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The phylogeny of arachnomorph arthropods and the origin of the Chelicerata

Trevor J. Cotton and Simon J. Braddy

ABSTRACT: A new hypothesis of the relationships between arachnomorph arthropods, and the origin of chelicerates, is presented based on a cladistic analysis of 34 taxa and 54 characters. The present study provides a detailed discussion of primary hypotheses of homology and includes a more complete range of terminal taxa than previous analyses. The analysis provides the first convincing synapomorphies for the Arachnomorpha, and suggests that the marrellomorphs are not arachnomorphs. The assignment of Cambrian 'great appendage' (or megacheiran) arthropods to the Arachnomorpha is confirmed, and potential synapomorphies uniting them with chelicerates are discussed and tested. Principal amongst these are the loss of the first cephalic appendages (the antennae), loss of the exopods of the second cephalic appendages and modification of the endopods of these appendages into spinose grasping organs. The Arachnomorpha consists of two major clades: (1) a 'chelicerate-allied' clade, including chelicerates, megacheirans, *Emeraldella, Sidneyia*, cheloniellids and aglaspidids, in which chelicerates and a paraphyletic group of megacherian arthropods form the sister group to the remaining taxa; and; (2) a 'trilobite-allied' clade, including trilobites, xandarellids, helmetiids, tegopeltids and naraoiids, the relationships of which are more fully resolved than in previous studies.

KEY WORDS: Arachnata, Arachnomorpha, Burgess Shale, Cambrian, Cheliceramorpha, cladistics, evolution, Trilobitoidea, Trilobitomorpha

The phylogeny of arthropods has been debated for over a century. Whilst five major groups, the extant Chelicerata, Hexapoda, Crustacea and Myriapoda, and the extinct Palaeozoic Trilobita, have more or less consistently been recognised, the relationships between these groups have been highly contentious (see Wheeler *et al.* 1993; Wills *et al.* 1995). Recently, however, some consensus has been reached on issues such as the monophyly of the euarthropods, and the sister group relationship between crustaceans and hexapods, forming the Pancrustacea (Budd 1996a; Akam 2000). Furthermore, all recent cladistic studies that have included fossil taxa have recognised trilobites and chelicerates as more closely related to each other than either group is to Pancrustacea (see e.g. Ax 1986; Bergström 1992; Weygoldt 1998; Wills *et al.* 1998a). This clade has variously been given the names Arachnomorpha (Størmer 1944, 1951; Briggs & Fortey 1989; Briggs *et al.* 1992; Wills *et al.* 1995; Weygoldt 1998), Lamellipedia (Hou & Bergström 1997) or Arachnata (Lauterbach 1973, 1980, 1983; Chen *et al.* 1997; Ramsköld *et al.* 1997; Edgecombe & Ramsköld 1999; although Lauterbach apparently later rejected the term Arachnata and included all the assigned taxa in the Chelicerata – see Müller & Walossek 1987, p. 53). The term Arachnata has recently been most extensively used, but the current concept of the group is closer to that of Størmer than of Lauterbach, and therefore, the earlier name Arachnomorpha, originally proposed by Heider (1913), is preferred here. This group can be defined as the most inclusive clade, including Chelicerata, but not Pancrustacea (following Chen *et al.* 1997; Ramsköld *et al.* 1997). According to this definition, the Arachnomorpha consists of the chelicerates and their stem group (*sensu* Ax 1986), as illustrated by Figure 1. Therefore, resolving arachnomorph phylogeny will have important implications for understanding early chelicerate evolution (Dunlop 1999).

In addition to the Trilobita and Chelicerata, Størmer (1944) included in his Arachnomorpha a seemingly highly disparate (Gould 1989, 1991) assemblage of Palaeozoic fossil arthropods, the Trilobitomorpha (Størmer 1944) or Trilobitoidea (Størmer 1959). These included various problematic arthropods from the famous Middle Cambrian Burgess Shale of British Columbia, Canada (see Conway Morris 1982; Briggs *et al.* 1994), and *Cheloniellon* and *Mimetaster* from the Devonian Hunsrück Slate of Germany (see Bartels *et al.* 1998). Since then, our knowledge of arachnomorph diversity has been transformed by the discovery of many new taxa from Cambrian Burgess Shale-type faunas, and to a lesser extent, later faunas from around the world. Of primary importance amongst these new *Lagerstätte* (reviewed by Conway Morris 1989, 1998) is the Chengjiang fauna from the Lower Cambrian of Yunnan, China (see Hou *et al.* 1991; Chen *et al.* 1996; Hou & Bergström 1997).

These new finds largely consist of taxa similar to those from the Burgess Shale. For example, the Chengjiang fauna includes taxa that are clearly closely related to *Helmetia* Walcott, 1918, *Tegopelte* Simonetta & Delle Cave, 1975 and *Alalcomenaeus* Simonetta, 1970 (Edgecombe & Ramsköld 1999). Similarly, the most widespread trilobitomorph group, the Naraoiidae (*sensu* Fortey & Theron 1994) or Nektaspida (*sensu* Hou & Bergström 1997), was originally known only from *Naraoia* Walcott, 1912 from the Burgess Shale. A number of related genera are now recognised from the Early Cambrian of Poland (*Liwia* Dzik & Lendzion, 1988), China (*Misszhouia* Chen *et al.*, 1997) and Greenland (*Buenaspis* Budd, 1999a), and the Ordovician of Sardinia (*Tariccoia* Hammann *et al.*, 1990) and South Africa (*Soomaspis* Fortey & Theron, 1994). *Naraoia* itself has now also been described from the Early Cambrian of Idaho, the Middle Cambrian of Utah (both Robison 1984) and from the Chengjiang fauna (Zhang & Hou 1985). However, some of the probable arachnomorphs from Cambrian exceptionally preserved faunas have no obvious affinities to others, despite detailed knowledge of their morphology. Notable among these are *Emeraldella* Walcott, 1912 and *Sidneyia*

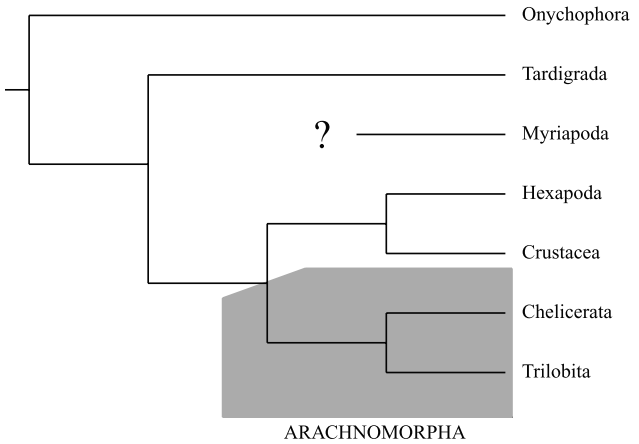

Figure 1 Widely accepted relationships between major arthropod groups, illustrating the Arachnomorpha concept followed here.

Walcott, 1911 from the Burgess Shale, *Retifacies* Hou *et al.*, 1989 from the Chengjiang fauna and *Phytophilaspis* Ivantsov, 1999 from the Lower Cambrian Sinsk Formation of Siberia.

Despite uniformally supporting an arachnomorph clade including the trilobites and various Cambrian trilobite-like or merostome-like arthropods, recent studies have largely failed to provide convincing synapomorphies for the group (Dunlop 1999). Here cladistic methods are used to address this problem, to rigorously assess the limits of the Arachnomorpha and to determine relationships within the arachnomorph group as a whole. The present study is based upon a new matrix that is more comprehensive than previous work in terms of both the range of characters considered and taxonomic sampling.

1. Previous studies

Since Størmer (1944), studies of the phylogeny of the Arachnomorpha have disagreed on the taxa that should be included in the group and on the relationships between them (Fig. 2). In the earliest relevant cladistic studies, Lauterbach (1980, 1983) and Ax (1986) suggested a particularly close relationship between chelicerates and a paraphyletic Trilobita, a hypothesis originally proposed by Raw (1957). Lauterbach and Ax argued that olenellid trilobites (reviewed by Palmer & Repina 1993) were the sister group to chelicerates and that other trilobites were the sister group to this clade. This idea has been extensively criticised. In particular, Lauterbach ignored all other arachnomorph taxa (including more plesiomorphic trilobites) and a wide range of characters that are potential trilobite synapomorphies (Fortey & Whittington 1989; Fortey 1990a; Ramsköld & Edgecombe 1991; Bergström & Hou 1998). To the present authors' knowledge, no subsequent author, except Weygoldt (1998), has accepted Lauterbach's hypothesis.

Most hypotheses of arachnomorph phylogeny have been presented as part of analyses of the phylogeny of arthropods as a whole. The pioneering cladistic work of Briggs & Fortey (1989) found that the crustaceans (and Cambrian 'crustaceanomorphs') were paraphyletic with respect to arachnomorphs (Fig. 2A). Within the arachnomorphs, a strongly pectinate paraphyletic group, including *Aglaspis* and various Burgess Shale arthropods, was primitive with respect to a clade of all other taxa. This consisted of a [*Habelia* (*Naraoia*, Trilobita)] group and a clade including the Burgess Shale 'great appendage' arthropods, *Burgessia*, *Sarotrocercus* and chelicerates (Fig. 2A). This work was subsequently revised (Briggs *et al.* 1992, 1993) to include a representative range of extant arthropods alongside a different selection of Cambrian taxa, coded for a greater number of characters. Whereas the earlier work used *Marrella* as an outgroup, the hypothesis of Briggs *et al.* (1992, 1993) was rooted using the lobopod *Aysheaia.* This study supported the monophyly of crustaceans and suggested a very different topology within the Arachnomorpha (Fig. 2B). Whereas *Sarotrocercus*, *Burgessia* and *Yohoia* were still placed close to the chelicerates, the other 'great appendage' taxa, *Alalcomenaeus* and *Leanchoilia*, were found to be basal arachnomorphs. Of the taxa placed in a basal paraphyletic assemblage in the earlier study, some remained basal (*Emeraldella* and *Sidneyia*), whereas others were now more closely related to chelicerates than trilobites (*Molaria*, *Aglaspis* and *Sanctacaris*).

In a further refinement, the work of Wills *et al.* (1995, 1998a) coded the previously analysed taxa for many new characters and considered a small number of additional taxa, notably from post-Cambrian Palaeozoic *Lagerstätte.* Whilst supporting the topology of major euarthropod clades found by Briggs *et al.* this analysis again proposed very different relationships within the Arachnomorpha (Fig. 2C). *Burgessia* was found to be the sister group to all other arachnomorphs, and a clade of trilobites, *Molaria* and *Naraoia*, the sister group to all remaining taxa. *Cheloniellon* and *Aglaspis* were successive sister groups to chelicerates. Notably, and unlike in previous analyses, most Burgess Shale arachnomorphs formed a large clade which was placed in opposition to the clade consisting of chelicerates, *Cheloniellion* and *Aglaspis.*

In contrast to these studies, Bergström (1992), Hou & Bergström (1997) and Bergström & Hou (1998) rejected parsimony as a phylogenetic criterion and developed an arthropod phylogeny (Fig. 2D) based on a small sample of characters. The possibility of any of the selected characters evolving convergently was excluded on purely methodological grounds. Bergström's interpretations of homology are also often unclear. For example, he used leg posture, which can rarely be adequately determined from fossils, as an important character (see Edgecombe & Ramsköld 1999, p. 281). Bergström's work has been extensively criticised (e.g. Schram 1993; Briggs 1998; Cotton 1999; Edgecombe & Ramsköld 1999), and these arguments are not repeated here.

The cladistic analysis of stem group chelicerates presented by Dunlop & Selden (1997) included only taxa that were found to be the most closely related to chelicerates by Wills *et al.* (1995, 1998a). The results of this analysis were largely unresolved (the published cladogram, fig. 17.3, is only one of 9450 most parsimonious trees), but supported the view of Wills *et al.* that *Cheloniellon* is more closely related to chelicerates than *Aglaspis.* However, Dunlop & Selden (1997, p. 232) noted that cheloniellids, aglaspidids and chelicerates may not form a monophyletic group with respect to all other arachnomorphs. Emerson & Schram (1997) analysed arthropod phylogeny on the basis of Arthropod Pattern Theory (Schram & Emerson 1991). Their results are also poorly resolved, and the topology of arachnomorph taxa highly unstable across the various treatments of their data they present (e.g. Emerson & Schram 1997, figs. 7.3A–C). Many of their characters are difficult to interpret outside the framework of the theory.

Edgecombe & Ramsköld (1999) recently presented a cladistic study of some arachnomorph taxa in an attempt to resolve the relationships of the Trilobita. Their work was an improvement on previous studies in that they included a comprehensive sample of both taxa and characters, and presented detailed discussions of the homology of these characters. Their results supported the monophyly of the Helmetiida (*sensu* Hou & Bergström 1997), Naraoiidae and Xandarellida (see Ramsköld *et al.* 1997) within an unresolved clade also including the Trilobita. *Sidneyia*, *Emeraldella* and *Retifacies* were found to

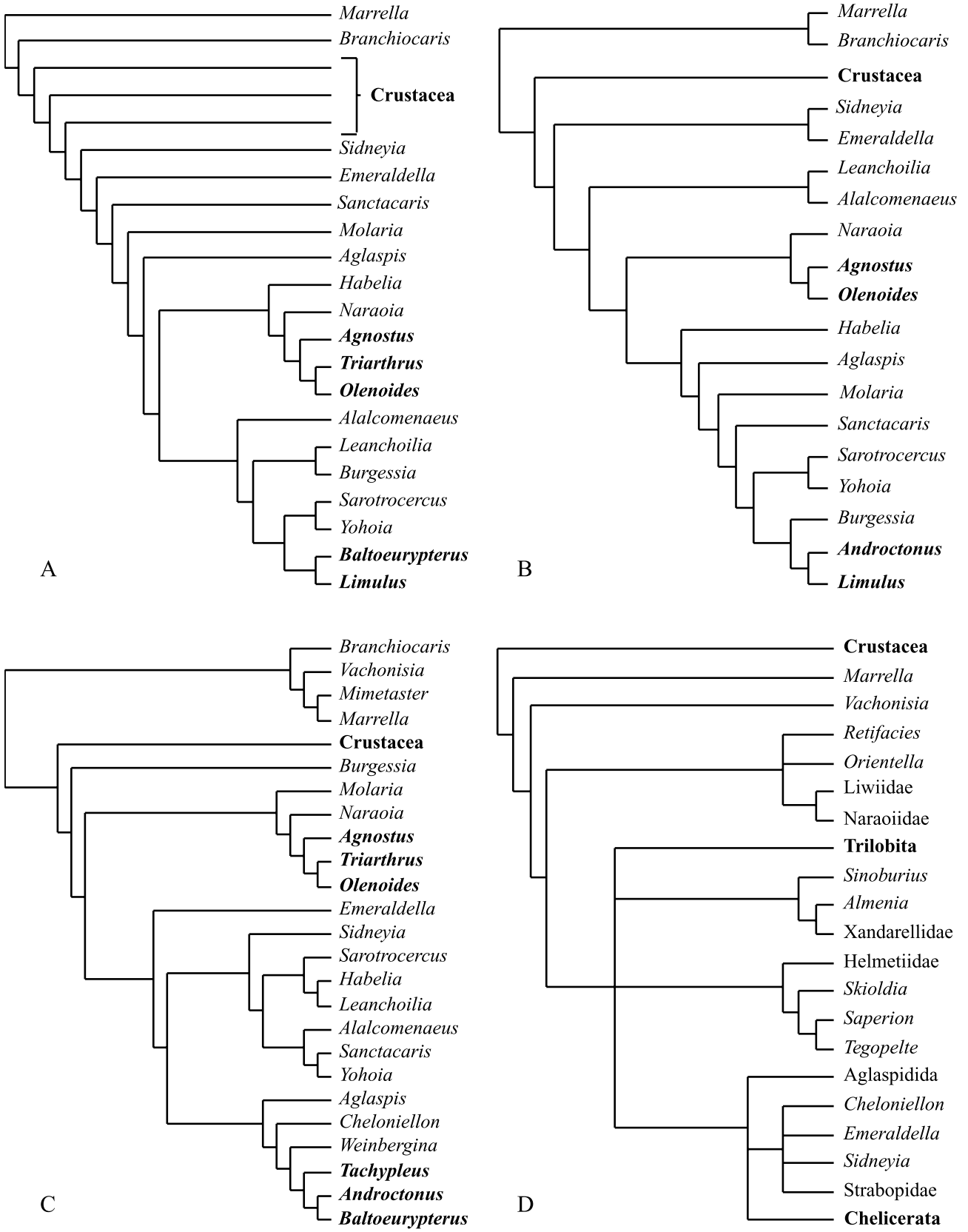

Figure 2 Previous hypotheses of arachnomorph phylogenys: (A) after Briggs & Fortey (1989, fig. 1; 1992, fig. 3), note that Crustacea are paraphyletic in this analysis; (B) after Briggs *et al.* (1992, fig. 3; 1993, fig. 1); (C) after Wills *et al.* (1995, fig. 1A; 1998a, fig. 2. 1); and (D) after Hou & Bergström (1997, fig. 88) (for monotypic families, the family names used by Hou & Bergström have been replaced with generic names). Taxa important for the recognition of an arachnomorph clade (i.e. trilobites, chelicerates and crustaceans; see text) are shown in bold type.

be more basal arachnomorphs on the basis of outgroup rooting with Marellomorpha. Unfortunately, Edgecombe & Ramsköld (1999) made no attempt to establish the monophyly of the group of 'trilobite-allied arachnates' that they included in their analysis, and did not consider the position of the chelicerates.

