17 The early history and phylogeny of the chelicerates

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17.1 INTRODUCTION

Chelicerata is one of the major arthropod groups, characterized by a body divided into two tagmata, prosoma and opisthosoma, while the name Chelicerata refers to the chelicerae, the chelate first pair of appendages. Chelicerates comprise the arachnids (spiders, scorpions, mites, etc.), the extinct eurypterids (sea scorpions) and the xiphosurans (horseshoe crabs). Among Recent groups the limits of the Chelicerata are well defined, i.e. arachnids and xiphosurans, though the position of pycnogonids (sea spiders) remains uncertain (King, 1973). Phylogenetic relationships within the Chelicerata remain unresolved (Weygoldt and Paulus, 1979; van der Hammen, 1989; Shultz, 1990). When fossil taxa are considered, the limits of the Chelicerata become less well constrained. This is especially true of various problematic arthropods: fossils such as aglaspidids (Raasch, 1939), chasmataspids (Caster and Brooks, 1956), *Sanctacaris* Briggs and Collins, 1988 and other Burgess Shale-type arthropods (see Conway Morris, 1992 for a review). Different authors at different times have expanded the definition of Chelicerata to include some of these problematic groups (e.g. Bergström, 1979) and a range of higher taxon nomenclature has been generated.

The history of chelicerate phylogeny can be traced back to Lankester's (1881) classic paper, 'Limulus, *an arachnid*' in which it was proposed that xiphosurans were related to arachnids, not crustaceans as had previously been thought. Lankester (1881) was not the first to propose this theory, but he argued the case most convincingly. To Lankester, Arachnida embraced arachnids, xiphosurans and eurypterids. Similarities between eurypterids and xiphosurans had already been identified (Nieszkowski, 1859) and these two groups were united in the taxon Merostomata (Woodward, 1866). Similarities between xiphosurans and trilobites were noted by, among others, Lockwood (1870), and similarities between scorpions and eurypterids were summarized by Woods (1909). However, the general consensus around the turn of the century was

that xiphosurans were closely related to eurypterids in the Merostomata, which were aquatic, and that together these were related to the arachnids, which were terrestrial (see Clarke and Ruedemann (1912) and Størmer (1944) for reviews of early work on chelicerate phylogeny). Heymons (1901) introduced the name Chelicerata for merostomes and arachnids, and this name became widely adopted.

Walcott (1912) described a number of unusual Cambrian fossils from the Burgess Shale and referred them to one of the four main arthropod groups (i.e. chelicerates, trilobites, crustaceans and atelocerates). Walcott (1912) placed some of these fossils in Merostomata and constructed an evolutionary tree showing how these taxa may have evolved into xiphosurans. Other problematic arthropod fossils which resembled merostomes, e.g. aglaspidids (Raasch, 1939) were also described in the early part of this century. Størmer (1944) reviewed these problematic arthropods and recognized a broad taxon, Arachnomorpha Heider, 1913, which comprised chelicerates (including aglaspidids), trilobites and the Trilobitomorpha Størmer, 1944; the latter comprising most of the problematic Burgess Shale-type Palaeozoic arthropods. Størmer (1944) concluded that chelicerates evolved from among the trilobitomorphs and subsequently Størmer (1959) recognized a taxon, Merostomoidea, for the most merostome-like of the trilobitomorphs. Other authors attempted to derive chelicerates from olenellid trilobites (Raw, 1957; Lauterbach, 1980). The Burgess Shale arthropods were subsequently reinterpreted as animals with unique body plans of uncertain affinity, unrelated to any of the four main arthropod groups. The Merostomoidea were redescribed by Bruton (1981), Whittington (1981) and Bruton and Whittington (1983), who argued on morphological grounds that none of these merostomoids could be classed as a chelicerate or a direct chelicerate ancestor. These revisions, and Briggs *et al.*'s (1979) removal of aglaspidids from Chelicerata (see below), left no Cambrian chelicerates, other than the dubi-

ous *Eolimulus* (see below) until Briggs and Collins (1988) described *Sanctacaris* as a chelicerate.

Kraus (1976) argued that Merostomata represented an aquatic grade of chelicerate, rather than a discrete taxon and Bergström (1979) further suggested that Arachnida could simply represent terrestrial chelicerates. A number of evolutionary models for the chelicerates and/or the arachnomorphs have been proposed (Fedotov, 1925; Beklemishev, 1944; Zakhvatkin, 1952; Dubinin, 1962; Sharov, 1966; Bristowe, 1971; Savory, 1971; Grasshoff, 1978; Bergström, 1979; Simonetta and Delle Cave, 1981; Starobogatov, 1990). A discussion of all these evolutionary models is beyond the scope of this present work, but most were based on general resemblances of the various fossils rather than distinct synapomorphies. The most widely accepted recent model was the cladistic analysis of Weygoldt and Paulus (1979). These authors included Aglaspidida in the Chelicerata as sister group of a taxon, Euchelicerata, which itself had a basic phylogeny of (Xiphosura (Eurypterida (Scorpiones + other arachnids))).

Recent authors (Wheeler *et al.*, 1993; Wills *et al.*, 1995) have rejected treating all the problematic groups as unrelated arthropods of uncertain affinity, the latter recognizing broad clades of arthropods: Crustacea, Marellomorpha, Atelocerata and Arachnomorpha, which include both the problematic fossils and extant groups. In these models the Chelicerata clearly evolved from among the Arachnomorpha (alternatively called Arachnata), a taxon comprising chelicerates, trilobites and the non-marellomorph problematic arthropods. However, a consensus on the phylogenetic position of chelicerates and what their immediate sister groups are among the arachnomorphs has proved difficult to establish (Briggs and Fortey, 1989; Briggs *et al.*, 1992; Wills *et al.*, 1994, 1995). In this paper we present a phylogenetic analysis and evolutionary model of the major chelicerate groups and those fossil taxa we consider their immediate outgroups. Based on this we attempt a new diagnosis of Chelicerata.

17.2 THE LIMITS OF CHELICERATA

Living chelicerates are represented by xiphosurans and arachnids. The extinct eurypterids are also clearly chelicerates. It is still unclear whether the pycnogonids (sea spiders) are chelicerates (see King, 1973) and their meagre fossil record does not help clarify the situation (Bergström *et al.*, 1980); though these authors suggested pycnogonids could be derived from primitive merostomes. Wheeler *et al.* (1993) placed pycnogonids as sister group to the chelicerates on a combination of morphological and ribosomal DNA evidence, though for now we regard pycnogonids as Arthropoda *incertae sedis* and have not included them in our analysis (see below). Other extant arthropods have in the past been referred to Chelicerata (Dahl, 1913), though of

these, pentastomids (tongue worms) are probably crustaceans (Abele *et al.*, 1989) and tardigrades are certainly not chelicerates but may have originated between the lobopods and stem group arthropods (Dewel and Dewel, 1997, this volume). Among fossil taxa, the Silurian–Triassic euthycarcinoids, originally thought to be crustaceans (Handlirsch, 1914), were suggested as being chelicerates by Riek (1964) based on their general resemblance to xiphosurans. However, the presence of antennae and apparently mandibulate mouthparts suggests that euthycarcinoids are atelocerates (McNamara and Trewin, 1993; Wills *et al.*, 1995).

Among arachnomorphs, the limits of Chelicerata have proved harder to define. Aglaspidids were for a long time included as chelicerates, either in Xiphosura (Størmer, 1944), Merostomata (Eldredge, 1974) or as sister group to the other chelicerates (Bergström, 1979; Weygoldt and Paulus, 1979). Briggs *et al.* (1979) removed aglaspidids from Chelicerata on the grounds they had only four or five cephalic appendages, none of which were chelicerae. *Sanctacaris* was described as a chelicerate by Briggs and Collins (1988), who placed it as the sister group to all other chelicerates, redefining Chelicerata to accommodate it. However, subsequent phylogenetic analyses (Briggs *et al.*, 1992; Wills *et al.*, 1994, 1995) (Figure 17.1), while placing *Sanctacaris* in the Arachnomorpha, do not place it as the sister group to other chelicerates (Wills, 1996), but as sister group to *Yohoia* (Wills *et al.*, 1995). Thus, *Sanctacaris* cannot be referred to Chelicerata without including the other Arachnomorpha, including trilobites.