Table 1 Authorship and important references for species included in cladistic analyses of arachnomorphs. Previous analyses by Briggs & Fortey (1989, 1992), Briggs *et al.* (1992, 1993), Wills *et al.* (1995, 1998a) and Edgecombe & Ramsköld (1999) informed the coding of many taxa, and are not listed.

Name and authorship	Other references
Alalcomenaeus cambricus Simonetta, 1970	Briggs & Collins (1999)
Buenaspis forteyi Budd 1999a	
Burgessia bella Walcott, 1912	Hughes (1975)
Cheloniellon calmani Broili, 1932	Broili (1933); Stürmer & Bergström (1978)
Cindarella eucalla Chen *et al.* 1996	Ramsköld *et al.* (1997).
Emeraldella brocki Walcott, 1912	Bruton & Whittington (1983); Briggs & Robison (1984)
Eoredlichia intermedia (Lu, 1940)	Shu *et al.* (1995); Ramsköld & Edgecombe (1996)
Fortiforceps foliosa Hou & Bergström, 1997	
Helmetia expansa Walcott, 1918	Briggs *in* Conway Morris (1982); Briggs, Erwin & Collier (1994)
Jianfengia multisegmentalis Hou, 1987b	Bergström & Hou (1991); Chen & Zhou (1997)
Kuamaia lata Hou, 1987a	Hou & Bergström (1997); Begström & Hou (1998)
	Edgecombe & Ramsköld (1999)
Leanchoilia superlata Walcott, 1912	Bruton & Whittington (1983); Briggs & Robison (1984)
Lemoneites Flower, 1968	Dunlop & Selden (1997)
Liwia plana (Lendzion, 1975)	Dzik & Lendzion (1988); Fortey & Theron (1994)
	Chen, Edgecombe & Ramsköld (1997)
Marrella splendens Walcott, 1912	Whittington (1971)
Mimetaster hexagonalis (Gürich, 1931)	Stürmer & Bergström (1976)
Misszhouia longicaudata (Zhang & Hou, 1985)	Bergström & Hou (1991); Chen *et al.* (1997); Hou & Bergström (1997)
Naraoia Walcott, 1912	Whittington (1977); Robison (1984); Zhang & Hou (1985)
	Chen *et al.* (1997)
Olenoides serratus (Rominger, 1887)	Whittington (1975a, 1980)
Paleomerus hamiltoni Størmer, 1956	Bergström (1971); Dunlop & Selden (1997)
Retifacies abnormalis Hou *et al.* 1989	Hou & Bergström (1997)
Saperion glumaceum Hou *et al.* 1991	Ramsköld *et al.* (1996); Hou & Bergström (1997)
Sidneyia inexpectans Walcott, 1911	Bruton (1981)
Sinoburius lunaris Hou *et al.* 1991	Hou & Bergström (1997) *Skioldia aldna* Hou & Bergström, 1997
Soomaspis splendida Fortey & Theron, 1994	Chen *et al.* (1997)
Tariccoia arrusensis Hammann *et al.* 1990	Fortey & Theron (1994); Chen *et al.* (1997)
Tegopelte gigas Simonetta & Delle Cave, 1975	Whittington (1985); Ramsköld *et al.* (1996)
Weinbergina opitzi Richter & Richter, 1929	Stürmer & Bergström (1981); Andersen & Selden (1997); Dunlop & Selden (1997)
Xandarella spectaculum Hou *et al.* 1991	Bergström & Hou (1991); Ramsköld *et al.* (1997);
	Hou & Begström (1997)
Yohoia tenuis Walcott, 1912	Whittington (1974)

2. Cladistic analysis

2. 1. Taxonomic scope

Thirty-four ingroup taxa were considered in the cladistic analyses. Of these, the majority were coded as individual species-level terminals, although higher taxonomic levels were employed in some instances. A complete list of species and genus-level terminals, along with details of authorship and other important references, is given in Table 1. Species-level terminals are referred to throughout by generic names only (except in Table 1), since the majority are assigned to monotypic genera. In addition to these ingroup taxa, a hypothetical outgroup was used for rooting, as discussed below.

Terminals were selected on the basis of the recent cladistic analyses of Wills *et al.* (1995, 1998a) and Edgecombe & Ramsköld (1999), and to a lesser extent, previous hypotheses of arthropod relationships. The majority of taxa that have been included in an arachnomorph group by previous authors are included in this study. Exceptions include *Agnostus*, *Habelia*, *Molaria*, *Sanctacaris* and *Sarotrocercus* (all of which were considered by Wills *et al.* but not Edgecombe & Ramsköld), the putative chelicerate *Offacolus*, and *Phytophilaspis.* The Agnostina are regarded as a clade within the Trilobita derived from Eodiscina (e.g. Fortey 1990a; Fortey & Theron 1994; Wills *et al.* 1998a) rather than stem group crustaceans (e.g. Shergold 1991; Bergström 1992; see Cotton 2002 for a detailed discussion and phylogenetic analysis). The Burgess Shale taxa *Habelia* Walcott, 1912, *Molaria* Walcott, 1912 and *Sarotrocercus* Whittington, 1981 and the Hunsrück Slate *Magnoculocaris blindi* (Briggs & Bartels 2001, 2002) are rather poorly known and hypotheses of their relationships constrained by too few characters.

Sanctacaris Briggs & Collins, 1988 and the probably closely related *Offacolus* Orr *et al.*, 2000 were both originally described as having chelicerate affinities. Sutton *et al.* (2002) added *Offacolus* to the matrix of Wills *et al.* (1995, 1998a), and found it to be nested within the Chelicerata, despite its biramous cephalic appendages. The material of *Sanctacaris* is in need of restudy; the homology of the cephalic appendages and ventral cephalic structures remain unclear (see Budd 2002 and Briggs & Collins 1988 for alternative schemes). The relationships of these 'sanctacarids' will be considered in detail later by Braddy and co-workers, following re-examination of *Sanctacaris*, and description of a new Chengjiang taxon (Babcock & Zhang in press) that is likely to have a profound impact on the interpretation of both *Sanctacaris* and *Offacolus.*

Phytophilaspis Ivantsov, 1999 shows a combination of features that may be homologous to those found in naraoiids (the

form of the pygidium), xandarellids (the eye slits and overlap of anterior thoracic segments by the head shield) and Trilobita (the hypostome with anterior and posterior lateral wings). Therefore, it potentially has a pivotal position in the phylogeny of the trilobite-allied Arachnomorpha. However, the interpretation of these features by Ivantsov (1999) requires confirmation, and adequately determining the homology of these structures would require restudy of the material.

The Xandarellida, known only from the Chengjiang fauna, were originally described as an arachnate clade (Ramsköld *et al.* 1997). All three valid genera, *Xandarella*, *Sinoburius* and *Cindarella*, were included in the analysis of Edgecome & Ramsköld (1999). They differ in important respects, and therefore, all three genera are included here to test the monophyly of this group in the context of a wider analysis.

Wills *et al.* (1995, 1998a) represented the Trilobita (except Agnostida) by *Olenoides*, the appendages of which are known from the Burgess Shale, and the Ordovician *Triarthrus* (see Cisne 1975, 1981; Whittington & Almond 1987). However, the present authors follow Edgecombe & Ramsköld (1999) in choosing *Olenoides* and *Eoredlichia* to represent the Trilobita. These are more basal trilobites (see e.g. Fortey 1990a, b) than *Triarthrus*, and consequently, are more likely to reflect the ancestral trilobite condition. The putative trilobite *Kleptothule* Budd 1995 from the Early Cambrian Sirius Passet fauna of North Greenland is not included. Its appendages are unknown, and homologies between exoskeletal features of this taxon and other arachnomorphs are uncertain.

The Naraoiidae or Nektaspida (reviewed above) are widely considered to be closely related to the trilobites, either as a paraphyletic assemblage of 'soft-bodied' trilobites (e.g. Shu *et al.* 1995, fig. 20B) or as the sister group of calcified trilobites (Fortey 1997; Whittington 1977). They have been included in the Trilobita by some authors. However, Edgecombe & Ramsköld (1999) found no particularly close relationship between naraoiids and trilobites (see above). In order to test the monophyly of the group, all described naraoiid genera are included except *Maritimella* and *Orientella* (both Repina & Okuneva 1969), which are probably pseudofossils (Robison 1984, p. 2).

Tegopelte from the Burgess Shale has also been considered a soft-bodied trilobite (Whittington 1985). Ramsköld *et al.* (1996) revised the exoskeletal morphology of *Tegopelte* and noted similarities to the Chengjiang taxa *Saperion* and *Skioldia.* This relationship has been confirmed by cladistic analysis (Edgecombe & Ramsköld 1999). An undescribed large arthropod from the Soom Shale *Lagerstätte* (Aldridge *et al.* 2001, fig. 3.4.4.2) is probably a tegopeltid (Braddy & Almond 1999). The Helmetiidae, based on *Helmetia* Walcott, 1918 from the Burgess Shale, are united with the tegopeltid group in the Helmetiida (Hou & Bergström 1997; Edgecombe & Ramsköld 1999). *Helmetia* is rather poorly known, and awaits redescription, but is very similar to *Kuamaia lata* Hou, 1987a, *Kuamaia muricata* Hou & Bergström, 1997 and *Rhombicalvaria acantha* Hou, 1987a from Chengjiang. There are no significant differences between these Chinese taxa, and their taxonomy may be over split (Delle Cave & Simonetta 1991; Hou & Bergström 1997). The morphology of *Kuamaia lata* is known in some detail and it is coded here, along with *Helmetia* and all three tegopeltid genera.

Delle Cave & Simonetta (1991, table 1) compared several taxa to *Tegopelte* and *Helmetia.* Of these, only *Retifacies* is known in enough detail to make coding worthwhile. *Tontoia* and *Nathorstia* (both Walcott, 1912) are *nomina dubia* (see Whittington 1985, 1980, respectively) and only the exoskeleton is known of *Urokodia* Hou *et al.*, 1989 and *Mollisonia* Walcott, 1912. *Retifacies* has been placed near a trilobite-naraoiid-helmetiid clade (Delle Cave & Simonetta 1991; Edgecombe & Ramsköld 1999) or as sister group to the naraoiids (Hou & Bergström 1997).

There is a long history of comparing *Emeraldella* and *Sidneyia* with chelicerates (following Størmer 1944), but the position of these taxa in cladistic studies has been highly variable (see Fig. 2). According to the hypothesis of Bergström, these taxa, along with the Aglaspidida and Cheloniellida, form a clade that is the sister group to the chelicerates. More usually, aglaspidids or cheloniellids have been considered sister taxon to the chelicerates, and these Burgess Shale taxa more distantly related.

A cheloniellid-chelicerate clade was supported by Wills *et al.* (1995, 1998a) and Stürmer & Bergström (1978; also Bergström 1979), and Simonetta & Delle Cave (1981) and Delle Cave & Simonetta 1991) placed the cheloniellid *Triopus* as ancestral to all chelicerates. The Cheloniellida (*sensu* Dunlop & Selden 1997) are represented by *Cheloniellon* herein since the appendages of other cheloniellid taxa are unknown.

It has also repeatedly been suggested that chelicerates evolved from aglaspidids (e.g. Starobogatov 1990), and aglaspidids have been included in the Chelicerata by some authors (Størmer 1944; Weygoldt & Paulus 1979). The coding of aglaspidids is considered in detail in Section 2.2. *Lemoneites* (Flower 1968) and *Paleomerus* (Størmer 1956; Bergström 1971) have been assigned to the Aglaspidida by some authors (see Hou & Bergström 1997, pp. 96–97). They are included to facilitate comparison with the results of Dunlop & Selden (1997). *Lemoneites* is particularly problematic (R. A. Moore, pers. comm. 2004), and both taxa are known from very few characters – hence, the present authors have investigated the implications of their exclusion from the analysis (see Section 2.6). The aglaspidid-like arthropod *Kodymirus vagans* Chlupác & Havlícek 1965 from the Lower Cambrian of the Czech Republic (redescribed and compared to eurypterids by Chlupác 1995) is excluded from the present study because features of its morphology that are well known generally agree with those of *Aglaspis.*

The phylogeny of crown group chelicerates is a matter of considerable debate, but most authors have considered pycnogonids, xiphosurans and eurypterids as early divergent groups within Chelicerata (Dunlop 1999). These hypotheses are represented here by coding a generalised pycnogonid and eurypterid, and the Devonian synziphosurine *Weinbergina* (Stürmer & Bergström 1981). *Weinbergina* is the best-known synziphosurine and is more likely to represent the primitive condition of xiphosurans than modern examples. The phylogeny of the Xiphosura has recently been studied by Anderson & Selden (1997). Coding for Eurypterida follows the recent work of Dunlop & Selden (1997), Dunlop (1998), Braddy *et al.* (1999) and Dunlop & Webster (1999). Coding for pycnogonids follows general works on the group (e.g. King 1973; Fry 1978), the reconstruction of the pycnogonid stem group by Bergström *et al.* (1980) and recent work on pycnogonid phylogeny (Munilla 1999; Arango 2002). The pycnogonid family Ammotheidae is generally accepted as the most plesiomorphic extant group (Arango 2002).

Two groups of Palaeozoic fossil taxa have been included in the Arachnomorpha by some authors, but considered less closely related by others. *Marrella* from the Burgess Shale and two Devonian taxa, *Mimetaster* and *Vachonisia*, have generally been considered to form the clade Marrellomorpha (Whittington 1971; Stürmer & Bergström 1976; Bergström 1979; Wills *et al.* 1995). This has been thought to be the sister group to other arachnates (Stürmer & Bergström 1976), a basal schizoramian or a basal euarthropod group (see Fig. 2). Bergström (1979) included the Carboniferous Cycloidea in the

Marrellomorpha, but there is considerable evidence that these are rather derived crustaceans (see Schram *et al.* 1997) and they are not considered further. The Burgess Shale taxon *Burgessia* has also been placed in the Marrellomorpha (Hou & Bergström 1997), but was not found to belong to this clade in most analyses. Størmer (1944) placed *Burgessia* in a comparable systematic position to *Marrella*; he included both in the Arachnomorpha, but excluded them from the Merostomoidea. *Marrella*, *Mimetaster* and *Burgessia* were included in the present study to assess whether the marellomorphs should be included in the Arachnomorpha and test the affinities of *Burgessia.*

The Cambrian 'great appendage' arthropods (the Megacheira of Hou & Bergström 1997) have been nested within the Arachnomorpha in most cladistic studies (e.g. Briggs & Fortey 1989, Wills *et al.* 1995, 1998a; Emerson & Schram 1997). Briggs & Fortey (1989, 1992) recognised megacheiran taxa as particularly closely related to chelicerates (Fig. 2A), while other authors (Bergström 1992; Hou & Bergström 1997; Budd 2002) have considered megacheirans to be primitive euarthropods, or ancestral to some (but not all) crustaceans (Delle Cave & Simonetta 1991, and references therein). Since the monophyly of the megacheirans has not usually been supported, the present authors have included nearly all described taxa. These include *Leanchoilia*, *Alalcomenaeus* and *Yohoia* from the Burgess Shale, and *Fortiforceps* and *Jianfengia* from the Chengjiang fauna. Excluded from this study are: *Actaeus* Simonetta, 1970 from the Burgess Shale, which may be a synonym of *Alalcomenaeus* (Briggs & Collins 1999); *Alalcomenaeus*? *illecebrosus* (Hou 1987b, see Hou & Bergström 1997) from the Chengjiang Fauna, which is probably a chimaera (Briggs & Collins, 1999); and the poorly preserved *Leanchoilia*? *hanceyi* from the Middle Cambrian of Utah (Briggs & Robison 1984).

According to the definition given above, any assessment of the limits of the Arachnomorpha needs to consider the phylogenetic position of these taxa relative to crustaceans. To this end, a generalised crustacean, intended to represent the plesiomorphic crustacean condition, was included as an ingroup taxon. There has been considerable disagreement over the most basal crustacean group (see Wills 1997, pp. 194–5; Schram & Hof 1998, pp. 245–8). The coding used here largely follows Walossek & Müller's (1990, 1997, 1998) and Walossek's (1993) concept of the crustacean stem group, but is intended to be conservative so that coding on the basis of other theories of crustacean origins would be similar.

2.2. Aglaspidida

The morphology of the appendages of aglaspidids is poorly known, having been described from three species of body fossil, *Aglaspis spinifer* Raasch, 1939, *Flobertia kochi* Hesselbo, 1992 and *Khankaspis bazhanovi* Repina & Okuneva, 1969, and trace fossil evidence (Hesselbo 1988). Of these, the appendages of *Aglaspis*, described by Raasch (1939), Briggs *et al.* (1979) and Hesselbo (1992), are by far the best known. The appendages of *Flobertia* (described by Raasch 1939 as *Aglaspis barrandei*, and Hesselbo 1992) agree with those of *Aglaspis.* However, the appendages of *Khankaspis* show a different morphology, but have only been poorly illustrated and described (Repina & Okuneva 1969). This material suggests the presence of lobate exopods with lamellate setae. This taxon is probably correctly assigned to aglaspidids (*cf.* Whittington 1979, p. 258), on the basis the central position of the dorsal eyes and presence of genal spines, although Hou & Bergström (1997, p. 96) suggested that its broad tail spine may indicate that it is a strabopid.

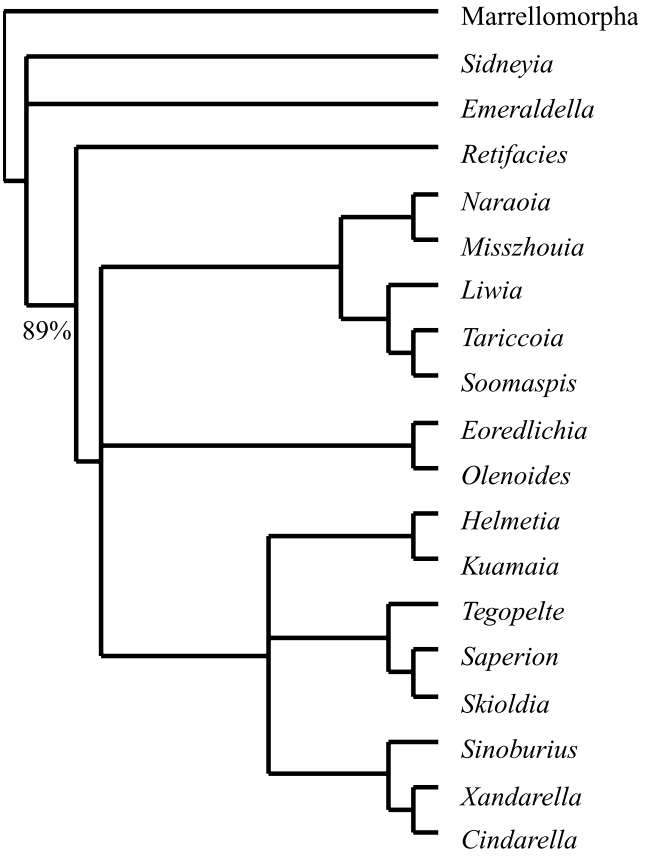

Figure 3 Majority rule consensus of 'trilobite-allied' arachnate phylogeny, after Edgecombe & Ramsköld (1999, fig. 3).

It remains unclear whether lamellate exopods are absent in some aglaspidids (*Aglaspis*) and present in others (*Khankaspis*), or whether the apparent differences in appendage morphology between these taxa are a result of preservational bias alone. A possible preservational analogue is provided by some Chengjiang taxa, in which the exopods are very poorly preserved and the endopods of the cephalic appendages are preserved as impressions in the dorsal head shield in a similar manner to those of *Aglaspis.* This is presumably because the endopods were more convex and more heavily sclerotised than the exopods. This mode of appendage preservation is most clearly seen in *Misszhouia longicaudata* (see Chen *et al.* 1997, fig. 2a–d), but is also found in *Sinoburius* (see Hou & Bergström 1997) and possible protaspides of *Naraoia* (Hou *et al.* 1991).

Here, a generalised aglaspidid is coded in two different ways to accommodate this uncertainty. In both codings, they are considered to have possessed a pair of antenniform appendages, followed by 11 pairs of pediform endopods, on the head and first eight thoracic tergites (Briggs *et al.* 1979; Hesselbo 1988, 1992). According to one interpretation (coded as Aglaspidida 1), all the appendages are uniramous; the exopod is lost throughout. According to the other (Aglaspidida 2), exopods consisting of a single lobe fringed with lamellate setae (Repina & Okuneva 1969, pl. 15, figs 1, 3 & 4) are present on at least some appendages, but their distribution and attachment are considered unknown.

2.3. Outgroup rooting

A hypothetical plesiomorphic euarthropod was included to allow outgroup rooting. Many of the characters considered could be coded unambiguously on the basis of recent discussions of the arthropod stem group (Budd 1996b, 1997, 1999b).

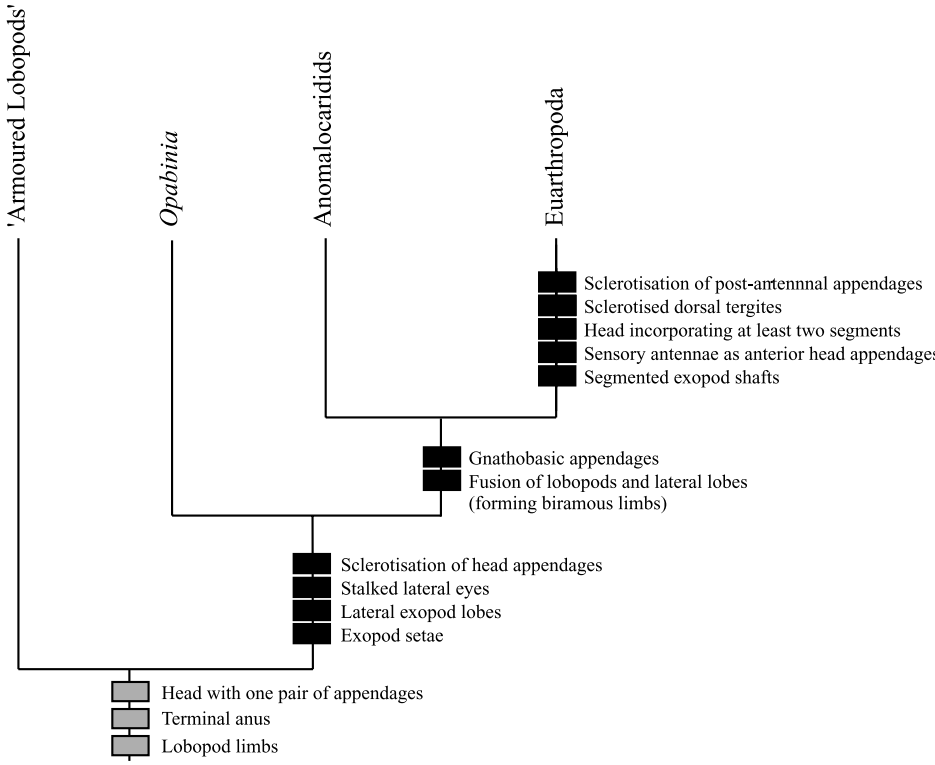

Figure 4 Reconstruction of the euarthropod stem group used to inform coding of hypothetical outgroup. Gross topology largely follows Budd (1996b, fig. 9; 1997, fig. 11.10). Solid boxes indicate unambiguous apomorphies and shaded boxes character states which are plesiomorphic for the Arthropoda.

The ancestral euarthropod is here considered to have possessed a head with antennae only, and a series of post-cephalic biramous limbs with gnathobases. The hypothesised pattern of the evolution of plesiomorphic euarthropod characters is shown in Figure 4. The use of a hypothetical outgroup is somewhat unsatisfactory, but only affects the relationship between the major clades (Arachnomorpha, Crustacea and Marrellomorpha); the topology within the arachnomorphs was unaffected by the use of this outgroup, since identical results were obtained with unrooted analyses, or by rooting with Crustacea, *Marrella* or both.

2.4. Characters and coding

Most previous cladistic analyses, with the notable exception of Edgecombe & Ramsköld (1999), have included only brief discussions of the primary hypotheses of homology involved in character construction and coding. Therefore, a full discussion of most characters is provided here. Descriptions of characters and character states, below, are arranged by organ system or body region in approximate anterior to posterior order. The distribution of character states across all taxa is shown in the data matrix (Table 2).

The terminology of morphological features in arachnomorphs is often confused. Terminology developed for chelicerates, trilobites and crustaceans has variously been applied to taxa included in this study, so some attempt is made to clarify terminology herein. Where appropriate, the present authors' terminology follows Edgecombe *et al.* (2000) and Wheeler *et al.* (1993), but following Scholtz (1997), the protocerebral 'segment' is considered to be acronal and, consequently, the deutocerebral segment to be the first true segment. Therefore, the antennae (or antennulae of crustaceans) belong to the first cephalic segment.

The present authors have attempted to include as complete a set of characters as possible. However, characters requiring hypotheses of homology between podomeres (e.g. the number of podomeres in endopods of thoracic appendages; Wills *et al.* 1998a, character 51) were not considered, following Edgecombe *et al.* (2000, p. 157). Secondly, some characters used by Bergström (e.g. Hou & Bergström 1997, p. 109), such as appendage posture and mode of feeding, were excluded, following Edgecombe & Ramsköld (1999). Finally, some characters of the ventral surface of the head were not coded, as discussed below and illustrated in Figure 7. The present authors do not include all potential synapomorphies for the Chelicerata as the status of many of these is debated (see e.g. Shultz 1990, 2001; Dunlop & Selden 1997; Weygoldt 1998; Wheeler & Hayashi 1998; Dunlop 1999; Edgecombe *et al.* 2000).

Two methods for the coding of inapplicable characters in phylogenetic analysis have been used. First, inapplicable character states can be coded as missing data. A complex structure may comprise characters: 'absent/present' and 'state1/state2', with taxa lacking the structure coded as absent for the first character and as missing data for the second. Some authors have regarded this method as problematic because it may lead to reconstruction of impossible ancestral states, and hence, unjustified trees (Platnick *et al.* 1991; Strong & Lipscomb 1999). The alternative is to code the second character as a third 'not applicable' state in taxa that lack the structure. These methods are equivalent to Pleijel's (1995) coding methods C and B, respectively. In the present study, inapplicable characters are treated as missing data for most analyses because coding them as a distinct character state reduces character independence and effectively weights the inapplicable character, and hence, could result in them dominating the analysis. The effects of this assumption were investigated by using a distinct character state in some analyses (see Section 2.6) and inapplicable characters are shown as distinct to 'true' missing data (using the symbol '-') in the matrix (Table 2).

2.4.1. Anterior cephalic appendages and head segmentation. 1. Appendages of the first segment (antennae): (0) present; and (1) absent. The majority of taxa considered in the present study

Table 2 Data matrix for cladistic analyses of arachnomorphs: (?) missing data; and (–) inapplicable characters. Letters indicate multistate uncertainty codings, as follows: (A) 34, (B) 02, (C) 01, (D) 134, (E) 12.

	1	1111111112	2222222223	3333333334	4444444445	5555
	1234567890	1234567890	1234567890	1234567890	1234567890	1234
OUTGROUP	0000000000	0?0––00000	0000000400	0000000000	000–0000––	–0–0
Aglaspidida 1	001A000001	0––––––0001	0000000001	1001000000	0012110?––	–101
Aglaspidida 2	00?A00000?	010––?0101	0000000001	1001000000	0012110?––	–101
Alalcomenaeus	1113–20100	010––10000	000000D00	1001000000	000–0101––	–110
Buenaspis	??????????	0?????????B	??0010?00	10?1000010	000–0?1110	10–0
Burgessia	0003000000	010––00012	–0000040–0	000?002000	000–0001––	–100
Cheloniellon	0014000001	010––00101	0000001 0–0	1001000001	0010110?––	–0–1
Cindarella	0006000000	0110000110	0000001 0–0	1011002100	010–101100	00–0
Crustacea	0003000000	000––01000	0000004 0–0	0000000000	000–0?00––	–100
Emeraldella	0015000000	0110000102	–0000000–0	1001000000	0011111 01––	–101
Eoredlichia	0003000010	0110000100	1000003111	1002000000	000–101100	10–0
Eurypterida	1116–11001	110––10101	0001004100	1001000000	0013010 1––	–100
Fortiforceps	0114–00000	010––10010	000000D00	1001000000	000–0101––	–110
Helmetia	???3?????10	?1????01?0	0?000120–0	1002000001	100–001101	00–0
Jianfengia	1114–10000	010––10110	000000D00	1001000000	000–0101––	–100
Kuamaia	000?0000?0	0110100100	0100012 0–0	1002000001	100–001101	00–0
Leanchoilia	1113–20100	010––1011B	000000D00	1001000000	000–1101––	–100
Lemoneites	??????????	0?????????1	?00??00??1	10?1000000	0012 0?0?––	–10?
Liwia	0????1?????	0??????????	0????0???0	10?1001010	000–0?1110	00–0
Marrella	0011000000	000––01002	–000?000–0	000?002000	000–0000––	–0–0
Mimetaster	0012000000	000––0101C	000??000–0	0001002000	000–0000––	–0–0
Misszhouia	0003000010	0111000100	0000001 0–0	11––200010	000––01100	10–0
Naraoia	0003100010	0111000100	0000001 0–0	11––200010	000––01100	?0–0
Olenoides	0003000010	0110000101	1000003111	1002000000	000–011100	00–0
Paleomerus	??????????	0?????????1	0000?0???1	10??000000	000–0?0?––	–10?
Pycnogonida	1114–11001	11––––0011	0001004 0–0	000?000000	001?0000––	–100
Retifacies	0003000000	010––00100	0000000 0–0	1001000000	000–101100	0100
Saperion	0????2?????	0?10100110	0100012 0–0	11––11––00	100––?1100	10–0
Sidneyia	0010100001	010––00100	0000000??0	1001000000	0012110 1––	–101
Sinoburius	0004000000	01????01?0	0110001 0–0	1001002100	010–001101	00–0
Skioldia	0????2?????	0?????????0	0100012 0–0	11––11––00	100––?1100	10–0
Soomaspis	??????????	01????????B	000010?0–0	10?1001010	000–0?1110	10–0
Tariccoia	??????????	01????????B	000010?0–0	10?1001010	000–0?1110	10–0
Tegopelte	000?0000??	01????011?	0?0001E0–0	10––E1––00	?00––01100	10–0
Weinbergina	1116–11001	110––10101	0001004100	1001000000	0012010 1––	–100
Xandarella	0004000000	0111000100	0010001 0–0	1011002100	010–10110?	00–0
Yohoia	1114–10001	110––10?10	000000D00	1001000000	0012010 1––	–110

possess a single pair of long, uniramous, multi- and annulated antennae at the anterior of the head, which presumably had a sensory function, as found in Crustacea, Myriapoda and most members of Hexapoda (i.e. proturans do not have antennae). These appendages are likely to be a synapomorphy of the Euarthropoda (e.g. Scholtz 1997; Walossek & Müller 1997), and therefore, the outgroup is coded as State 0. The anteriormost head appendages of most Cambrian megacheiran arthropods, which have been called 'great appendages' following Walcott (1912), consist of a small number of robust, spinose podomeres. Uniquely, *Fortiforceps* has a pair of short antennae anterior to the 'great appendages' (Hou & Bergström 1997, pp. 34–8). Therefore, it appears likely, that the 'great appendages' are the appendages of the second cephalic segment, and the antennae are lost in megacheirans other than *Fortiforceps.* This, of course, depends on recognising the 'great appendages' as homologous in all of these taxa, as discussed below (Character 2). Homology of the megacheiran anterior appendages with the second cephalic appendages of trilobites was previously suggested by Størmer (1944, p. 124) on the basis of their post-oral position.