Chen *et al.* (1995) described *Fuxianhuia* from the Lower Cambrian Chengjiang fauna as a basal euarthropod. Wills (1996) coded this fossil into his (Wills *et al.*, 1995) dataset and concluded that *Fuxianhuia* was a chelicerate, specifically sister group of arachnids and eurypterids on the synapomorphy of opisthosomal differentiation, a character we regard as synapomorphic for all chelicerates (see below). Edgecombe *et al.*'s reply to Wills rejected this interpretation (a view with which we concur), questioning Wills's (1996) coding of *Fuxianhuia* characters and pointing out that his model requires re-evolution of antennae and exopods on the trunk appendages and does not fit the known chelicerate fossil record. Babcock (1996) also proposed a Chengjiang arachnomorph as an early Cambrian chelicerate, though this fossil does not fit Chelicerata as we define it. In response to this trend of 'chelicerate spotting' among the early arthropod-bearing Lagerstätten, a new look at the limits of Chelicerata is clearly warranted.

17.3 PHYLOGENETIC ANALYSIS

We investigated the phylogeny and early history of the chelicerates to determine the boundary between chelicerates and non-chelicerates and hence diagnostic characters for the Chelicerata. To this end we undertook a cladistic analysis
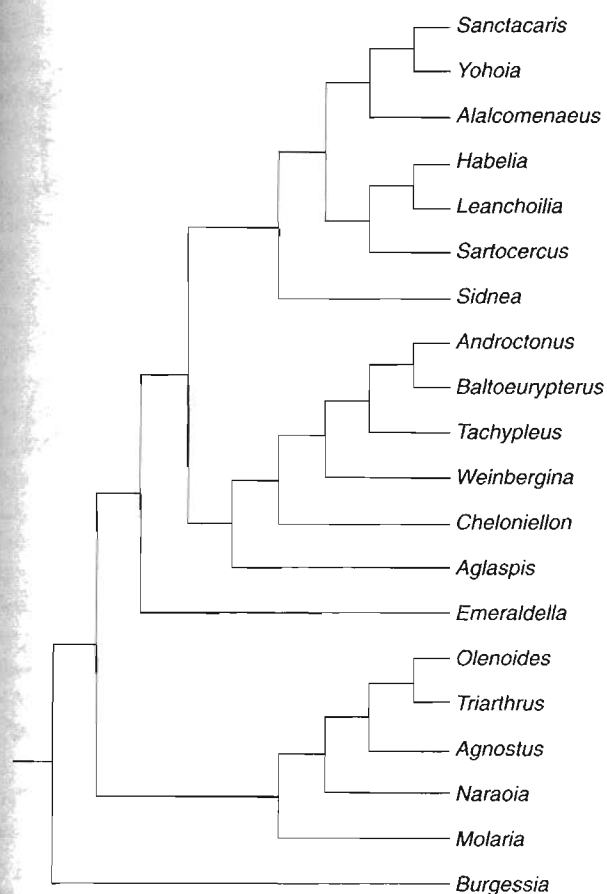
Figure 17.1 Phylogeny of the Arachnomorpha clade of the Palaeozoic arthropods. (After Wills *et al.*, 1995, Figure 1A.)

using MacClade 3.04 and PAUP 3.1.1 of those taxa known to be chelicerates, i.e. xiphosurans, eurypterids and arachnids. Wills *et al.* (1995) placed Chelicerata + *Cheloniellon* + *Aglaspis* as a clade within Arachnomorpha and in our analysis we investigated this clade in more detail. We included the major chelicerate groups, aglaspidids *sensu stricto* and other genera referred to Aglaspidida (treated as separate genera), *Cheloniellon* and similar forms, and a number of problematic genera such as *Chasmataspis. Sanctacaris* is omitted from the analysis since in most recent phylogenies it is placed as sister group to other non-chelicerate Arachnomorpha (see above). Taxa known only from isolated carapaces, such as *Eolimulus*, were also excluded. Characters and character states are listed below and the data matrix is given in Table 17.1.

17.3.1 TAXA INCLUDED IN THE ANALYSIS

(a) *Neostrabops* (Figure 17.2(A))

The Upper Ordovician arthropod *Neostrabops* Caster and Macke, 1952, is a poorly preserved fossil from Stonelick

Creek, Ohio. It is 4 cm long and is one of a group of fossils which resemble *Cheloniellon* (see below) in overall appearance, though many of its characters are unknown. The telson inferred by Caster and Macke (1952) in *Neostrabops* is not present in the fossil and appendages are absent.

(b) *Duslia* (Figure 17.2(B))

The Upper Ordovician arthropod *Duslia* Jahn, 1913 from the Barrandian area of the Czech Republic was originally interpreted as a polyplacophoran. This 9- to 12-cm-long arthropod is distinguished by a characteristic fringe of spines around the body. Appendages are not known and no eyes are preserved. *Duslia* has been referred to trilobites and cheloniellid arthropods (see Chlupač, 1988 for a review). Chlupač (1988) redescribed *Duslia* and concluded that it probably belonged in the Trilobitomorpha, rather than Trilobita, and that its systematic position was probably analogous to *Cheloniellon*.

(c) *Triopus* (Figure 17.2(C))

Triopus Barrande, 1872 is an Ordovician arthropod, about 4 cm long, possibly from the same horizon in the Czech Republic as *Duslia* (Chlupač, 1988). It was originally thought to be a trilobite. The holotype was reported lost (Chlupač, 1965), but was rediscovered and figured by Chlupač (1988). *Triopus* has been compared with aglaspidids (Chlupač, 1965), while Bergström (1968) interpreted it as a poorly preserved xiphosuran. Though incomplete and lacking appendages, *Triopus* resembles *Cheloniellon* and is therefore included in this analysis.

Table 17.1 Data matrix used in the phylogenetic analysis.

| | | 1 | | 2 | |
Characters	12345	67890	12345	67890	12345
Neostrabops	11000	00???	?1000	0????	????0
Duslia	11000	001??	?1100	01?4?	????1
Triopus	11???	?????	??100	0????	????0
Pseudarthron	111??	?????	??100	0????	????0
Cheloniellon	11100	00000	01100	01040	000?0
Paleomerus	10000	000??	?2000	00?0?	????0
Strabops	10000	00???	?2000	00?0?	????0
Aglaspidida	10010	000?0	02000	00110	?00?0
Lemoneites	1000?	?????	?2000	10?0?	????0
Weinbergina	10001	1?010	02110	10001	100?0
Bunodes	10001	110??	?1111	10?0?	????0
Kasibelinurus	10001	110??	?0110	10?1?	????0
Xiphosurida	10011	11010	00113	10012	10000
Diploaspis	10000	010??	?3002	30?4?	?00?0
Chasmataspis	10010	010??	?3002	3001?	?00?0
Eurypterida	10000	01011	13000	20013	?1000
Scorpiones	10000	01011	13000	20034	20110
Other arachnids	10000	01011	13000	10024	30010

0–4 = alternative character states. ? = character state uncertain. See text for details.
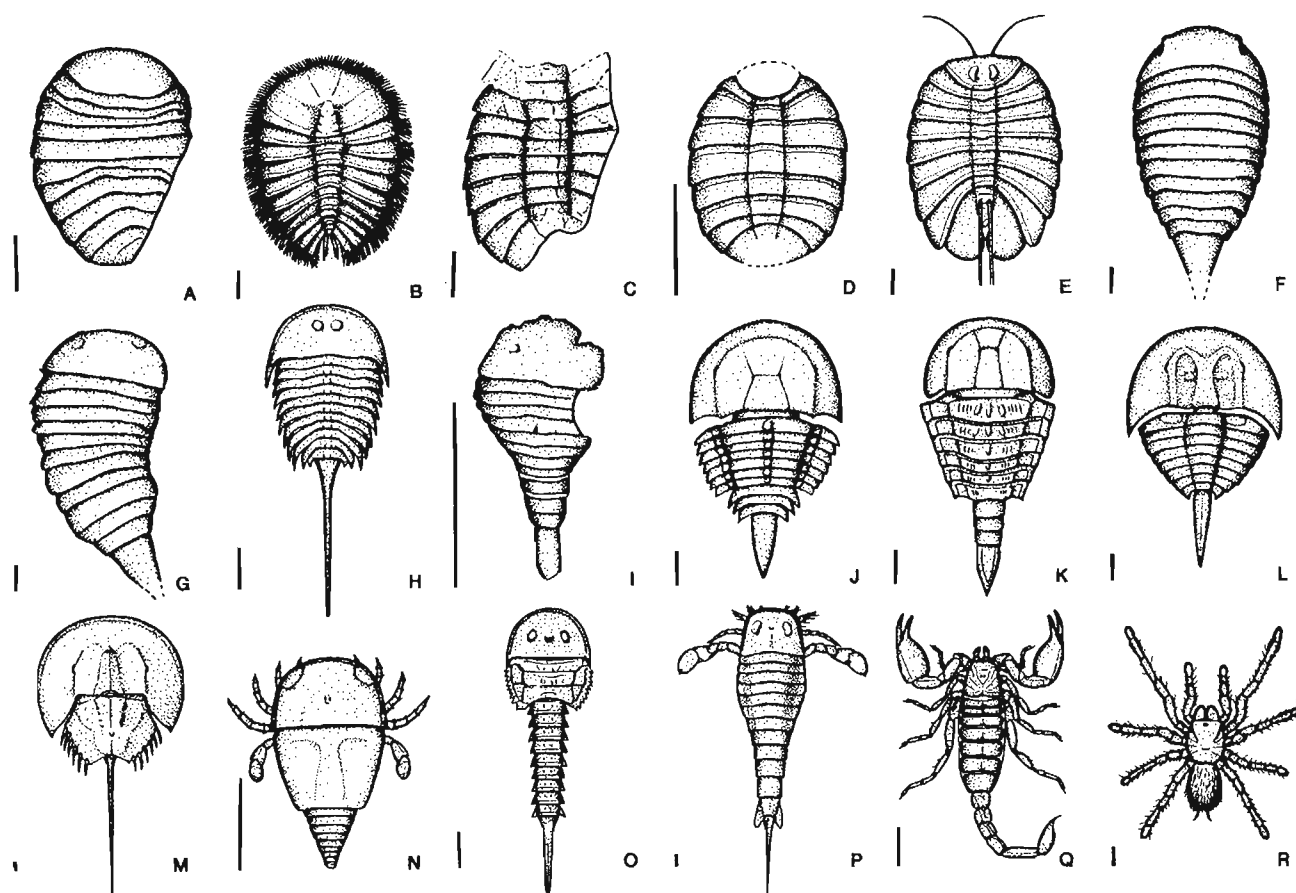
Figure 17.2 Reconstructions of the 18 taxa considered in the phylogenetic analysis, or of representative examples of the groups. A, *Neostrabops*. B, *Duslia*. C, *Triopus*. D, *Pseudarthron*. E, *Cheloniellon*. F, *Paleomerus*. G, *Strabops*. H, *Aglaspis*. I, *Lemoneites*. J, *Weinbergina*. K, *Bunodes*. L, *Kasibelinurus*. M, *Limulus*. N, *Diploaspis*. O, *Chasmataspis*. P, *Baltoeurypterus*. Q, *Chaerilus*. R, *Poecilotheria*. After various sources. Scale bars equal 1 cm.

(d) *Pseudarthron* (Figure 17.2(D))

Pseudarthron Selden and White, 1984 is from the Upper Silurian of Lesmahagow, Scotland. It is about 16 mm long, and resembles *Cheloniellon*, but the prosoma is poorly preserved and the appendages are absent. These authors discussed its phylogenetic affinities with extant groups, including isopods, myriapods and chelicerates and a number of fossil genera, including the Devonian *Oxyuropoda* Carpenter and Swain, 1908, and the Carboniferous *Camptophyllia* Gill, 1924. Selden and White (1984) suggested that resemblances between *Pseudarthron*, *Oxyuropoda* and *Camptophyllia* were due to convergence, hence the latter two genera were omitted from our analysis.

(e) *Cheloniellon* (Figure 17.2(E))

The Lower Devonian arthropod *Cheloniellon* Broili, 1932, from the Hunsrück Shale, Germany, was originally described as a crustacean. Following a detailed re-description by Stürmer and Bergström (1978) its morphology became known in greater detail and these authors suggested that it was a late representative of a group of trilobitomorphs which gave rise to Chelicerata. Wills *et al.* (1995) included *Cheloniellon* in their phylogenetic analysis and placed it among the Arachnomorpha, as sister group to the xiphosurans, eurypterids and arachnids, with aglaspidids as sister group to *Cheloniellon* + Chelicerata. *Cheloniellon* is 6–10 cm long and is not particularly merostome-like in appearance; it has antennae, lacks a telson and the prosoma-opisthosoma boundary is poorly defined. However, it has gnathobasic appendages and, bearing in mind Wills *et al.*'s (1995) placement, we included *Cheloniellon*, and the similar forms: *Neostrabops*, *Pseudarthron*, *Duslia* and *Triopus*, in our analysis.

(f) *Paleomerus* (Figure 17.2(F))

The Lower Cambrian *Paleomerus* Størmer, 1956 (see also Størmer 1955) from Sweden is one of the oldest arthropods

and is one of the most primitive-looking merostome-like arthropods known. *Paleomerus* is about 8 cm long, though none of the three *Paleomerus* fossils is well preserved and appendages are unknown.

(g) *Strabops* (Figure 17.2(G))

The Cambrian *Strabops* Beecher, 1901, is about 10 cm long and known from a single specimen from Missouri, USA, which shows the dorsal surface only. It was described by Clarke and Ruedemann (1912) as a eurypterid, based on a count of 12 opisthosomal segments (in fact it has 11), who interpreted it as the most primitive member of that group. Bergström (1971) removed *Strabops*, *Neostrabops* and *Paleomerus* (see above) from the Aglaspidida and referred them to an unnamed order of the Merostomoidea, though Briggs *et al.* (1979) doubted whether this was justified. These three genera show neither a typical aglaspidid carapace nor strongly curved margins of the tergites; we treat *Strabops*, *Neostrabops* and *Paleomerus* as separate taxa in our analysis. Note that the appendages figured in Clarke and Ruedemann's (1912, plate 1) reconstruction of *Strabops* are hypothetical. It proved difficult to find any significant characters to distinguish *Strabops* from *Paleomerus*.

(h) Aglaspidida (Figure 17.2(H))

Aglaspidids are primarily Cambrian fossils, first described by Hall (1862) who interpreted them as crustaceans, but are best known from the monograph of Raash (1939), who referred them to Merostomata. Aglaspidids have recently been recorded from the upper Lower Ordovician (D. Siveter, personal communication). Aglaspidids are 2–10 cm long and have been regarded as a taxon within Xiphosura (Størmer, 1955), a separate taxon of the Merostomata (Eldredge, 1974) or as a separate taxon of Chelicerata (Weygoldt and Paulus, 1979; Bergström, 1979). However, Briggs *et al.* (1979) removed Aglaspidida from Chelicerata, preferring not to assign them to any higher taxon within Arthropoda. Aglaspidida has become something of a 'bucket taxon' for non-trilobite arthropods which resemble xiphosurans (Størmer, 1955; Chlupač and Havlicek, 1965). Some taxa were removed from Aglaspidida by Bergström (1971). One aglaspidid genus, *Beckwithia* Resser, 1931, was described as having a fused tail plate and was thus raised to a family separate from other aglaspidids by Raasch (1939); it was placed in a monotypic order by Bergström (1979). *Beckwithia* has been interpreted as central to the evolution of the chelicerates (Starobogatov, 1990) and/or the arachnids in particular (Bergström, 1979). Hesselbo (1989) redescribed *Beckwithia* and found no evidence for the tail plate, and thus returned the genus to the order Aglaspidida. Another problematic genus is *Kodymirus* Chlupač and Havlicek, 1965, which was described as having 12 opisthosomal segments, as opposed to the 11 seen in typical aglaspidids such as *Aglaspis*. However, their photographs of the

specimen suggest that even more segments may be present in the fossil. A supposed Carboniferous aglaspidid (Youchong and Shaowu, 1981) does not resemble typical aglaspidids, having fewer than 11 segments and lacking a carapace with genal spines and we regard it as an arthropod of uncertain affinity. The aglaspidids form a distinct group of arachnomorph arthropods and a revision of their constituent genera is clearly warranted. For the purposes of this analysis we regard Aglaspidida as a morphologically distinct group characterized by an 11-segmented opisthosoma, postanal plates, a tail spine, and a carapace bearing genal spines. We relied on the descriptions of Briggs *et al.* (1979) and Hesselbo (1989, 1992) for determining characters and character states.