The classical view of chelicerate head segmentation maintains that they too have lost the antennae and the chelicerae are the appendages of the second cephalic segment. Recent revisions of arthropod phylogeny have uncritically accepted this homology (Edgecombe *et al.* 2000; Giribet *et al.* 2001), which is based largely on neuroanatomy. The 'chelicero-neuromer', which innervates the chelicerae, seems to be homologous with the tritocerebrum associated with the second cephalic appendage pair of mandibulates (see Weygoldt 1979; Winter 1980). Although some uncertainty exists over the position of pycnogonids within Arthropoda, and the homology of their cephalic segmentation is poorly understood, this view is also supported by the presence of pre-cheliceral appendages in a pycnogonid larva (Larva D of Müller & Walossek 1986) from the Upper Cambrian of Sweden (Walossek & Dunlop 2002). *Cheloniellon* also has a pair of pre-oral pediform appendages, considered homologous to the chelicerae, in addition to its antennae. Thus, despite recent neontological studies that indicate that the chelicerae are homologous to the antennae of mandibulates, based on patterns of *Hox* gene expression (Damen *et al.* 1998; Telford &

Thomas 1998), and developmental data (Mittmann & Scholtz 2003), morphological evidence from fossils supports the view that chelicerates have lost the antennae. The *Hox* gene evidence suffers from a lack of comparative data from diverse mandibulates, especially primitive crustaceans (see Akam 2000), and the use of *Hox* gene expression boundaries as markers for segmental homology has been criticised (e.g. Abzhanov *et al.* 1999, although relating to posterior *Hox* patterns). Wills *et al.* (1998a, pp. 43 & 48) considered the chelicerae to be appendages of the second (deutocerebral) segment, but curiously, in support of this, cited Schram (1978) who unambiguously followed the homology scheme used in the present study.

The anterior-most appendages of *Aglaspis* were originally described as chelicerae (Raasch 1939), which lead to their classification in the Chelicerata (e.g. Størmer 1944). However, the morphology of these appendages (see Briggs *et al.* 1979) is more similar to that of antennae. They are narrow relative to the thoracic endopods, of relatively even diameter proximally and the podomeres are apparently weakly defined. Hesselbo (1988, 1992) also argued that the anterior appendages of *Aglaspis* are likely to be antennae. The distal parts are unknown (and hence, so is their length, *cf.* Wills *et al.* 1998a, p. 58) and there is no evidence that they were chelate, contrary to the coding of Wills *et al.* (1998a, character 31). Nothing is known about the anterior appendages of *Buenaspis*, *Lemoneites* or *Paleomerus*, and this character is accordingly coded as missing data in these taxa.

2. Form of endopod of appendages of the second segment: (0) pediform; and (1) anteriorly directed raptorial appendage with reduced number of podomeres and terminal podomeres bearing spines on distal margins. As discussed above, chelicerae and 'great appendages' are both likely to represent the appendages of the second segment. They also differ from the assumed primitive biramous euarthropod limb in similar ways, and therefore, are likely to be homologous modifications of these appendages. The homology of 'great appendages' and chelicerae was originally proposed by Henriksen (1928) and supported by Størmer (1944), but to the present authors' knowledge, no modern author has discussed this possibility.

Both 'great appendages' (Figs 5A, D, E) and chelicerae (Figs 5B, C) are equipped with strong spinose projections on the outer (dorsal) side of the distal margins of the terminal podomeres that are lacking on the proximal podomeres. Secondly, the number of podomeres in both chelicerae and 'great appendages' is more or less reduced compared to the number in the endopods of biramous limbs. In the case of 'great appendages', they are significantly more robust than those of posterior endopods, a situation that is matched in some chelicerates. The homology of the 'great appendages' of *Alalcomenaeus*, *Leanchoilia*, *Yohoia*, *Jiangfengia* and *Fortiforceps* is supported by all of these features, and is widely accepted (e.g. Wills *et al.* 1998a, character 31; Hou & Bergström 1997; Bergström & Hou 1998; Hou 1987a). Only Hou & Bergström (1991, p. 183) have suggested, albeit in passing, that the 'great appendages' of all these taxa may be convergent, a view they appear to have changed. The endopods of the appendages of other taxa are locomotory legs, which either lack strong spines or have spinose extensions that are invariably on the medial (ventral) surface and are stronger on the proximal podomeres than the distal ones (e.g. *Misszhouia*; Fig. 6A). In the latter case, these spines form part of the feeding system, along with the gnathobases, and are often located around the middle of the podomere rather than limited to the distal margin. These endopods are directed ventrolaterally, as opposed to anteriorly in the case of both chelicerae and 'great appendages'. The modified second appendages of *Marrella* resemble this plesiomorphic condition, here referred to as 'pediform', except in their anterolateral orientation. In some Recent crustaceans, this appendage is modified into a second antenna, but in stem-group crustaceans, it is pediform (e.g. Walossek & Müller 1997, 1998). This character is coded as missing data in a number of taxa for which the morphology of the second segment appendage is unknown.

Some authors (Dzik 1993; Chen & Zhou 1997; Dewel & Dewel 1997; Budd 2002) have suggested that the 'great appendages' are homologous with the anterior appendages of anomalocaridids and the anomalocaridid-like *Opabinia* and *Kerygmachela* (see Budd 1996b, 1999b, respectively). The anterior appendages of most anomalocaridids and other Cambrian lobopodians differ from megacheiran 'great appendages' in that they consist of a large number of segments. Moreover, there is considerable morphological evidence that anomalocaridids are part of the euarthropod stem group (Wills *et al.* 1995, 1998a) and not closely related to the 'great appendage' taxa (cf. Budd 2002), with the possible exception of *Parapeytoia.* 'Great appendage' taxa share a suite of derived characters with other crown group euarthropods, including sclerotised dorsal tergites, the incorporation of more than one pair of appendages into the head, sclerotisation of the endopods and strong differentiation of the head, that were excluded from Budd's (2002) analysis. The relationships of anomalocaridids will be considered in detail later by Braddy and co-workers.

3. Exopod of appendages of the second segment: (0) present; and (1) absent or much reduced. The raptorial appendages of the second segment (chelicerae and 'great appendages') are uniramous, as are the corresponding pediform appendages of *Marrella*, *Mimetaster*, *Emeraldella*, *Cheloniellon* and *Sidneyia.* The plesiomorphic euarthropod state is found in most other arachnomorphs, including trilobites, where the biramous second segment appendages are undifferentiated from those of posterior segments (Edgecombe *et al.* 2000, character 78). The exopods of these appendages are also present in basal members of the crustacean crown group (Edgecombe *et al.* 2000, character 79) and in stem group crustaceans (Walossek 1993; Walossek & Müller 1997, 1998).

4. Number of head segments: (0) 1; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6; and (6) 7. The coding of this character by Edgecombe & Ramsköld (1999, character 2) explicitly referred to the number of limb pairs present in addition to the antenna. Here, the number of post-acronal segments present in the head is coded, following Wills *et al.* (1998a, character 29). In taxa that lack an antenna, the number of somites is inferred to be one greater than the number of cephalic appendage pairs (cf. Wills *et al.* 1998a), as described above.

Stürmer & Bergström (1978) suggested that the head of *Cheloniellon* is defined primarily on the basis of appendage tagmosis, rather than the fusion of segments under a single cephalic-shield (cf. Hou & Bergström 1997, pp. 98–9). According to this view, the head consists of both the cephalic tergite and the anteriormost free tergite that share uniramous, gnathobasic appendages. Wills *et al.* (1998a) coded *Cheloniellon* as having six somites incorporated into the head, and therefore, presumably accepted this suggestion. There is no evidence that the first free tergite of *Cheloniellon* was incorporated into the head (except perhaps functionally), and the present authors prefer to code the number of somites under the cephalic shield. In *Sidneyia*, there is a series of uniramous, strongly gnathobasic appendages, similar to those of *Cheloniellon*, posterior to the head shield. All of these appendages would presumably have to be considered part of the head based on appendage differentiation, according to the view of Stürmer & Bergström (1978). Some autapomorphic states are included

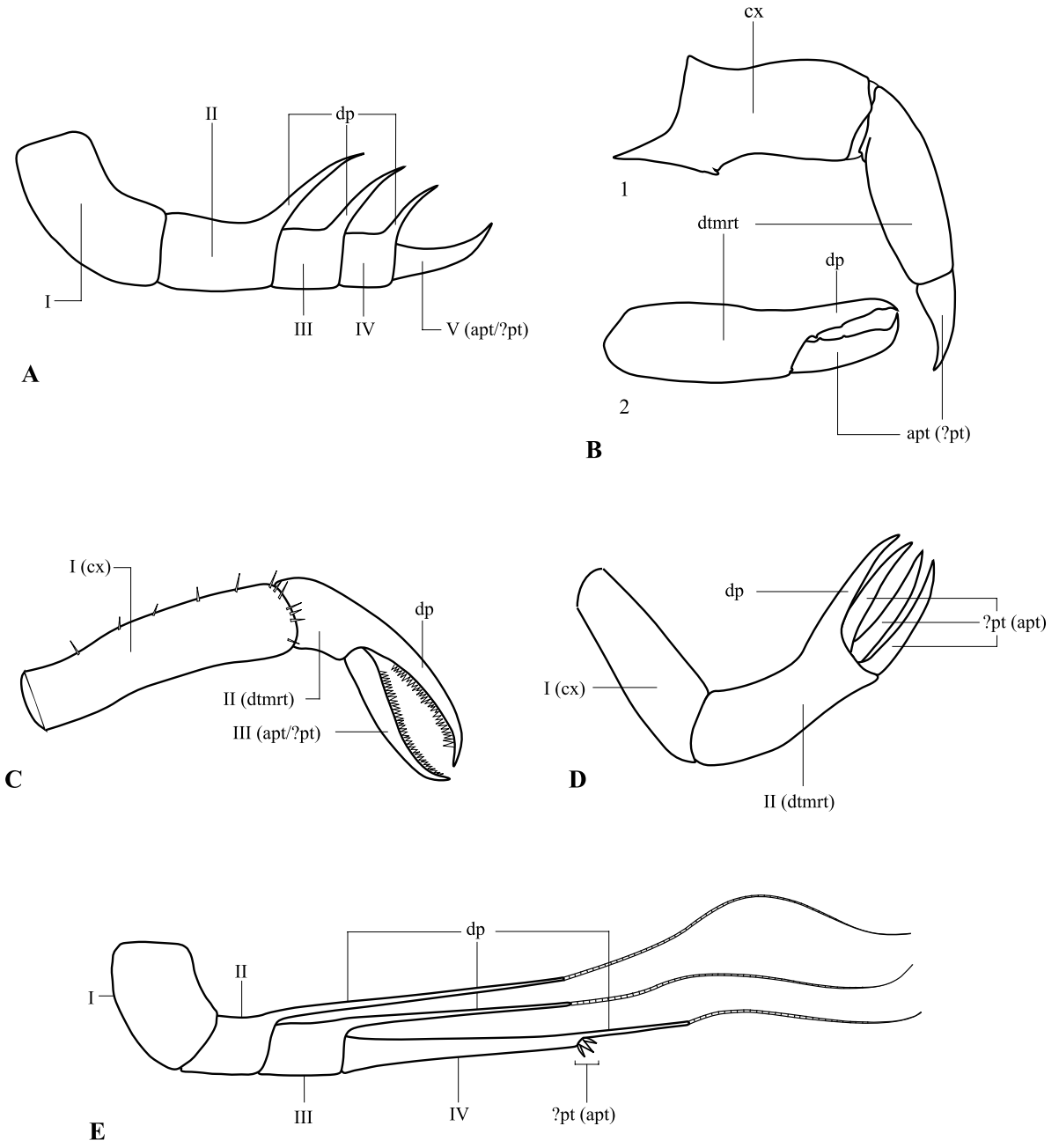

Figure 5 Diagrammatic reconstructions of raptorial second-segment appendages in lateral view (except where otherwise stated) and approximate life orientation, showing suggested homology of appendage elements (in brackets). Roman numerals indicate position in the podomere series and do not necessarily imply homology. (A) 'Great appendage' of *Fortiforceps* (after Hou & Bergström 1997); (B) Left chelicera of *Leiobunum aldrichi* (Arachnida: Opiliones), (1) in medial perspective and (2) distal parts in anterior perspective (after Shultz 2000); (C) Chelifore of *Nymphon* (Pycnogonida), (after Child 1997); (D) 'Great appendage' of *Yohoia* (after Whittington 1974, fig. 2); (E) 'Great appendage' of *Leanchoilia* (modified after Bruton & Whittington 1983). Not to scale. Abbreviations: (apt) apotele (probably homologous with the mandibulate pretarsus); (cx) coxa; (dtmrt) deutomerite; and (pt) pretarsus.

(none for *Sidneyia*, one for *Marrella* and six for *Emeraldella*) since these will become informative if the character is treated as ordered.

Edgecombe & Ramsköld (1999, p. 265) described a novel form of cephalic tagmosis. The present authors tentatively accept their suggestion that, in trilobite-like taxa, the fourth pair of biramous cephalic appendages was directly under the cephalo-thoracic junction. This may explain previous confusion about the number of such appendages incorporated into the trilobite cephalon (e.g. Cisne 1975; Whittington 1975a; Bergström & Brassel, 1984). However, Edgecome & Ramsköld accept the view of Chen *et al.* (1977, p. 7) that only the first three biramous limbs of *Misszhouia* were structurally and functionally part of the head. Therefore, it seems more acceptable to code these taxa as having only four post-acronal somites than to use the coding scheme of Edgecombe & Ramsköld (1999). The partial integration of the first thoracic somite under the head shield could be considered to be a form of overlap of the trunk by the head shield (i.e. a distinct state of character 9 of Edgecombe & Ramsköld 1999, or Character 37 herein). Derived states of this character would then potentially be synapomorphic for a clade including xandarellids, naraoiids, helmetiids, tegopeltids and trilobites. However, since the degree of overlap in taxa with the fourth biramous appendages under the cephalo-thoracic articulation is identical to that found between thoracic tergites (State 0 of Character

37), it is here preferred to regard this as a distinct character (Character 9, herein).

The coding of *Alalcomenaeus* by Wills *et al.* (1998a) as having four post-acronal somites is accepted here, but for different reasons. Briggs & Collins (1999) have recenty demonstrated that *Alalcomenaeus* possessed two pairs of biramous appendages on the head in addition to the great appendages. This would equate to three head somites according to the homology scheme of Wills *et al.* (1998a). Here, the antennae are inferred to be lost, and therefore, four segments incorporated into the head.

Recently, a number of authors have agreed that the plesiomorphic condition for euarthropods is a four-segmented head, as found in stem group crustaceans (Scholtz 1997; Walossek 1993; Walossek & Müller 1997, 1998; Edgecombe *et al.* 2000). However, reconstruction of the euarthropod stem group clearly indicates that even crownward taxa had a head consisting of only the antennal segment and acron, as found in tardigrades and onychophorans. Therefore, it seems that the four-segmented head is pleisomorphic only for crown group euarthropods. Some fully arthropodised fossil taxa also have a shorter head that may be pleisomorphic, such as the two-segmented head of *Marella*. *Retifacies* is coded following the recent redescription of Hou & Bergström (1997), rather than on the basis of the coding by Edgecombe & Ramsköld (1999), for which they provide no explanation. A partial uncertainty coding is used for *Aglaspis*, in which the number of post-antennal cephalic appendages is either three or four (Briggs *et al.* 1979).