(i) Xiphosura (Figures 17.2(I–M))]

The Xiphosura were traditionally seen as the most primitive chelicerates and incorporated the Aglaspidida in some schemes (see above). Significant accounts of xiphosuran phylogeny and systematics include Størmer (1952, 1955), Novojilov (1962), Eldredge (1974), Bergström (1975) and Selden and Siveter (1987). A recent analysis by Anderson and Selden (1997) concluded that class Xiphosura comprise the order Xiphosurida, supported by distinct autapomorphies (see below), and a paraphyletic group of genera, the synziphosurines. This differs from previous interpretations in which the synziphosurines were regarded as a distinct taxon, Synziphosurida, of equal rank to Xiphosurida (Eldredge, 1974). It has been suggested that arachnids evolved from among the synziphosurines (Beall and Labandeira, 1990) and this hypothesis merits consideration. For the purpose of this analysis we included the Xiphosurida (Figure 17.2(M)) as one taxon and selected four of the synziphosurines to include as separate taxa: *Lemoneites* Flower, 1968 (Figure 17.2(I)) is the oldest and smallest of the synziphosurines and which shows the most plesiomorphic character states. *Weinbergina* Richter and Richter, 1929 (Figure 17.2(J)) is one of the most intensively studied synziphosurines (Stürmer and Bergström, 1981), also included by Wills *et al.* (1995) in their analysis. *Bunodes* Eichwald, 1854 (Figure 17.2(K)) is perhaps the most arachnid-like of the synziphosurines. *Kasibelinurus* Pickett, 1993 (Figure 17.2(L)) emerged as the sister group of the Xiphosurida in Anderson and Selden's analysis. The supposed Cambrian xiphosuran *Eolimulus* (Möberg, 1892) is only known from a carapace and is not included in the analysis. From an analysis of these taxa it should be possible to test whether any of the other chelicerate groups is sister taxon to all Xiphosura, or to a particular synziphosurine.

(j) *Diploaspis* (Figure 17.2(N))

Størmer (1972) described two Devonian fossils, *Diploaspis* and *Heteroaspis*, from Germany and referred them to Chasmataspida. These small (2 cm) fossils were described

as having a 12-segmented opisthosoma with three fused anterior segments and a postabdomen of nine ring-like segments similar to *Chasmataspis* (see below). The postabdomens of *Diploaspis* and *Heteroaspis* are short, not elongate as in *Chasmataspis*. The posteriormost prosomal appendage of *Diploaspis* is a eurypterid-like paddle. The preservation of some of this Devonian material is patchy and there is a suspicion that these taxa might represent a composite of a number of different fossils. The characters used to distinguish *Diploaspis* from *Heteroaspis* are of no phylogenetic significance and since *Diploaspis* is better preserved, it is used in our analysis. Eldredge (1974) placed Chasmataspida as the sister group of Eurypterida on account of the possession of paddles in some eurypterids and some chasmataspids. Bergström (1979) placed Chasmataspida as the sister group of Xiphosurida on the basis of the following characters: chilaria (unknown in *Chasmataspis*), chelate legs, and lamellate book-gills. *Diploaspis* was figured on a separate lineage leading to the arachnids. For the purposes of this analysis *Chasmataspis* and *Diploaspis* are treated as separate taxa.

(k) *Chasmataspis* (Figure 17.2(O))

The Ordovician fossil *Chasmataspis* Caster and Brooks, 1956 from Tennessee is about 5 cm long, with an aglaspidid-like carapace and an opisthosoma consisting of a 'buckler' of three segments, fused both dorsally and ventrally, and an elongate postabdomen of nine reduced, ring-like segments. Caster and Brooks (1956) described *Chasmataspis* as a 'merostomaceous arachnomorph' and erected a new order, Chasmataspida, which they referred to Merostomata. The affinities of Chasmataspida are discussed above. An unpublished Cambrian trace fossil from Texas may have been made by a chasmataspid.

(l) Eurypterida (Figure 17.2(P))

The eurypterids were traditionally allied to the Xiphosura in the Merostomata (Størmer, 1944, 1955), though more recently they have generally been placed as the sister group of the arachnids (Weygoldt and Paulus, 1979; Shultz, 1990). The relationship between eurypterids and scorpions is controversial (see below). Significant accounts of eurypterid phylogeny and systematics include Clarke and Ruedemann (1912), Størmer (1955, 1974), Dubinin (1962), Caster and Kjellesvig-Waering (1964), Waterston (1979) and Tollerton (1989). A number of genera, originally placed in the Cyrtoctenida Størmer and Waterston, 1968, were removed from Eurypterida by Tollerton (1989). Cyrtoctenids have a large, domed, carapace, a reduced genital appendage and a cleft metastoma. However, since they show the two eurypterid autapomorphies of a genital appendage and metastoma (albeit modified) we prefer to retain Cyrtoctenida as a taxon within Eurypterida. In this analysis Eurypterida is regarded as a single taxon, with stylonurids

interpreted as the most primitive eurypterids (Størmer, 1955) in the determination of characters and character states.

(m) Scorpiones (Figure 17.2(Q))

Scorpions are the oldest arachnids and are widely perceived as the most primitive members of the group (Pocock, 1893). The interpretation of the earliest fossil scorpions as aquatic (Pocock, 1901) is a strong argument against the traditional split of chelicerates into the aquatic Merostomata and terrestrial Arachnida. The obvious similarities between scorpions and eurypterids (see Clarke and Ruedemann (1912), Kjellesvig-Waering (1986) and Sissom (1990) for reviews), led some authors to propose that eurypterids evolved from scorpions (Versluys and Demoll, 1920), that scorpions evolved from the eurypterids (Beklemeshev, 1944; Sharov, 1966; Bristowe, 1971) and/or that scorpions are more closely related to eurypterids than the rest of the arachnids (Grasshoff, 1978; Starobogatov, 1990). Other authors have regarded scorpions as true arachnids (Petrunkevitch, 1949; Shultz, 1990). Fossil scorpion phylogeny was extensively revised by Kjellesvig-Waering (1986), though many of his higher taxa, based on the nature of the respiratory organs, have not been adopted by subsequent authors (Stockwell, 1989; Jeram, 1994). The scorpions are treated as a separate taxon from the non-scorpion arachnids in this analysis, which allows us to test the hypotheses that scorpions are either sister group of the eurypterids (Grasshoff, 1978) (in which case Arachnida is paraphyletic), or sister group of the non-scorpion arachnids (Weygoldt and Paulus, 1979), (in which case Arachnida remains monophyletic). We cannot test Shultz's (1990) model in which Arachnida are monophyletic and opilionids are the sister group of (scorpions + (pseudoscorpions + solifuges)) without expanding the analysis to include all the arachnid orders, which is beyond the scope of this analysis.

(n) Other arachnids (Figure 17.2(R))

The phylogeny of the arachnid orders (including scorpions) has been investigated by a number of authors and significant accounts of arachnid phylogeny include: Pocock (1893), Petrunkevitch (1949), Zakhvatkin (1952), Dubinin (1962), Savory (1971), Firstman (1973), Grasshoff (1978), Weygoldt and Paulus (1979), Lindquist (1984), van der Hammen (1989) and Shultz (1990). For the purpose of this analysis we regard all the non-scorpion arachnids as a single taxon, termed Lipostena by Weygoldt and Paulus (1979). There is a general consensus about which characters are primitive for arachnids (Shultz, 1990, Figure 3, modelled plesiomorphic states in arachnids, though this model included scorpions as arachnids) such as an undivided carapace bearing median and lateral eyes, a 12-segmented opisthosoma plus a telson and such conventions were used when coding non-scorpion arachnid characters.

17.3.2 CHARACTERS AND CHARACTER STATES

For the purpose of this analysis all characters are assumed to be unordered and polarity has not been argued, though autapomorphies and synapomorphies have been identified where appropriate. The alternative character states are noted in the text.

Character 1 (Body tagmosis)

A body divided into two distinct tagmata, a prosoma and opisthosoma, is present in all taxa under consideration and is coded as (1).

Character 2 (Carapace margin)

A distinctly procurved posterior margin of the carapace is only seen in the genera *Neostrabops*, *Triopus*, *Duslia*, *Pseudarthron* and *Cheloniellon* and is synapomorphic for these taxa (1), compared with the straight or slightly recurved posterior carapace margin seen in all other taxa (0).

Character 3 (Carapace size)

A highly reduced carapace, less than half the width of the opisthosoma, is synapomorphic for *Pseudarthron* (where its size can be estimated from the preserved tergites) and *Cheloniellon* (1), compared with the broad carapaces of all other taxa under consideration (0). This character is uncertain in *Triopus*.

Character 4 (Genal spines)

Strongly developed genal spines (1) are present in aglaspidids, *Chasmataspis* and xiphosurids. The carapaces of all other taxa lack genal spines (0). This character is unknown in *Triopus* and *Pseudarthron*.

Character 5 (Ophthalmic ridges)

An ophthalmic ridge, a discrete ridge on the carapace bearing the eyes, is seen in all xiphosurids and the synziphosurines *Weinbergina*, *Bunodes* and *Kasibelinurus*, and is synapomorphic for these taxa (1). The carapaces of all other taxa lack ophthalmic ridges (0). The carapaces of *Lemoneites*, *Triopus* and *Pseudarthron* are poorly preserved or unknown and this character is coded as uncertain in these taxa.

Character 6 (Cardiac lobes)

A cardiac lobe in the centre of the carapace is seen in *Weinbergina*, *Bunodes*, *Kasibelinurus* and xiphosurids and is synapomorphic for these taxa (1). The carapaces of all other taxa lack a cardiac lobe (0). The carapaces of *Lemoneites*, *Triopus* and *Pseudarthron* are poorly preserved or unknown and this character is coded as uncertain in these taxa.

Character 7 (Median eyes)

Median eyes, or ocelli, are present in xiphosurans, *Chasmataspis*, *Diploaspis* [where their presence is inferred in comparison to the related and better preserved carapace of *Heteroaspis* in which median eyes are clearly present (Størmer, 1972, plate 5)], eurypterids, scorpions and other arachnids. Median eyes are synapomorphic for these taxa (1). Median eyes are absent in the other taxa under consideration (0). The carapaces of *Lemoneites*, *Triopus* and *Pseudarthron* are poorly preserved or unknown and this character is coded as uncertain in these taxa.

Character 8 (Lateral eyes)

Lateral eyes are absent in *Duslia* where this is interpreted as an autapomorphic condition (1). Lateral eyes are present (0) in all other taxa where the carapace is sufficiently well preserved. The carapaces of *Neostrabops*, *Strabops*, *Lemoneites*, *Triopus* and *Pseudarthron* are poorly preserved or unknown and this character is coded as uncertain in these taxa.

Character 9 (Prosomal appendage 1)

The first prosomal appendage of *Cheloniellon* is antenniform (0). This appendage was interpreted as antenniform in aglaspidids (Hesselbo, 1992), though the evidence from his plates is not convincing and this character is coded as uncertain. A chelate first prosomal appendage, (i.e. a chelicera) is present in *Weinbergina*, xiphosurids, eurypterids, scorpions and arachnids (1). The first appendage of the remaining taxa is unknown.

Character 10 (Divided femur)

Shultz (1990) regarded a walking leg femur divided into two podomeres to be the plesiomorphic state in arachnids, including scorpions (and retained in taxa such as solifuges and ricinuleids) and also to be present in eurypterids (Selden, 1981). A divided femur (0) is coded as absent in *Cheloniellon*, Aglaspidida, *Weinbergina* and Xiphosurida and a divided femur (1) is present in eurypterids, scorpions and the other arachnids. This character is coded as unknown in all other taxa. Appendages are known from both chasmataspid taxa and while they appear not to have a divided femur, their preservation makes it is difficult to be certain which podomeres should be homologized with the chelicerate femur and this character is coded as uncertain.

Character 11 (Basitarsus)

The tarsus of prosomal appendages 3–6 in eurypterids, scorpions and other arachnids is subdivided into a basitarsus and telotarsus. A basitarsus on these appendages is absent in *Cheloniellon*, Aglaspidida, *Weinbergina* and Xiphosurida (0) and present in eurypterids, scorpions and other arachnids (1). This character is coded as uncertain in all other taxa. Chasmataspids may possess a basitarsus, but as noted above there are problems homologizing podomeres and this character is coded as uncertain.

Character 12 (Opisthosomal segment number)
The taxa under consideration show a range of visible opisthosomal segment counts. *Kasibelinurus* and xiphosurids have nine segments (0), a synapomorphy of these taxa. *Neostrabops*, *Cheloniellon*, *Duslia* and *Bunodes* have 10 segments (1). *Paleomerus*, *Strabops*, *Lemoneites*, *Weinbergina* and aglaspidids have eleven segments (2). *Diploaspis*, *Chasmataspis*, eurypterids, scorpions and other arachnids have twelve segments (3), a synapomorphy of these taxa. A transient 13th segment is cited by some authors as being present during scorpion embryology. Total opisthosomal segment number in *Triopus* and *Pseudarthron* is unknown and this character is coded as uncertain in these taxa.

Character 13 (Opisthosomal axial region)
A discrete opisthosomal axial region is present in *Cheloniellon*, *Pseudarthron*, *Duslia*, *Triopus*, *Bunodes*, *Weinbergina*, *Kasibelinurus* and all xiphosurids (1). This axial region was interpreted as an adaptation for enrolment in xiphosurans (Eldredge, 1974). An opisthosomal axial region is absent in the remaining taxa (0).

Character 14 (Opisthosomal segment 1)
Opisthosomal segment 1 is highly reduced in all xiphosurids and in *Weinbergina*, *Bunodes* and *Kasibelinurus* and all xiphosurids (1) and is synapomorphic for these taxa. Opisthosomal segment 1 is fully expressed in the remaining taxa (0).

Character 15 (Opisthosomal tergite fusion)
Fusion of tergites 2 and 3 into a diplotergite is autapomorphic for *Bunodes* (1) in this analysis. Fusion of the first three opisthosomal segments into a discrete buckler is synapomorphic for *Diploaspis* and *Chasmataspis* (2). Fusion of the opisthosomal tergites into a thoracetron is autapomorphic for Xiphosurida (3). Some derived arachnids have fused opisthosomal segments, but here they do not form a thoracetron. The tergites of all remaining taxa are coded as unfused (0).

Character 16 (Opisthosomal differentiation)
The last three opisthosomal segments of *Lemoneites*, *Weinbergina*, *Bunodes* and many non-scorpion arachnids are ring-like and form a discrete postabdomen (1). The last five opisthosomal segments of eurypterids and scorpions form a postabdomen (2). The last nine opisthosomal segments of *Diploaspis* and *Chasmataspis* form a postabdomen (3). The remaining taxa show no differentiation of the opisthosoma (0).

Character 17 (Furcal rami)
Paired furcal rami at the posterior end of the opisthosoma are present in *Duslia* and are also present in *Cheloniellon* as elongate structures (1). Furcal rami are not seen in the remaining taxa (0). The posterior opisthosoma of *Neostrabops*, *Triopus* and *Cheloniellon* is not preserved and this character is coded as uncertain in these taxa.

Character 18 (Postanal plates)
Postanal plates are autapomorphic for aglaspidids (1) and not recorded in other taxa where the ventral surface is known, i.e. *Cheloniellon*, *Weinbergina*, xiphosurids, *Chasmataspis*, eurypterids and both scorpion and non scorpion arachnids (0). This character is coded as uncertain in the remaining taxa.

Character 19 (Telson shape)
The telson is broad, but tapering in *Paleomerus*, *Strabops*, *Lemoneites*, *Weinbergina* and *Bunodes* (0). The telson (or tail spine incorporating opisthosomal segments in xiphosurans) is longer and more styliform in Aglaspidida, *Kasibelinurus*, xiphosurids, *Chasmataspis* and eurypterids (secondarily modified into a broad structure in some eurypterids) (1). The telson is subdivided in those non-scorpion arachnids which retain a telson, such as palpigrades and uropygids (an autapomorphy) (2) and is modified into a sting in scorpions (an autapomorphy) (3). The telson is absent in *Cheloniellon*, *Duslia* and *Diploaspis* (4). The posterior opisthosoma is unknown in *Neostrabops*, *Triopus* and *Pseudarthron* and this character is coded as uncertain in these taxa.