5. Orientation of the antennae: (0) directed anterolaterally; (1) strongly deflected laterally; and (2) placed well inside shield margin, curing posteriorly from a transverse proximal element (cf. Edgecombe & Ramsköld 1999, character 3). The anterior appendages of *Aglaspis* (see character 1) are clearly directed anterolaterally, and it is presumed that they continued past the head shield margin. The anterior appendages of arthropod stem group taxa such as *Aysheaia*, *Kerygmachela* and *Anomalocaris* are either directed anterolaterally or ventrally, but are not strongly-deflected laterally. Therefore, the outgroup is coded as State 0. This character is coded as missing data for taxa where the presence of antennae is equivocal (those coded as missing data for Character 1), and as inapplicable in taxa where the antennae are considered absent (coded as State 1 for Character 1).

6. Length of distal spines on terminal podomeres of endopods of second segment appendages: (0) absent or shorer than podomeres; (1) subsequal to length of podomeres; and (2) longer than the entire podomere series. The spinose projections of the raptorial appendages described above vary in length. In chelicerae (Figs 5B,C) and some 'great appendages' (e.g. those of *Yohoia*, Fig. 5D), the most distal spine is equal in length to the spinose terminal podomere, forming a chelate structure. In *Fortiforceps* (Fig. 5A), the spines are short relative to the lengths of the podomeres, but in *Alalcomenaeus* and *Leanchoilia* (Fig. 5E), they are extremely long, so that the spines are much longer than the entire podomere series. As described above, in taxa with pediform endopods of the second segment appendages, spines on the distal podomeres are short or entirely absent.

7. Chelicerae: (0) absent; and (1) present. Despite their similarities to 'great appendages', the chelicerae of the euchelicerates and chelifores of the pycnogonids are clearly distinct, and have been widely recognised as a chelicerate synapomorphy. Chelicerae differ from any 'great appendages' by the combination of a smaller number of podomeres, the presence of only a single terminal element and only a single spinose projection on the dorsal side of the podomere series (Fig. 5). Amongst extant chelicerates, only the pycnogonid *Pallenopsis* has chelicerae of four podomeres, comparable to the number in 'great appendages'. Bergström *et al.* (1980) considered that the chelifores of the Devonian pycnogonid *Palaeoisopus* also consist of four segments, but this is not well supported by their figures.

8. Distal spines of second segment endopods terminating in annulated flagellae: (0) absent; and (1) present. It is widely recognised (e.g. Størmer 1944; Simonetta 1970; Bruton & Whittington 1993; Briggs & Collins 1999) that the terminal parts of the extended spines of *Alalcomenaeus* and *Leanchoilia* formed annulated flagellae. Nothing similar is known from homologous appendages of any other arthropod, although similar processes may have operated in the transformation of the endopod as a whole into the second antennae of derived crustaceans and in the origin of multiramous antennulae (first antennae) in malacostracans.

2.4.2. Posterior appendages. 9. Appendages of first thoracic somite underneath the cephalo-thoracic articulation: (0) absent; and (1) present (cf. Edgecombe & Ramsköld 1999, character 2). For a discussion of this character, see Character 4 herein.

10. Exopods of appendages of third to fifth segments: (0) present; and (1) reduced or absent. A number of taxa have uniramous appendages on the third to fifth segments. In most, these segments are incorporated into the head (*Yohoia*, chelicerates), but in others, all (e.g. in *Sidneyia*) or some (e.g. in *Cheloniellon*) of these segments are post-cephalic. In all cases, the appendage is morphologically similar to the endopods of biramous limbs of other taxa and/or other segments, and it is interpreted that the exopod is lost.

11. Endopods of thoracic appendages: (0) present; and (1) reduced or absent. The opisthosomal appendages of chelicerates lack endopods or have the endopods much reduced (e.g. *Limulus*, Siewing 1985, fig. 838; Shultz 2001), a situation that is also found in the uniramous thoracic appendages of *Yohoia* (Whittington 1974). It has been suggested that *Helmetia* (Briggs *et al.* 1994) lacks endopods, but pending a redescription of this genus and considering that they have been documented in the otherwise very similar *Kuamaia*, this is coded as uncertain.

12. Exopod shaft of numerous podomeres, each bearing a single seta: (0) present; and (1) absent. The exopods of crustaceans (at least plesiomorphically, see e.g. Walossek & Müller 1998, figs 5·5 & 5·6), and of *Marrella* and *Mimetaster* have multi-annulated shafts, with each podomere bearing a single seta. In other taxa the exopod shafts consist of one of two lobes bearing numerous setae.

The polarity of exopod segmentation is uncertain. The lateral flaps of stem group arthropods such as *Opabinia* (Whittington 1975b; Budd 1996b) and anomalocaridids (e.g. Hou *et al.* 1995) are certainly unsegmented, but as suggested by Budd's (1996b, fig. 8) reconstruction, this does not necessarily suggest the form of the primitive euarthropod exopod. Rather, segmentation may have been a result of the sclerotization of the cuticle of the exopod shaft. The outgroup was coded as uncertain for this character. According to the first interpretation of aglaspidid appendage morphology (coded as Aglaspidida 1), the exopods are lacking on all appendages, and consequently, this and all other characters describing exopod morphology are coded as inapplicable.

13. Exopod shaft differentiated into proximal and distal lobes: (0) absent; and (1) present. Ramsköld & Edgecombe (1996; Edgecombe & Ramsköld 1999, character 26) have discussed the distribution of the trilobite-type bilobate exopods recognised by this character (Fig. 6A). Among taxa included here that were not considered by Edgecombe &

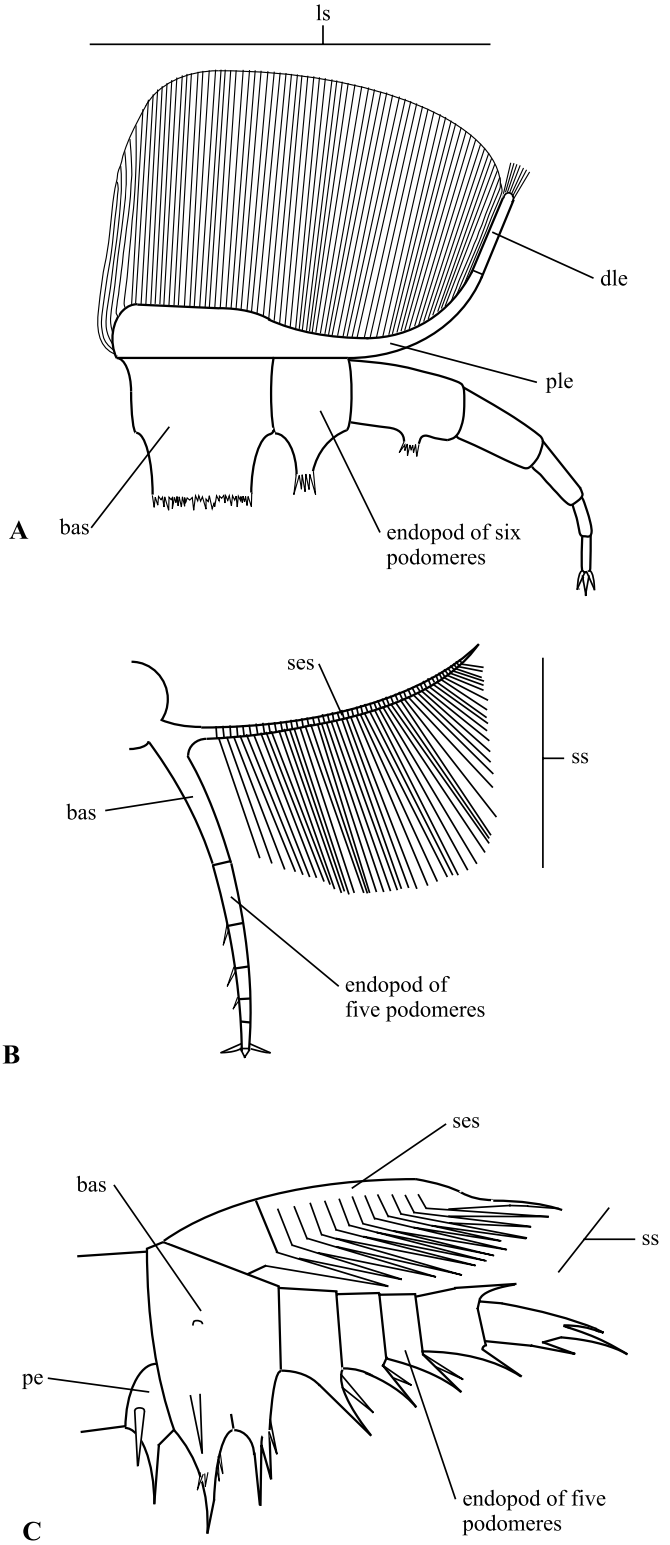

Figure 6 Diagrammatic reconstructions of (A) arachnomorph and (B, C) non-arachnomorph biramous appendages: (A) The 'trilobite-type' biramous appendage of *Misszhouia longicauda* (after Chen *et al.* 1997); (B) Appendage of *Marrella splendens* (after Whittington 1971); (C) Appendage of the stem-lineage crustacean *Martinssonia elongata,* (after Müller & Walossek 1997, 1998). Not to scale. Abbreviations: (bas) basis; (dle) distal lobe of exopod shaft; (ls) lamellar exopod setae; (pe) proximal endite or pre-coxa; (ple) proximal lobe of exopod shaft; (ses) segmented exopod shaft; and (ss) spinose exopod setae.

Ramsköld (1999), exopods consist either of a single flattened lobe or a homonomous series of podomeres (Fig. 6B, C). No stem group euarthropod has a bilobate exopod, and the outgroup is consequently also coded as State 0.

14. Proximal lobe of exopod: (0) flattened lobe; and (1) slender shaft.

15. Distal lobe of exopod: (0) small to moderate sized flap, with short to moderately long attachment to proximal lobe; and (1) large, teardrop-shaped, with long attachment to proximal lobe. Neither of these characters can be coded for taxa that do not have an exopod differentiated into proximal and distal lobes (Character 13, State 1) without asserting the homology of the single-lobed exopod with one of these parts. The coding of Edgecombe & Ramsköld (1999, p. 280) implicitly homologizes the exopods of *Sidneyia* and *Retifacies* with the proximal lobe. In these taxa, this view is perhaps supported by the presence of lamellate exopod setae, which match those of the trilobite-type proximal lobe. However, in other taxa with a single-lobed exopod, such as *Alalcomenaeus* (see Briggs & Collins 1999), the exopod is fringed with sharp spines, like the distal lobe of differentiated exopods. Alternatively, the bilobate exopod may have originated from the division of a primitively single-lobed structure. The single-lobed exopod is not clearly homologous with either lobe of divided exopods, and both these characters are consequently coded as inapplicable to taxa without differentiated proximal and distal exopod lobes. Consequently (see Character 13 herein), these characters can only be coded for taxa that were previously considered by Edgecombe & Ramsköld (1999), and their coding is followed here, except in the cases of *Sidneyia* and *Retifacies.*

16. Exopod shaft is a deep, rounded flap: (0) absent; and (1) present. All bilobate (Character 13) and segmented (Character 12) exopod shafts are long and relatively narrow structures (see Fig. 6), whereas some single-lobed exopod shafts have the form of rounded flaps. These flap-like exopod shafts are large compared to the length of the setae and at least half as deep as they are long. This appendage structure is found in chelicerates and 'great appendage' arthropods.

17. Medially-directed exopod setae: (0) absent; and (1) present. Walossek & Müller (1998, p. 194) suggested that the tilting of exopod setae towards the endopod in post-antennular limbs with a multi-annulated exopod was an autapomorphy uniting crustaceans and all members of the crustacean stem group (the crustacean total group *sensu* Ax 1986; see Fig. 6C). This character is shared with the marellomorphs *Marrella* and *Mimetaster* (see Fig. 6B; Stürmer & Bergström 1976; Bergström 1979, fig. 1·3A, B). In other taxa, the setae either surround the entire margin of the exopod shaft or are directed dorsally (Fig. 6A). The identification of setae on the dorsal surface of the lateral flaps in *Opabinia* (Budd 1996b) suggests that the condition in marellomorphs and crustaceans is derived.

18. Lamellate exopod setae: (0) absent; and (1) present. Lamellate exopod setae, originally described from trilobites, are a classic synapomorphy of the Arachnomorpha (see e.g. Bergström 1992; Hou & Bergström 1997, pp. 42–3). They are perhaps best known from *Misszhouia* (see Chen *et al.* 1996, Hou & Bergström 1997; Fig. 6A). These setae differ from the more spinose setae of other taxa (Fig. 6C) in that they are wide and flat, and imbricate over the length of the exopod shaft. The setae of *Marrella* (Fig. 6B) and similar taxa have variously been considered lamellate (Bergström 1979) or non-lamellate (Bergström 1992). Since they do not imbricate and do not seem to be strongly flattened (Whittington 1971; Stürmer & Bergström 1976, fig. 9a), *Marrella* and *Mimetaster* are coded as State 0. The setae of *Helmetia*, as shown in Briggs *et al.* (1994, fig. 141), seem to be of the lamellate type. The setae of *Sinoburius* have been described by Hou & Bergström (1997, p. 85) as similar to those of *Misszhouia.* Only the setae are known of the appendages of *Buenaspis* (Budd 1999a), and these also appear to be of the trilobite-type.

The homology of the book-gill lamellae of xiphosurans with lamellar setae was supported by Walossek & Müller (1997, p. 149) and Edgecombe *et al.* (2000, p. 174), but rejected by Stürmer & Berström (1981) on the grounds that *Weinbergina* possesses *Limulus*-like gill lamellae and fringing setae. Book-gills have also been described from a eurypterid (Braddy *et al.* 1999). There are certainly major morphological differences between book-gills and trilobite-type exopods. Following most recent opinion, and pending further study, *Weinbergina* and Eurypterida are coded as possessing lamellate setae.

The form of the setae of *Yohoia* is uncertain (Whittington 1974); the spinose setae seen in the most common reconstruction (Gould 1989; Briggs *et al.* 1994) are not justified by the specimens. Amongst other great appendage arthropods, the form of the setae appears to vary; those of *Jianfengia* (see Chen & Zhou 1997, p. 74) and *Leanchoilia* (see Bruton & Whittington 1983) are lamellate, while those of *Fortiforceps* (Hou & Bergström 1997) and *Alalcomenaeus* (Briggs & Collins 1999) are spinose and less densely packed.

19. Gnathobase on basis and/or prominent endites on endopod: (0) present; and (1) absent (cf. Edgecombe & Ramsköld 1999, character 29; Wills *et al.* 1998a, characters 36 & 59). The presence of gnathobases on the appendages of some anomalocaridids (Hou *et al.* 1995) and their general distribution amongst non-arachnomorph euarthropods suggests that State 0 is plesiomorphic. The homology of the various endites and gnathobasic structures found in euarthropods is in need of careful assessment, and therefore, a very general coding (following Edgecombe & Ramsköld) is used for this character.

2.4.3. Eyes. 20. Position of lateral facetted eyes: (0) ventral and stalked; (1) dorsal and sessile; and (2) absent (cf. Edgecombe & Ramsköld 1999, character 4). Partial uncertainty coding is used for a number of taxa where the dorsal surface is known, but the ventral morphology is not, and therefore, the presence of ventral eyes cannot be discounted. For example, there is good evidence that *Leanchoilia* lacked dorsal sessile eyes, but ventral stalked eyes may have been present (as in *L. hanceyi*, see Briggs & Robison 1984), and a (02) partial uncertainty coding is used. This is also the case in many naraoiids, such as *Buenaspis.* However, only the outline of the head shield of *Liwia* is known, and the absence of dorsal eyes in the reconstruction of Dzik & Lendzion (1988) is conjectural. It is unclear whether the autapomorphic condition of stalked dorsal eyes in *Mimetaster* (see Stürmer & Bergström 1976) is homologous with State 0 or State 1, and a partial uncertainty coding is also used.