Character 20 (Opisthosomal appendages)
Pediform appendages running the length of the opisthosoma are present in aglaspidids and *Cheloniellon* (0). Pediform appendages are restricted to opisthosomal segment 1 in *Weinbergina* (1). We believe this appendage to be opisthosomal (Anderson's 1973 review of xiphosuran embryology suggests the chilaria belong to opisthosomal segment 1), not prosomal as suggested by Stürmer and Bergström (1981). This appendage is modified into chilaria in xiphosurids (an autapomorphic state) (2), may be modified into the metastoma of eurypterids (3), though an alternative interpretation of the metastoma is that they are the fused epicoxa of prosomal appendage 6 (S. Braddy, personal communication), (an autapomorphic state) and is lost in scorpions, though a transitory limb bud appears during scorpion embryology (Anderson, 1973) and all other arachnids (4). The appendages of the remaining taxa are unknown and this character is coded as uncertain in these taxa.

Character 21 (Respiratory organs)
A series of pairs of gills running the length of the opisthosoma is present in *Cheloniellon* (0). Five pairs of respiratory organs are seen in *Weinbergina* and xiphosurids (1), four pairs are seen in scorpions (2) and two pairs of lamellate respiratory organs are primitively present in non-scorpion

arachnids (3). Eurypterids have five pairs of branchial chambers, but it is unclear whether they all contained book-gills. The number of gills in eurypterids and the remaining taxa is coded as uncertain.

Character 22 (Genital appendage)

A genital appendage on the underside of the opisthosoma is autapomorphic for eurypterids (1) and is absent in all remaining taxa where the ventral surface is known (0), i.e. *Cheloniellon*, aglaspidids, *Weinbergina*, xiphosurids, scorpions and other arachnids. This character is coded as uncertain in the remaining taxa.

Character 23 (Pectines)

Pectines, paired, probably sensory, structures on the underside of the opisthosoma, are autapomorphic for scorpions (1) and are absent in all remaining taxa where the ventral surface are known (0), i.e. *Cheloniellon*, aglaspidids, *Weinbergina*, xiphosurids, eurypterids and other arachnids. This character is coded as uncertain in the remaining taxa.

Character 24 (Slit sensilla)

Slit sensilla are sensory cuticular strain gauges which are synapomorphic for scorpions and non-scorpion arachnids (1). They are absent in xiphosurids and eurypterids (0) and unknown in all remaining taxa.

Character 25 (Marginal spines)

A fringe of spines on the prosoma and opisthosoma is autapomorphic for *Duslia* (1) and is absent in all remaining taxa (0).

17.4 DISCUSSION

Using these 18 taxa and 25 characters we have produced a cladogram (Figure 17.3) with a tree-length of 46 and a consistency index of 0.83. The cladogram is one of a number of equally parsimonious trees. This analysis has identified a number of well supported clades and highlights problems in resolution, particularly with respect to poorly preserved taxa.

17.4.1 PALEOMERUS AND STRABOPS

These two Cambrian genera are the most primitive-looking of the taxa considered in this analysis. Bergström (1971) removed these genera from Aglaspidida, which is supported by our analysis since they lack aglaspidid apomorphies (e.g. genal spines). It proved impossible to find meaningful characters to separate *Paleomerus* and *Strabops* and we regard them as sister groups in the analysis (Figure 17.3), though there are no synapomorphies to support this. In the evolutionary model below these taxa are treated as part of the same lineage, a primitive stem group from which
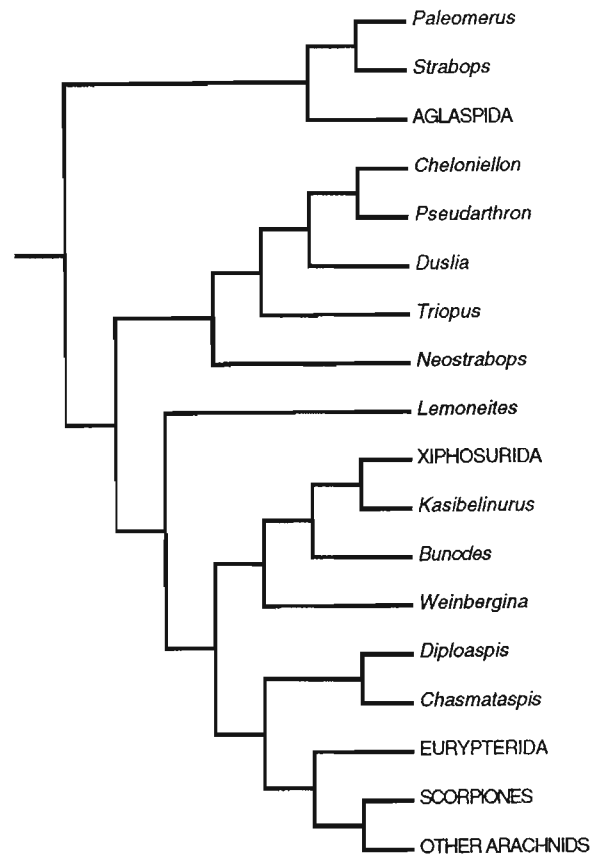

Figure 17.3 Cladogram of the major chelicerate groups and their outgroups. The cladogram has a tree length of 46 and a consistency index of 0.83 and is one of a number of equally parsimonious trees.

Chelicerata, Aglaspidida and Cheloniellida can be derived. Despite the spectacular Chengjiang finds, *Paleomerus* is perhaps the best model of a primitive arachnomorph.

17.4.2 AGLASPIDIDA

The aglaspidids form a distinct group with an autapomorphy of postanal plates. The development of genal spines and an elongate telson is probably convergent with the chasmataspids and later xiphosurids, presumably reflecting a similar mode of life. Aglaspidids represent a distinct taxon within the Arachnomorpha, though as noted above, a number of problematic arthropods have been referred to Aglaspidida and the group as a whole needs revision. The position of Aglaspidida relative to the other taxa in the analysis is difficult to resolve. It is equally parsimonious to place aglaspidids as sister group to either *Paleomerus/Strabops* or the Chelicerata and aglaspidids share no synapomorphies with any of these groups. Since they originate in the Cambrian and lack opisthosomal differentiation we prefer to place aglaspidids as sister group to the

Paleomerus/Strabops lineage, rather than as sister group of the Chelicerata.

17.4.3 CHELONIELLIDA

Neostrabops, *Duslia*, *Triopus*, *Pseudarthron* and *Cheloniellon* form a clade for which the name Cheloniellida Broili, 1932 is available. This clade is supported by the synapomorphy of a procurved posterior margin of the carapace. Loss of the telson and the presence of paired furcal rami may also be synapomorphic for this group, though these characters are only seen in the two taxa where the terminal end of the opisthosoma is known. Antennae may have been present in all five taxa, but are only known from *Cheloniellon*. Relationships of the five taxa within this clade are harder to resolve; *Neostrabops* lacks a well-defined opisthosomal axial region which places it as sister group to the other cheloniellids. The two youngest taxa, *Pseudarthron* and *Cheloniellon*, are sister groups sharing the synapomorphy of a highly reduced carapace. The positions of *Duslia* and *Triopus* are difficult to resolve, though *Duslia* has well-defined autapomorphies of lateral eyes absent and a marginal fringe of spines. The cheloniellids are not chelicerates (as diagnosed below), nor can they readily be envisaged as chelicerate ancestors on account of their synapomorphies (procurved carapace margin, loss of telson, ?furcae). In this analysis it is equally parsimonious to place cheloniellids as sister group to Chelicerata [as in Wills *et al.*'s (1995) model], sister group to aglaspidids and *Paleomerus/Strabops* or sister group to all other taxa in the analysis. Since cheloniellids are currently known from the Ordovician (*Paleomerus*, *Strabops* and most Aglaspidida being known from the Cambrian) we follow Wills *et al.* (1995) and adopt the sister group to Chelicerata model (Figures 17.3 and 17.4). In any case, cheloniellids appear to represent a distinct taxon within the Arachnomorpha.

17.4.4 CHELICERATA

Chelicerata, restricted to *Lemoneites*, xiphosurans, chasmataspids, eurypterids and arachnids in this analysis, is a monophyletic group. We question the referral of certain Cambrian taxa to Chelicerata (Briggs and Collins, 1988; Babcock, 1996; Wills, 1996). The presence of chelicerae, the traditional diagnostic character of chelicerates, is difficult to prove in many of the fossil taxa under consideration. However, in this analysis we recognize alternative diagnostic characters for Chelicerata: (1) presence of median eyes and/or median ocular tubercle; and (2) differentiation of the opisthosoma into a preabdomen and postabdomen (mesosoma and metasoma are alternative terms, but usually used with reference to the presence of opisthosomal appendages which cannot be seen in all taxa). This opisthosomal differentiation is not seen in Xiphosurida, but is present in the synziphosurines and as the pygidium of the arachnid orders

Palpigradi, Trigonotarbida, Araneae, Amblypygi, Uropygi, Acari and Ricinulei (Shultz, 1990).

17.4.5 *LEMONEITES*

These small, problematic, Ordovician fossils were originally referred to Aglaspidida, but show some synziphosurine features (Flower, 1968). Anderson and Selden (in press) excluded *Lemoneites* from Xiphosura. In our analysis it is equally parsimonious to place *Lemoneites* as sister group to chasmataspids + eurypterids + arachnids, to the Xiphosura or to all other chelicerates. *Lemoneites* shows opisthosomal differentiation, supporting its referral to Chelicerata, but its poor preservation makes determining diagnostic characters such as the xiphosuran autapomorphy of ophthalmic ridges impossible. With respect to its simple morphology, Ordovician age and lack of explicit xiphosuran synapomorphies, we prefer to place *Lemoneites* as sister group to all other chelicerates, and it is probably a reasonable model for a common ancestor of Chelicerata.

17.4.6 XIPHOSURA

In this analysis the Xiphosura emerge as a monophyletic group within Chelicerata united on the synapomorphies of ophthalmic ridges, a cardiac lobe and a reduced opisthosomal segment 1. An axial region of the opisthosoma (convergent with cheloniellids) also characterizes xiphosurans. The presence of these synapomorphies makes it difficult to derive any of the remaining chelicerate groups from among the Xiphosura (Beall and Labandeira, 1990); the status of *Lemoneites* was discussed above. Our analysis of the Xiphosura is essentially the same as that of Anderson and Selden (1997) where the synziphosurines form a series of plesions with Xiphosurida as a crown group characterized by the autapomorphies of chilaria and opisthosomal segments fused into a thoracetron.

17.4.7 CHASMATASPIDA

Chasmataspis, with its genal spines and elongate postabdomen, and the smaller, squatter *Diploaspis/Heteroaspis* group (the two genera may be synonymous with differences resulting from preservation) appear quite different. However, they emerge as sister groups, sharing the synapomorphies of fusion of the first three opisthosomal segments and a postabdomen of nine ring-like segments. This supports the referral of both groups to a separate chelicerate taxon, Chasmataspida. The position of the Chasmataspida within Chelicerata is harder to resolve and we place chasmataspids as the sister group of (Eurypterida (Scorpiones + other arachnids)) with which they share the synapomorphies of 12 opisthosomal segments. We find no synapomorphies in favour of Eldredge's (1974) placement of chasmataspids as sister group of eurypterids alone,
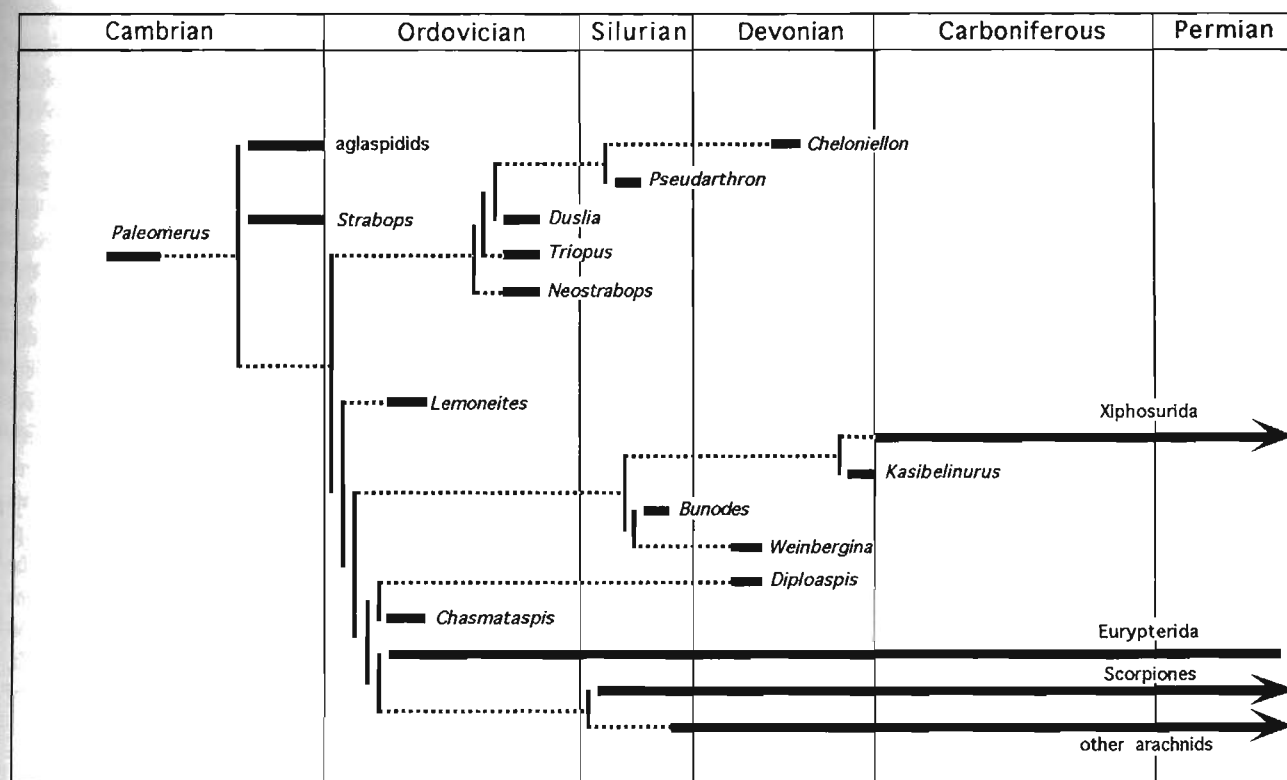
Figure 17.4 Evolutionary tree of the major chelicerate groups and their outgroups derived from the cladogram and the stratigraphic record. Vertical lines show inferred relationships, solid horizontal lines the fossil record, dashed lines are ghost lineages.

and since chasmataspids lack ophthalmic ridges their inclusion in Xiphosura (Selden and Siveter, 1987) is unsupported. However, on the current characters it is equally parsimonious to place chasmataspids as sister group to any one of eurypterids, scorpions or other arachnids. Chasmataspids' nine-segmented postabdomen could be interpreted as part of a trend towards increasing postabdominal differentiation (a scorpion/eurypterid character), while their three-segmented preabdomen suggests they may only have had two or three pairs of gills which is closer to the non-scorpion arachnid condition. Since a number of characters are unknown in chasmataspids the model in Figure 17.3 is most parsimonious. Restudy of the original chasmataspid material would be welcome to resolve some of these uncertain characters and their phylogenetic position. Chasmataspids are a group of rare, Palaeozoic chelicerates; their synapomorphy of opisthosomal differentiation suggest they are not ancestral to any other chelicerate group, but may represent an offshoot of an early arachnid/eurypterid radiation.