Whittington (1974) was somewhat equivocal about the nature of the lateral lobes anterior to the head shield of *Yohoia.* These more closely resemble the ventral stalked eyes of *Alacomenaeus*, as recently described by Briggs & Collins (1999), than either Whittington's (1974) or subsequent (e.g. Gould 1989, fig. 3·18; Briggs *et al.* 1994, fig. 153) reconstructions suggest. In a well preserved specimen showing the dorsal aspect (USNM 57696, Whittington 1974, pl. 2, figs 1–3) and in a laterally compressed specimen (USNM 57694, Whittington 1974, pl. 1, fig. 1), they are clearly seen to be stalked and relatively small lobate structures. That these structures are likely to represent stalked ventral eyes was reflected in the coding of Wills *et al.* (1998a, characters 26 & 27).

21. Visual surface with calcified lenses, bounded with circumocular suture: (0) absent; and (1) present.

22. Dorsal bulge in exoskeleton accommodating drop-shaped ventral eyes: (0) absent; and (1) present.

23. Eye slits: (0) absent; and (1) present.

Characters 21 to 23 are used exactly as described by Edgecombe & Ramsköld (1999, character 5). Character 21 is inapplicable to taxa that do not possess eyes (Character 20, State 2).

24. Dorsal median eyes: (0) absent; and (1) present. Dorsal median eyes on a tubercle are considered a synapomorphy of the Chelicerata (Dunlop & Selden 1997; Dunlop 1999). The nature and position of the structures interpreted as dorsal median eyes in *Mimetaster* (Stürmer & Bergström 1976, p. 83–4) are regarded as equivocal.

2.4.4. Ventral cephalic structures. Many characters of the ventral surface of the euarthropod head (see Fig. 7) of potential phylogenetic utility are poorly known in many important taxa. In particular, the presence of pre-hypostomal frontal organs (Fig. 7A, C–E) is not coded herein (see Edgecombe & Ramsköld 1999, p. 272). Definitive evidence of the absence of these structures is available for very few taxa, and the homology of these structures with the maculae of the trilobite hypostome (see Fig. 7B) and the frontal organs of the crustacean labrum (e.g. see Müller & Walossek 1987, p. 39) is uncertain. Secondly, the detailed homology of the trilobite hypostome with that of other putative arachnomorphs is unclear, and consequently, a very broad definition is used herein. For example, various pre-hypostomal sclerites (Fig. 7A, D) in other arachnomorphs may have been incorporated, along with a primitive hypostome, into a single sclerite that is recognised as the hypostome in trilobites. The structure of the hypostome (e.g. the presence of paired anterior wings dorsal to the antennae, Fig. 7B, C) may also be a source of additional characters.

25. Expanded cephalic doublure: (0) absent; and (1) present, maximum width more than 30% length of head shield or more than 25% width of pygidium. Chen *et al.* (1996) suggested that the wide doublure of *Soomaspis* and *Tariccoia* is a synapomorphy uniting these taxa. The doublure of *Buenaspis* (see Budd 1999a) is poorly known, but based on the width of the heavily crushed region of the cephalic margin and the position of a possible impression of the edge of the doublure in one specimen (Budd, 1999a, pl. 1, fig. 1), it also appears to be rather wide (i.e. greater than 30% of the length of the head shield). Following Edgecombe & Ramsköld's coding of *Sidneyia*, the present authors do not consider the postero-median expansion of the doublure of, for example, *Emeraldella* or *Retifacies* (see Bruton & Whittington 1983; Hou & Bergström 1999, respectively) to be homologous with State 1, but to represent the hypostome (see Character 26).

26. Anteromedian margin of cephalon notched, accomodating strongly sclerotised plate: (0) notch and plate absent; and (1) notch and plate present (cf. Edgecombe & Rasmköld 1999, character 10). The apomorphic state (illustrated in Fig. 7D) is only known in the taxa discussed by Edgecombe & Rasmköld (1999). Reconstructions of *Yohoia* show a rounded lobe between the eyes (see Character 20) anterior to, and distinct from, the head shield, which resembles the anterior sclerite recognised here. This seems to be a misinterpretation. Specimens preserved in dorsal aspect (USNM 57696, Whittington 1974, pl. 2, figs 1–3) and lateral aspect (USNM 57694, Whittington 1974, pl. 1, fig. 1; USNM 155616, Whittington 1974, pl. 5, fig. 2) seem to clearly show that this 'median lobe' is a downward curving, pointed, extension of the head shield.

27. Hypostomal sclerite: (0) median extension of the doublure, with no suture; (1) natant, sclerite not in contact with doublure; (2) with narrow overlap with pre-hypostomal sclerite; (3) narrow attachment to doublure at hypostomal suture; and (4) absent. The homology of hypostomes and labrums has been discussed by Haas *et al.* (2001) and Budd (2002). The euarthropod labrum is likely to represent a posteroventral extension of the pre-segmental acron (Scholtz

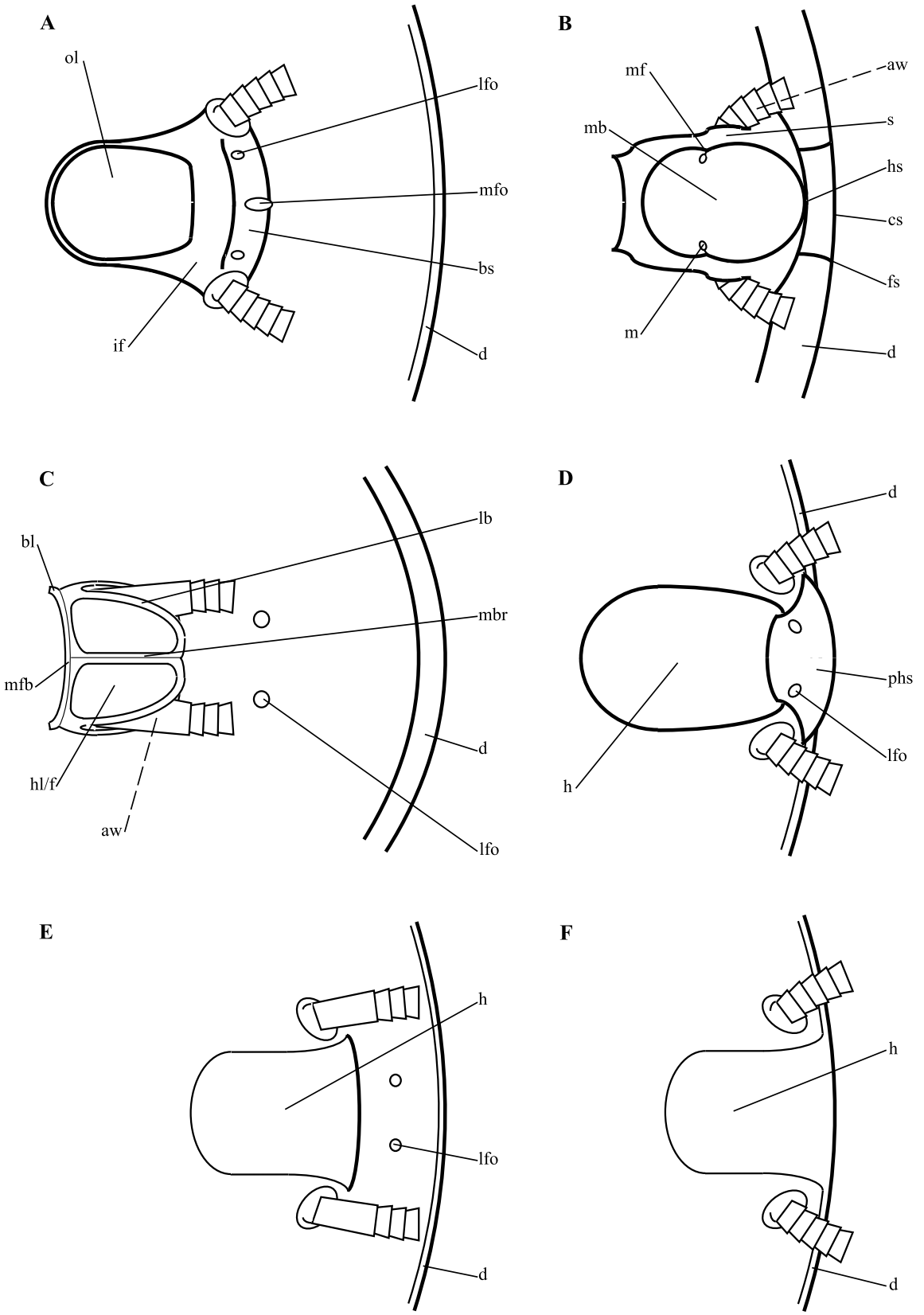

Figure 7 Ventral reconstructions of arachnomorph arthropod heads: (A) *Misszhouia longicaudata* (after Chen *et al.* 1997, figs 2–4, 7); (B) *Ceraurinella typa* (after Chen *et al.* 1997, fig. 7); (C) *Agnostus pisiformis* (after Müller & Walossek 1987); (D) *Kuamaia lata* (after Edgecombe & Ramsköld 1999, figs 3.2, 5 & 6); (E) *Cindarella eucala* (after Ramsköld *et al.* 1997); and (F) *Emeraldella brocki* (after Bruton & Whittington 1983). Not to scale. Abbreviations: (aw) anterior wing, beneath antennae; (bs) boomerang-shaped sclerite; (bl) blade-like process of posterior wing; (d) doublure of head-shield; (cs) connective suture; (f) fenestra; (fs) facial suture; (h) hypostome; (hl) hypostomal lobe (emerging through fenestrae of *Agnostus*); (hs) hypostomal suture; (if) intervening field of hypostomal complex; (lb) lateral bridge; (lfo) lateral frontal organ; (mb) median body; (mbr) median bridge; (mf) median furrow; (mfb) mouth field bridge; (mfo) median frontal organ; (ol) ovate lobe; and (phs), pre-hypostomal sclerite. Post-antennal appendages and distal parts of antennae omitted.

1997). This structure is often sclerotised and covers the mouth ventrally. It is this sclerite that is here identified as the hypostome. Therefore, this character is considered absent in taxa lacking a sclerite covering the mouth, irrespective of the morphology and position of the labrum itself, which at least partly covers the mouth in all euarthropods other than pycnogonids (see Edgecombe *et al.* 2000, p. 167). The 'fleshy labrum' of crustaceans does not appear to be sclerotised, and a hypostome is consequently considered to be absent. Although many derived features are associated with the crustacean labrum, this is not a good reason to consider it non-homologous with the hypostome-bearing structure of other arthropods, as Walossek & Müller (1990) argued.

In many taxa, the mouth is covered by a posteromedian extension of the doublure, here considered to represent the hypostome (e.g. *Emeraldella*, Fig. 7F; *Aglaspis*, see Hesselbo 1992, fig. 5.2). In others, the hypostome is separated from the doublure either by a suture, a pre-hypostomal sclerite (e.g. *Kuamaia lata*, Fig. 7D; *Saperion glumaceum*, see Edgecombe & Ramsköld 1999, figs 3 & 4) or an intervening region of unsclerotised cuticle (the natant condition of Fortey 1990b, e.g. *Cindarella eucala*, Fig. 7E). The homology of pre-hypostomal sclerites and hypostomes in helmetiids, trilobites and naraoiids (see Fig. 7) has been discussed by Chen *et al.* (1996) and Edgecombe & Ramsköld (1999), but it is as yet unclear whether any of the character states described here are derived from any other. They are treated here as distinct, and the character as unordered, pending further study.

No hypostome has been identified in *Yohoia* (see above), *Alalcomenaeus*, *Jianfengia*, *Fortiforceps* or *Leanchoilia*, and there is certainly no broad posterior extension of the doublure in any of these taxa. Since there is also no pre-hypostomal sclerite, they have received a (134) partial uncertainty coding. The attachment of the hypostome of *Tegopelte* is unclear, but it does not seem to be attached to any doublure (Whittington 1985), and therefore, it is given an uncertainty (12) coding.

The 'rostrum-like structure' on the ventral surface of *Lemoneites* appears to be similar in morphology and position relative to the anterior margin of the head shield (Flower 1968, pl. 8, figs 4 & 13) to that described from *Aglaspis*, and is coded as State 0. In many taxa, the hypostome is unknown, but in only a small number can it be coded reliably as absent. Hughes' (1975) suggestion that the hypostome of *Burgessia* is absent is accepted preliminarily, but an extension of the doublure may be visible in some of Hughes' figures. Fortey (pers. comm. 2000) also doubts Hughes' assertion.

28. Visible ecdysial sutures: (0) absent; and (1) present. The marginal ecdysial sutures of chelicerates and the dorsal sutures of trilobites are almost certainly not homologous, but the presence of sutures and their position (see Character 29) are coded separately to allow this to be tested. Wills *et al.* (1998a, Character 2) coded marginal sutures as present in *Sidneyia*, following Bruton's (1981) suggestion, but this is considered equivocal here.

29. Position of ecdysial sutures: (0) marginal; and (1) dorsal. This character is inapplicable to taxa lacking ecdysial sutures (Character 28, State 0). Dorsal sutures, whilst present in the representatives of the Trilobita coded here, are probably not a synapomorphy of trilobites as a whole, but for a clade of trilobites excluding the Olenellida (Whittington 1989; Fortey 1990a).

2.4.5. Exoskeletal tergites and thoracic tagmosis. 30. Mineralised cuticle: (0) absent; and (1) present. Calcification of the exoskeleton is one of the most convincing synapomorphies of the Trilobita (Fortey & Whittington 1989; Ramsköld & Edgecombe 1991; Edgecombe & Ramsköld 1999, Character 1). Cuticle mineralisation is also coded as present in aglaspidids following Briggs & Fortey (1982), who suggested that the aglaspidid exoskeleton was originally phosphatic. *Paleomerus* probably also had a mineralised cuticle, but Hou & Bergström (1997, p. 97) argued that it was likely to be calcareous. An undescribed Silurian aglaspidid may also have had an originally calcitic cuticle (Fortey & Theron 1994, p. 856). Because of the uncertainty about the chemical composition of the exoskeleton in these forms, cuticle mineralisation is coded as potentially homologous in all these taxa, and no attempt is made to code separate states for phosphatic and calcareous mineralisation.

31. Trunk tergites with expanded lateral pleurae covering appendages dorsally: (0) absent; and (1) present. Whilst the presence of paratergal folds may be a synapomorphy at the level of the Euarthropoda (Boudreaux 1979; Wägele 1993; Edgecombe *et al.* 2000, Character 142), these are, at most, small reflections of the margin of the tergites in most euarthropods. In arachnomorph taxa, these are expanded to form large lateral pleurae that cover the appendages dorsally (see e.g. *Limulus* and *Triarthus* in Boudreaux 1979). This is inferred to be the case in some taxa where dorsal features and appendages are poorly known, on the basis of their possession of tergites with wide pleural regions. This feature was suggested as typical of lamellipedians (=arachnomorphs) by Hou & Bergström (1997, pp. 42–3).

The arrangement of the thorax of *Marrella*, *Mimetaster* and *Burgessia* differs from that of all the other taxa considered here in that the appendages seem to be attached to the lateral margins of the body. The trunk tergites do not cover the appendages and seem to lack pleurae entirely, although they are covered by a posterior extension of the head shield in *Burgessia*. This character has been clearly described in *Mimetaster* (Stürmer & Bergström 1976, pp. 87–90, fig. 8) and *Burgessia* (Hughes 1975, p. 421).

32. Free thoracic tergites: (0) present; and (1) absent. Following Edgecombe & Ramsköld (1999, Character 16), a number of taxa lack functional post-cephalic articulations, and consequently, lack free thoracic tergites. Despite this, they code these taxa for a number of characters relating to the structure of thoracic tergites (e.g. their characters 18 and 19). These characters are treated here as inapplicable to taxa without free tergites and the definition of this character has been modified from that of Edgecombe & Ramsköld (1999) to make this more explicit.

33. Decoupling of thoracic tergites and segments: (0) absent; and (1) present. Ramsköld *et al.* (1997) described this character of *Cindarella* and *Xandarella*, where the thoracic tergites correspond to a variable, increasing posteriorly, number of appendage pairs. This character cannot be coded for taxa in which free thoracic tergites are absent (Character 32, State 1).

34. Tergite articulations: (0) tergites non-overlapping; (1) extensive overlap of tergites; and (2) edge-to-edge pleural articulations. In most of the taxa considered here, the thoracic tergites overlap considerably and relatively evenly over their width. This contrasts with the primitive euarthropod condition, where the tergites do not overlap medially, as seen in stem group crustaceans. In trilobites, such as *Helmetia* and *Kuamaia* (see Edgecombe & Ramsköld 1999, character 18), overlap of thoracic tergites is limited to a well-defined axial region, and the lateral pleurae meet edge-to-edge.

The thoracic articulations of naraoiids with free thoracic tergites are, in some ways, similar to those of trilobites, with a strong overlap medially that is lacking abaxially, and anterolateral articulating facets (Budd 1999a; Ramsköld & Edgecombe 1999). However, the distribution of these features

in other trilobite-like arachnomorphs is unclear and a restrictive coding is used here. The present authors do not consider that this character can be applied reliably to the fused thoracic tergites of *Saperion*, *Tegopelte* and *Skioldia*, and it is coded as inapplicable to all taxa lacking free thoracic tergites (Character 32, State 1).

35. Trunk effacement: (0) trunk with defined (separate or fused) tergite boundaries; (1) trunk tergite boundaries effaced laterally; and (2) trunk tergite boundaries completely effaced (cf. Edgecombe & Ramsköld 1999, Character 15)]. Contrary to Edgecombe & Ramsköld (1999), the present authors consider *Skioldia* and *Saperion* to show a distinct form of tergite effacement, where the fused tergite boundaries are defined by furrows axially, but effaced laterally. The boundaries are effaced, at least laterally, in *Tegopelte*, but the axial region of the exoskeleton is unknown, which accordingly, is given a multistate uncertainty coding.

36. Cephalic articulation fused: (0) absent; and (1) present. In *Tegopelte*, *Saperion* and *Skioldia*, the articulation of the head with the thorax is non-functional and the entire exoskeleton forms a single tergite.

37. Head shield overlap of thoracic tergites: (0) overlap absent or identical to overlap between thoracic segments; (1) head shield covers first thoracic tergite only; and (2) head shield covers mutliple anterior trunk tergites.

38. Head shield articulates with reduced anterior thoracic tergite: (0) absent; and (1) present. Amongst taxa showing a posteriorly expanded head shield, i.e. one that overlaps the thorax, Edgecombe & Ramsköld (1999, Character 9) identified two distinct character states. One of these – overlap of only the anteriormost thoracic tergite – was limited to taxa assigned to the Liwiinae (*sensu* Fortey & Theron 1994), and another – overlap of multiple tergites with attachment to a reduced anterior thoracic tergite – to the Xandarellida. None of the additional taxa considered herein (including *Buenaspis*, which was assigned to the Liwiinae by Budd 1999a) shows these distinctive morphological features. However, the expanded head shields of *Marrella*, *Mimetaster* and *Burgessia*, which do not articulate with a narrow anterior thoracic tergite, may be homologous with the expanded head shields of xandarellids. To recognise this, the degree of overlapping of the thorax and the possession of the reduced anterior tergite are coded separately. These characters are both coded as inapplicable to taxa in which the head shield and thoracic tergites are fused (Character 36, State 1). The crustacean carapace, which is most similar to the head shield of *Burgessia*, is seemingly absent in stem group crustaceans (Walossek & Müller 1998).

39. Trunk narrowed anteriorly relative to head shield, widest posteriorly: (0) absent; and (1) present (cf. Edgecombe & Ramsköld 1999, Character 14). The anterior narrowing of the trunk caused by the reduction of opisthosomal segment 1 in xiphosurids (*Weinbergina*, of the taxa analysed here: Andersen & Selden 1997; Dunlop & Selden 1997, Character 14) is not considered to be homologous with the unusual shape of the thorax in naraoiids recognised by their coding.

40. Boundaries of anterior trunk segments reflexed anterolaterally: (0) absent, boundaries transverse or reflexed posterolaterally; and (1) present.

41. Joints between posterior tergites functional, anterior ones variably fused: (0) absent; and (1) present.

42. Posterior tergite bearing axial spine: (0) absent; and (1) present.

Characters 40 to 42 are coded following Edgecombe & Ramsköld (1999, characters 17, 19 & 23, respectively). In addition to the taxa considered here, a thoracic axial spine is present in some olenelloid trilobites (see Lieberman 1998, Characters 73 & 74) and in the aglaspidid *Beckwithia* (see Hesselbo 1989).

2.4.6. Posterior body termination. 43. Postabdomen of segments lacking appendages: (0) absent; and (1) present.

44. Length of postabdomen: (0) one segment; (1) two segments; (2) three segments; and (3) five segments. In some taxa, a variable number of posterior thoracic segments bear complete tubular tergites and lack appendages. In *Aglaspis*, autapomorphically, it seems that the posterior three thoracic segments lack appendages (Briggs *et al.* 1979; Hesselbo 1992), but have unmodified tergites. These situations are recognised as potentially homologous by the coding used here. Character 44 is coded as inapplicable to taxa lacking a postabdomen.

45. Posterior tergites strongly curved in dorsal aspect compared to anterior tergites: (0) absent; and (1) present. As recognised by Wills *et al.* (1998a, Character 17), in some taxa where the tergites are distinct, the curvature of thoracic tergites increases posteriorly so that the posterior tergites are highly curved to semicircular in dorsal aspect. This situation is not known from crustaceans (except isopods) or stem group arthropods.

46. Posterior segments reduced and with highly reduced appendages: (0) present; and (1) absent. In some taxa, there are a large number of posterior segments that are short sagitally and have appendages that are much reduced in size compared to anterior trunk appendages. These somites are incorporated into the pygidium in some taxa, but primitively, they are covered by tiny free trunk tergites. In the derived state, the trunk somites and limbs are of a relatively constant size. The distinction between these states can be seen when attempting to count the number of segments that make up the body. In taxa showing State 0, the number of segments is very high and difficult to count, whereas in other taxa, the number of post-cephalic segments is easily assessed.

47. Pygidium: (0) absent; and (1) present. A pygidium is recognised here as a posterior tagma consisting of a number of fused segments under a single tergite, which may or may not incorporate the post-segmental telson. This is different to the use of this term by Edgecombe & Ramsköld (1999), which follows Ramsköld *et al.* (1997), and very different to its use by Wills *et al.* (1998a, p. 53) as a synapomorphy of the Trilobita. The present authors' definition recognises the situation in *Retifacies*, where the spinose postsegmental telson is autapomorphically not fused to the pygidium, as homologous to other multisegmented posterior tagma, which include the telson. The distinction between the pygidium and an expanded post-segmental telson can also be seen in the position of the anus, which is consistently in the posteriormost pre-telsonic segment amongst putative arachnomorphs (see Character 48). In taxa with a pygidium, the anal segment is fused into the pygidium (see e.g. *Kuamaia*, Edgecombe & Ramsköld 1999, fig. 6), whereas in those taxa lacking a pygidium, the anus is between the final trunk tergite and the telson.

Ramsköld *et al.* (1997) argued that the posteriormost tergite of xandarellids (which incorporates the anal segment) is not homologous to the posterior tagma recognised as pygidia herein because posterior thoracic tergites also cover multiple segments in xandarellids (see Character 33). Evidence of segmentation of the pygidium in a variety of taxa suggests that the number of tergites fused to form the pygidium is greater than the number of appendages. For example, the pygidium of *Kuamaia* has two pairs of lateral spines, but at least four pairs of appendages (Hou & Bergström 1997; Edgecombe & Ramsköld 1999), and that of *Triarthrus* has only five axial rings posterior to the articulating ring, but over 10 pairs of appendages (Whittington & Almond 1987). The fact that decoupling of tergites and segments is evident in the thorax of

Xandarella and *Cindarella* does not necessarily suggest that a similar, more widespread, decoupling in pygidia is the result of a different developmental process, and hence, that they are non-homologous. Instead, the situation in the xandarellid thorax is potentially homologous to that found (more widely) in pygidia, and consequently, the terminal xandarellid tergite is a pygidium. It is unclear if decoupling of tergites and somites is primitively limited to the terminal tergite or primitively a property of the arachnomorph post-cephalon as a whole.

It has been suggested that the tiny pygidium of olenelloid trilobites, which probably best reflects the primitive trilobite state, consists only of the post-segmental telson (Harrington *in* Moore 1959), and therefore, is not a true pygidium. However, Whittington (1989) showed that the olenelloid pygidium consists of at least two, and possibly as many as five or six segments, and therefore, is likely to be homologous with the pygidium of other trilobites.

48. Position of the anus: (0) terminal, within telson; and (1) at base of telson. In crustaceans and stem group arthropods, the anus is terminal or otherwise situated in the telson (e.g. *Rehbachiella*, Walossek 1993, fig. 15D). In putative arachnomorphs, the anus is either at the junction of the posteriormost thoracic segment and the telson, or ventral within a fused pygidium. In the case of taxa with a pygidium, the anus is anterior to the posterior margin and, where known, positioned between the posteriormost pair of appendages, suggesting that it is anterior to the post-segmental telson (see e.g. *Olenoides*, Whittington 1980).

49. Pygidium with median keel: (0) absent; and (1) present. Edgecombe & Ramsköld (1999, Character 21) considered the presence of a median keel on the pygidium as a synapomorphy uniting *Soomaspis* and *Tarricoia.* They did not explain how this structure could be distinguished from the raised pygidial axis of trilobites. Homology of these structures is not supported here because the axis of more primitive trilobites (including *Eoredlichia*) is quite distinct morphologically from the naraoiid keel. Budd (1999a) noted the presence of a keel on the pygidium of *Buenaspis* and suggested (Budd 1999a, p. 102) that it may be an artefact of dorsoventral compaction. However, contrary to the coding of Edgecombe & Ramsköld (1999), a keel is visible on the pygidium of *Liwia convexa* (Dzik & Lendzion 1988, fig. 4C,D), preserved in full relief. Therefore, it seems unlikely that the keel is a taphonomic artefact.

50. Pygidium with broad-based median spine: (0) absent; and (1) present.

51. Pygidium with lateral spines: (0) present; and (1) absent. Edgecombe & Ramsköld (1999, Character 22) coded the presence of a median spine and two pairs of lateral spines as potentially homologous in *Sinoburius*, *Kuamaia* and *Helmetia.* The distribution of lateral spines is much wider than that of terminal spines, and therefore, they are coded separately here. In trilobites, it has widely been recognised that lateral spines represent the original segmentation of the pygidium. This cannot be the case for median spines. Characters 49 to 51 are not applicable to taxa lacking a pygidium (Character 47, State 0).

52. Expanded post-segmental telson: (0) absent; and (1) present. In a range of taxa, the posterior-most tergite is a large (relative to the thoracic tergites) structure that lacks any evidence of segmentation and is interpreted as representing an expanded tergite of the post-segmental telson, from which segments are released anteriorly during ontogeny. On the other hand, the posteriormost tergite of *Marrella*, and probably *Mimetaster*, is small compared to the thoracic tergites and rounded. This element probably represents the plesiomorphic euarthropod telson. The homology of this character in most taxa is clear, and only doubtful in *Retifacies*, in which it may be segmented. The figures of Hou & Bergström (1997) provide little unequivocal evidence for a telson in *Retifacies*, but the presence of this structure is very clear in colour photographs (e.g. Chen *et al.* 1996, fig. 198A). However, these figures, do not convincingly demonstrate the segmentation of the telson. *Retifacies* is interpreted here as being unique in possessing both a pygidium and an expanded post-segmental telson.

53. Telson shape: (0) spinose; and (1) paddle-shaped. The shape of the expanded telsons identified above varies from broadly spinose to flattened and paddle-like. This difference can be recognised both on the basis of the ratio of length to basal width (spinose telsons are relatively long) and by the change in width posteriorly (spinose telsons reduce in width posteriorly, whereas paddle-shaped telsons increase in width). In eurypterids, a wide range of telson shapes is found, including both character states described here. It is likely that the plesiomorphic condition is a spinose telson. This character is inapplicable to taxa lacking an expanded telson.

54. Post-ventral furcae: (0) absent; and (1) present. This character recognises the potential homology of unsegmented, paired structures that articulate with the segment immediately anterior to the telson. The potential homology of these structures (the post-ventral plates) in *Emeraldella* and *Aglaspis* was recognised by Wills *et al.* (1998a, Character 70), and in *Emeraldella* and *Sidneyia* by Edgecombe & Ramsköld (1999, Character 25). The homology of the segmented pygidial caudal furcae of *Olenoides* (see Whittington 1975a, 1980) with these structures is considered doubtful and coded as equivocal.

Despite their distinctive morphology, the long caudual furcae of *Cheloniellon* may be homologous with the furcae of *Aglaspis*, *Emeraldella* and *Sidneyia.* This is supported by the caudal furcae of the Ordovician cheloniellid *Duslia*, which are more similar in morphology to those of *Emeraldella* than of *Cheloniellon.* Chlupác (1988, pp. 614–16) considered these structures to be on the terminal tergite in *Duslia.* However, a faint tergite boundary is apparent posterior to the attachment of the furcae (see Chlupác 1988, pl. 57, fig. 4). Therefore, they are considered here to have been attached to the pre-telsonic segment, as in *Cheloniellon.* Chlupác (1988) and Dunlop & Selden (1997) supported a close relationship between *Duslia* and *Cheloniellon.*

2.5. Methods

All analyses were carried out using PAUP* Version 4.0b4a (Swofford 1999), and unless otherwise stated, used heuristic searches with one thousand random addition sequence replicates. The software packages MacClade Version 3.07 (Maddison & Maddison 1997) and RadCon (Thorley & Page 2000) were used for comparing trees and investigating patterns of character evolution. Tree length and other statistics (the Consistency Index, CI; and Retention Index, RI) were calculated by PAUP* and MacClade with uninformative characters excluded. Analyses were run separately using each of the different codings for aglaspidids.

Characters were treated as unordered and of equal weight in most analyses. To assess the influence of this assumption, four of the eight multistate characters, which have states that are intermediate between others (Wilkinson 1992), were treated as ordered in some analyses. These characters are the number of cephalic segments (Character 4), the length of raptorial appendage spines (Character 6), the degree of overlap of the thorax by the head-shield (Character 37) and the number of segments making up the postabdomen (Character 44). The last of these is uninformative when not ordered because only one taxon shows each of states 0, 1 and 3.

Support for individual nodes was assessed by bootstrap analysis (Felsenstein 1985) and by calculating Bremer support

indices (Bremer 1988, 1994). These methods measure two distinct aspects of support for phylogenetic hypotheses. Trees or nodes may be considered well supported (1) to the extent to which alternative topologies are much less parsimonious, as measured by the support index (Wilkinson 1996), or (2) where they are consistent with a large proportion of characters, so that character sampling is unlikely to have had much influence on topology, as assessed by bootstrapping (Page 1996). Bootstrapping was performed with 100 bootstrap replicates, each of 10 addition sequence replicates. Bremer support indices are based on heuristic searches with 100 addition sequence replicates.

Three pairs of terminals are included in Table 2 that, apart from missing data, are coded identically. These are *Helmetia* and *Kuamaia*, *Soomaspis* and *Tariccoia,* and *Saperion* and *Skioldia.* These pairs are 'taxonomic equivalents'; removing the taxon with most missing data will not influence the position of the other. They can be recoded as single terminals according to the principal of safe taxonomic reduction (Wilkinson 1995a, b) and were not considered separately in the analyses presented here. Therefore, cladistic analyses were carried out on the basis of 33 terminals. Edgecombe & Ramsköld (1999) ignored this, and coded the same three pairs of taxa, and *Eoredlichia* and *Olenoides*, identically for their more limited set of characters.