17.4.8 EURYPTERIDA AND ARACHNIDA

Eurypterida is a monophyletic group within Chelicerata, characterized by a metastoma and a genital appendage. Eurypterids share no unique synapomorphies with xiphosurans, supporting Kraus's (1976) interpretation that the traditional concept of Merostomata (i.e. Xiphosura + Eurypterida) is artificial. Scorpions have autapomorphies of pectines and a sting, supporting the interpretation that they are not ancestral to any other arachnid order, while the other arachnids have a primitive condition of two pairs of respiratory organs and a segmented telson. Eurypterids, scorpions and arachnids form a well-supported clade with the synapomorphies of a divided femur and a basitarsus (though either of these characters may be present in chasmataspids). Resolving the interrelationships of these three taxa is difficult since scorpions share a number of characters with both eurypterids and other arachnids. Both eurypterids and scorpions have a postabdomen of five segments and this is a potential synapomorphy of these groups. In this respect, the other arachnids with a postabdomen (primitively) of three segments are closer to the xiphosurans. The models of Weygoldt and Paulus (1979) and Shultz (1990) in which scorpions and non-scorpion arachnids are placed together to form a monophyletic Arachnida is supported by the synapomorphies of slit sensilla and lack of appendages on opisthosomal segment 1 [though these are present as transient limb buds during scorpion embryology (Anderson, 1973)].

Certain characters (not used in the analysis) of both scorpions and non-scorpion arachnids are almost certainly convergent terrestrial adaptations, e.g. gills modified to book-lungs, preoral digestion and trichobothria. Part of the problem is resolving which characters of eurypterids and arachnids are synapomorphies and which are convergences associated with a terrestrial habitat. In addition to this, most of the widely cited eurypterid/scorpion similarities (e.g. 12 opisthosomal segments, abdominal plates, compound lateral eyes, etc.) are symplesiomorphic and postabdominal differentiation emerges as the only useful synapomorphy. The Weygoldt and Paulus (1979) model in which Arachnida is monophyletic concurs most closely with our analysis, though we do not feel that arachnid monophyly is proven.

17.4.9 OTHER TAXA

A number of other Middle Cambrian arachnomorph taxa resemble the Lower Cambrian *Paleomerus* with a simple division of the body into two tagma plus a telson in some (e.g. *Molaria*, *Habelia*, *Sidneya* and *Emeraldella*). It is conceivable that a number of these taxa could be derived from the *Paleomerus/Strabops* lineage and investigating these relationships represents an area for future work. We regard this present study as a framework, identifying three major arachnomorph clades: cheloniellids, aglaspidids and chelicerates. These three taxa are probably not a monophyletic group (Figure 17.3), rather part of a Cambrian radiation of arachnomorph arthropods whose relationships remain to be resolved.

17.5 EVOLUTIONARY TREE

The cladogram (Figure 17.3) was superimposed on the stratigraphic ranges (using both published and unpublished data) of these taxa to produce an evolutionary model (Figure 17.4). The *Paleomerus/Strabops* lineage (the two taxa cannot be separated in the analysis) is the oldest group, predating the Burgess Shale-type faunas; a number of arachnomorph taxa could be derived from this morphologically simple lineage. Aglaspidids can be derived from this group, and underwent a late Cambrian radiation, surviving to the Ordovician. Cheloniellids are relatively young, appearing in the late Ordovician through to the Lower Devonian, though the model predicts their occurrence in the Cambrian. Chelicerates can also be derived from a *Paleomerus/Strabops*-like ancestor. The occurrence of *Lemoneites*, *Chasmataspis* and the oldest eurypterids indicates that chelicerates had appeared by at least the early Ordovician. There is an unpublished trace fossil which may have been made by an Upper Cambrian chasmataspid and would therefore extend the range of Chelicerata back into the Cambrian.

Removing *Lemoneites* from Xiphosura, means the first synziphosurines are Silurian. The stratigraphic occurrences of the Xiphosura was discussed by Anderson and Selden (1997) and Xiphosurida (the classic 'living fossils') do not appear until the Lower Carboniferous. The other chelicerate groups, chasmataspids, eurypterids and arachnids again appear to be part of a late Cambrian radiation, though the arachnids themselves are not known until the Silurian. Chelicerata are at least Ordovician in age, but with the exception of eurypterids, the Ordovician fossil record for chelicerates is poor. The model shows a long range extension for *Diploaspis*, xiphosurans and arachnids and predicts that xiphosurans (or their ancestors) and the *Diploaspis* ancestor should be found in the Cambrian and that arachnids (or their ancestors) should be found in the Ordovician. There is also a significant ghost lineage for Xiphosurida and its Upper Devonian synziphosurine sister group, *Kasibelinurus*, relative to the other synziphosurines (see the fuller analysis of Anderson and Selden, 1997). If scorpions are sister group to eurypterids both they and non-scorpion arachnids should be present in the Ordovician. At present, we lack the fossil evidence to investigate this early phase of chelicerate evolution and radiation.

17.6 SYSTEMATICS

CHELICERATA HEYMONS, 1901

Diagnosis
Arthropods with body divided into two tagmata: prosoma, covered by a primitively undivided carapace bearing both median and lateral eyes, and bearing six pairs of appendages, first of which (chelicerae) are chelate; and opisthosoma of 12 or fewer segments in which opisthosomal appendage 1 may be present and pediform, but in which subsequent opisthosomal appendages are plate-like and bear respiratory organs. Some degree of opisthosomal differentiation into a pre- and postabdomen developed. Post-anal telson primitively present.

Remarks
This diagnosis restricts Chelicerata to arachnids (including scorpions), eurypterids and xiphosurans (including synziphosurines) and is essentially a restatement of Heymons's (1901) concept of Chelicerata, but now including the chasmataspids. It excludes *Sanctacaris* (which lacks opisthosomal differentiation) and *Fuxianhuia* (which has biramous opisthosomal limbs), the remaining Arachnomorpha and pycnogonids (though pycnogonids have median eyes and their highly reduced opisthosoma would not show differentiation and is clearly derived). We note the following provisos: The chelicerae in some arachnids (e.g. spiders) are modified from the chelate state, into 'clasp-knife' structures. The arachnid orders Palpigradi and

Solifugae have a divided carapace. In our analysis this would represent a derived state permitting prosomal flexibility, rather than a primitive character, as implied in the phylogenies of Savory (1971) and Grasshoff (1978). Scorpions have been interpreted as having 13 opisthosomal segments (van der Hammen 1989), partly based on a reported transitory pregenital embryological segment-bearing appendages. However, Anderson's (1973) detailed review of scorpion embryology noted transitory limb buds on the pregenital segment which are later reabsorbed. These limb buds were still part of a groundplan of a seven-segmented preabdomen and a five-segmented postabdomen, supporting the interpretation that scorpions have 12, not 13, opisthosomal segments.

17.7 CONCLUSIONS

1. Chelicerata Heymons, 1901 belongs to a broad clade of arthropods, the Arachnomorpha Heider, 1913.
2. Chelicerata is monophyletic, diagnosed as above, and is restricted to *Lemoneites*, Xiphosura, Chasmataspida, Eurypterida and Arachnida.
3. Eleven opisthosomal segments appears to be primitive for Chelicerata, as occurs in *Lemoneites*, Xiphosura and outgroups such as *Paleomerus*. Chasmataspida are not xiphosurans and are placed as the sister group of Eurypterida + Arachnida, with which they share the synapomorphy of 12 opisthosomal segments.
4. Xiphosura, Eurypterida, Chasmataspida and Scorpiones all possess autapomorphies and thus none is ancestral to any other chelicerate group. Arachnida emerges as a monophyletic taxon while Merostomata is paraphyletic.
5. The Ordovician *Lemoneites* appears very close to the origins of the chelicerates, but is too poorly preserved to resolve whether it is a primitive synziphosurine, sister group to chasmataspids, eurypterids and arachnids, or a sister group to all other chelicerates.
6. Presence of chelicerae is difficult to determine in many Lower Palaeozoic fossils and the presence of median eyes (or their tubercle) and some degree of differentiation in the opisthosoma into a preabdomen and postabdomen are better characters for recognizing a fossil chelicerate.
7. *Neostrabops*, *Duslia*, *Triopus*, *Pseudarthron* and *Cheloniellon* form a monophyletic group, Cheloniellida, placed as sister group to Chelicerata in this analysis, and is united on the character of a procurved posterior carapace margin.
8. (*Paleomerus*, *Strabops* + Aglaspidida) represents the sister group to Chelicerata and Cheloniellida. Aglaspidids represent a poorly defined group which warrants revision and it is difficult to resolve the position of aglaspidids relative to chelicerates and the *Paleomerus/Strabops* lineage.
9. Cheloniellida, Aglaspidida and Chelicerata represent three distinct arachnomorph taxa, all of which could be derived from a *Paleomerus/Strabops*-like lineage, though their relationships to the other Arachnomorpha remain uncertain.

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