2.6. Results

Analysis with all characters unordered and using the 'Aglaspidida 1' coding found nine most parsimonious trees (MPTs), each 126 steps long (CI=0·556, RI=0·763). Using the 'Aglaspidida 2' coding resulted in 18 MPTs of length 125 (CI=0·560, RI=0·765). Nine of these 18 trees were those found with the first coding of aglaspidids. The strict component consensus (*sensu* Wilkinson 1994) of the 27 unique trees found across both analyses is shown in Figure 8. All trees supported the monophyly of the Marrellomorpha (*Marrella* and *Mimetaster*) and of a clade including all other taxa except Crustacea (Clade 1 of Fig. 8). The relationships between these two clades and the Crustacea were unresolved, equal numbers of trees in both analyses supported each of the topologies [Clade 1 (Crustacea, Marrellomorpha)] [Crustacea (Marrellomorpha, Clade 1)] and [Marrellomorpha (Crustacea, Clade 1)]. All trees placed *Burgessia* as the sister taxon to the rest of Clade 1 and supported the division of the rest of Clade 1 into two major sister groups. The topology of one of these clades (Clade 2), which included trilobites, helmetiids, tegopeltids, naraoiids, xandarellids and *Retifacies*, was stable with respect to the coding of aglaspidids. The other clade (Clade 3) consists of a clade of megacheirans and chelicerates (Clade 4), and a clade including aglaspidids, *Lemoneites*, *Paleomerus*, *Cheloniellon*, *Emeraldella* and *Sidneyia* (Clade 5). This latter clade is unresolved in the strict consensus of all 27 trees (Fig. 8) and the strict consensus of the 18 MPTs found using the 'Aglaspidida 2' coding, but was fully resolved in the consensus of the nine trees found with the 'Aglaspidida 1' coding. Within the megacheiran-chelicerate clade, all trees found *Fortiforceps* to be the sister group to all other taxa, *Yohoia* the sister group to chelicerates, and *Alalcomenaeus* and *Leanchoilia* to form a clade. *Jianfengia* is equally parsimoniously placed as the sister group to the *Yohoia*-chelicerate clade or as the sister group to this clade and the *Alalcomenaeus*-*Leanchoilia* clade.

Treating characters 4, 6, 37 and 44 as ordered had a minimal effect on most parsimonious topology. Nine MPTs of 136 steps (CI=0·515, RI=0·743) were found with the 'Aglaspidida 1' coding and 12 MPTs 135 steps in length (CI=0·519, RI=0·745) with the 'Aglaspidida 2' coding. These trees all supported a (Crustacea, Clade 1) clade excluding the marrellomorphs.

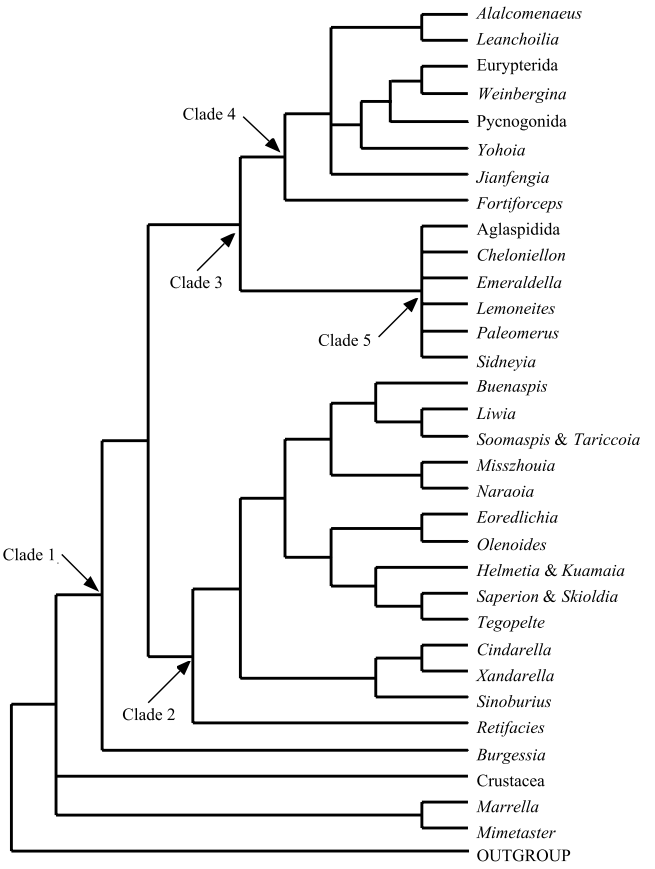

Figure 8 Strict consensus of 27 MPTs from four separate analyses of arachnomorph phylogeny with both interpretations of aglaspidid morphology, and with some characters treated as ordered or all characters unordered. Clades referred to in the text are numbered.

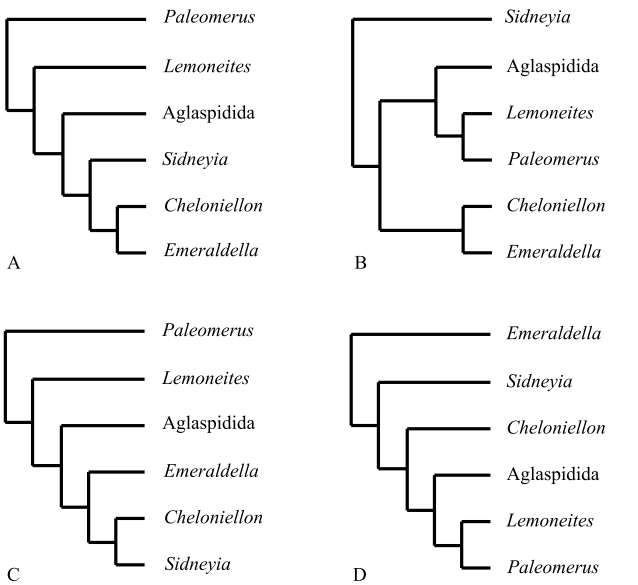

Figure 9 Alternative equally parsimonious resolutions of clade 5 of Fig. 8 (see Table 3).

Apart from this, the strict consensus of these 21 trees is identical to the consensus of the 27 trees found with all characters treated as unordered.

Across all analyses, four different topologies for Clade 5 (of Fig. 8) were found (Fig. 9). The distribution of these topologies across the four analyses described above, and across the same analyses repeated after reweighting of each character in proportion to their Rescaled Consistency Index (see Farris 1989) from the first analysis, is shown in Table 3. The instability of

Table 3 Numbers of most parsimonious trees supporting each of the alternative topologies for clade 4 of Fig. 7, under different analytical conditions: (RCI=Revealed Consistency Index)

Aglaspidid coding	Characters 4, 6, 36 and 43 ordered	Characters reweighted by RCI	*Paleomerus* and *Lemoneites* excluded	Topology (see Fig. 8)			
				A	B	C	D
1							9
1	X			3	3		3
1		X					6
1	X	X			3		
1			X				6
1	X		X		3		3
2						9	9
2	X			3	3	3	3
2		X					6
2	X	X			3		
2			X				6
2	X		X		3		3
Total				6	18	12	54

this clade was to some extent caused by the inclusion of *Lemoneites* and *Paleomerus*, which could each be coded for only 27 of the 54 characters used. Analysis with these two taxa excluded, and characters treated as unordered, found trees compatible only with Topology D of Figure 9, irrespective of the coding used for aglaspidids. Analysis with some characters treated as ordered and using either aglaspidid coding found three trees compatible only with Topology B of Figure 9 and three compatible only with Topology D of Figure 9. Therefore, Topology D is the preferred topology for Clade 5, as shown in Table 3.

One of the MPTs resulting from the 'Aglaspidida 2' coding (with all characters treated as unordered) was chosen as the basis for further discussion because this tree combined the preferred topology of Clade 5 with the (Crustacea, Clade 1) group that was favoured when some characters were treated as ordered. Bootstrap percentages and Bremer support values for this tree (using the Aglaspidida 2 coding) are shown in Figure 10. Apomorphies for all ingroup nodes of this tree are shown in Figure 10A.

3. Discussion

3.1. Phylogenetic results

The results of the cladistic analyses presented above are well-resolved and robust with respect to different analytical parameters. Most of the taxa considered form a clade (Clade 1 of Fig. 8) that is more closely related to chelicerates than to crustaceans in all analyses, and therefore, is recognised as the Arachnomorpha, as defined by Chen *et al.* (1996) and Ramskold *et al.* (1996). The monophyly of the Marrellomorpha was supported in all analyses. The marrellomorphs were found to be the sister group to a Crustacea+Clade 1 group in most MPTs, but in a minority of trees, formed the sister group to Clade 1 alone. According to the latter result, they should be included within the Arachnomorpha, but according to the first, excluded from it. Both of these alternatives have been supported in previous studies (e.g. Hou & Bergström 1997; Wills *et al.* 1998a, respectively). In addition to the marrellomorphs, the Fuxianhuiida Bousfield, 1995 and Canadaspidida have been placed in the Euarthropoda outside the main mandibulate and arachnomorph clades (Hou & Bergström 1997). Further study of these taxa, of the crustacean, or mandibulate, stem group and of the marrellomorphs is necessary before the position of the Marrellomorpha can be resolved. Provisionally, marrellomorphs are excluded from the Arachnomorpha, following the majority of analyses above and Wills *et al.* (1994).

The Burgess Shale arthropod *Burgessia* was placed as the sister group to remaining arachnomorphs in all analyses. Other Arachnomorpha form two major clades, one consisting of the 'trilobite-allied' arachnomorphs analysed by Edgecombe & Ramsköld (1999) here termed 'Trilobitomorpha' (defined as Trilobita and all taxa more closely related to Trilobita than Chelicerata), and the other ('chelicerate-allied') clade including chelicerates, 'great appendage' arthropods, aglaspidids, *Lemoneites*, *Paleomerus*, *Sidneyia* and *Emeraldella.* The latter is here termed 'Cheliceramorpha' (defined as Chelicerata and all taxa more closely related to Chelicerata than Trilobita). The topology of the 'trilobite-allied' clade was similar to that found by Edgecombe & Ramsköld (1999), but the present authors' results are more completely resolved, unambiguously supporting the sister-group relationship between trilobites and Helmetiida suggested in the previous study. Within the 'chelicerate-allied' clade, Aglaspidids, *Paleomerus*, *Lemoneites*, and the Burgess Shale *Emeraldella* and *Sidneyia* form a clade in opposition to megacheirans and chelicerates.

The present authors' analysis supports a new hypothesis of the origin of the chelicerates from within a paraphyletic assemblage of megacheiran arthropods and confirms pycnogonids as a sister group to the euchelicerates. Previous hypotheses of the chelicerate sister group (see Section 1) are much less parsimonious. The shortest trees supporting a *Cheloniellon*-chelicerate clade are six steps longer than the MPTs, and those supporting an aglaspidid-chelicerate clade, seven steps longer. All megacheirans and chelicerates are united by the flap-shaped rounded exopods and modification of the second cephalic segment endopods into anteriorly directed spinose raptorial organs, which share a number of detailed similarities. A clade including all of these taxa, apart from *Fortiforceps*, is supported by the synapomorphic loss of the antennae (or antennulae of crustaceans) and the longer length of spinose projections of the second cephalic appendage endopods. Within this clade, *Yohoia* shares the loss of cephalic exopods, the loss of thoracic endopods and a postabdomen of tubular tergites with chelicerates.

The poor resolution of Clade 5 (of Fig. 8) was partly a result of the poor preservation of, and consequent high proportion of missing data for, *Lemoneites* and *Paleomerus.* When these two

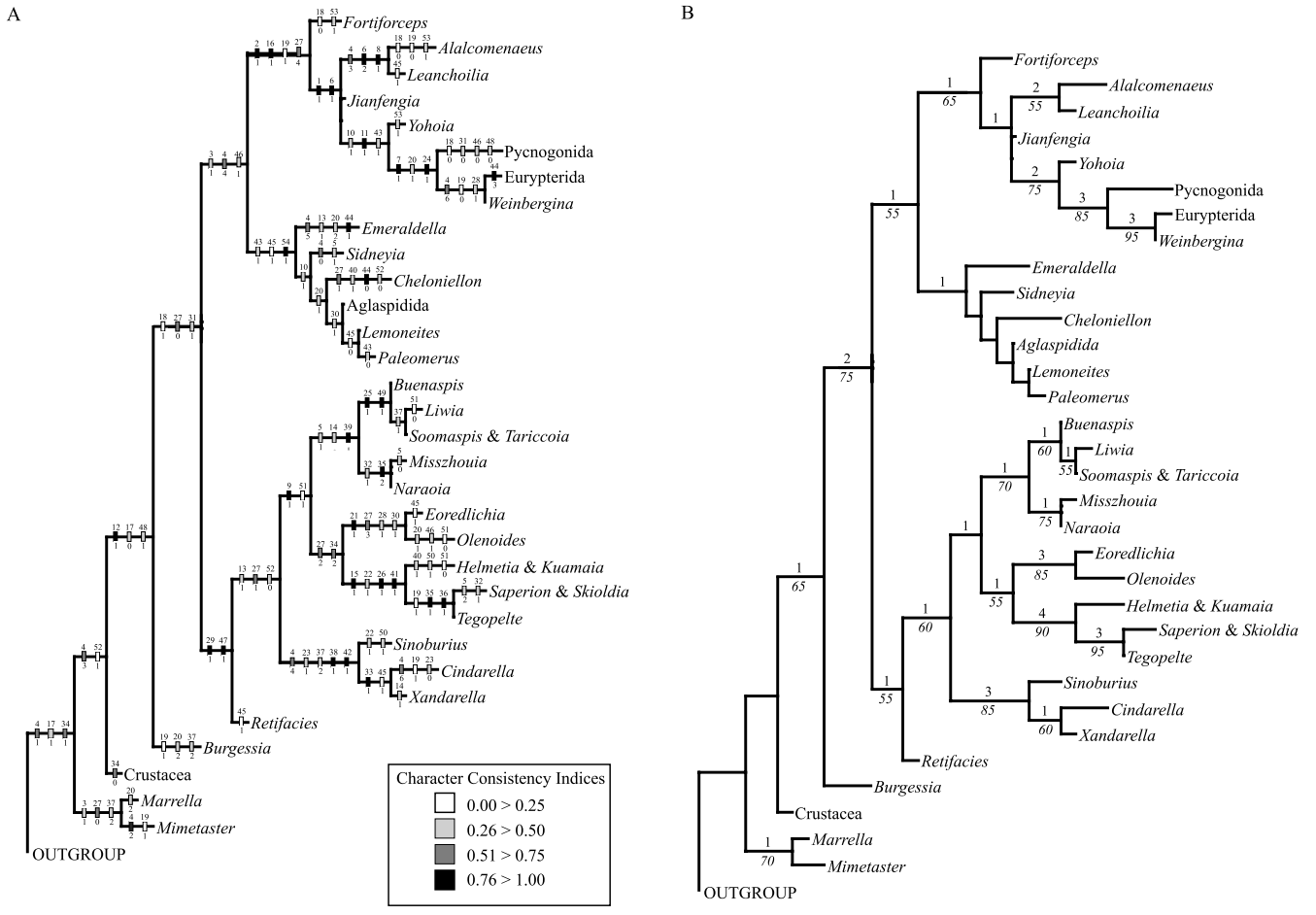

Figure 10 One of 18 equally parsimonious cladograms with 'Aglaspidida 2' coding and all characters unordered that is most congruent with results from other analyses. Non-terminal branch lengths scaled to reflect number of apomorphies. (A) ACCTRAN apomorphy scheme. Character numbers, shown above boxes, and states, shown below boxes, as in Table 2 and the text. Character consistency indices are indicated by shading. (B) Levels of support for individual nodes. Bremer support indices shown in bold type above branches. Bootstrap percentages in italic type below branches for all nodes with relative frequencies greater than 50%.

taxa were excluded from the analyses, only two (B and D) of the four topologies found in the complete analysis remained most parsimonious (see Fig. 9 and Table 3). Secondly, Bremer support values throughout much of the 'chelicerate-allied' clade (Clade 3 of Fig. 8) were improved when these taxa were excluded (see Fig. 11).

Dunlop (1999, p. 258) suggested that, in reconstructing the chelicerate stem lineage, 'we might predict that the two most significant changes towards the chelicerate condition are the reduction of the antennae and the formation of the next appendages into a claw'. According to the hypothesis presented here, both of these adaptations were achieved in Early Cambrian chelicerate ancestors. The recognition of the loss of the antennae in the stem group of the chelicerates, and the phylogenetic hypothesis presented here, suggest that chelicerates are most closely related to taxa with only a single additional segment fused to the crown group euchelicerate head of four fused somites. Previous hypotheses have derived chelicerates from Palaeozoic arthropods with a longer head (e.g. *Cheloniellon*, Stürmer & Bergström 1978; *Sanctacaris*, Briggs & Collins 1988; *Emeraldella*, Bruton & Whittington 1983). The plesiomorphic pattern of head segmentation is matched in pycnogonids; Bergström *et al.* (1980) suggested that only the anterior four pairs of appendages are incorporated into the head. This supports the view that pycnogonids are primitive with respect to other chelicerates, which show more or less complete fusion of this primitive head and three thoracic segments, including Solpugida and Pseudoscorpiones.

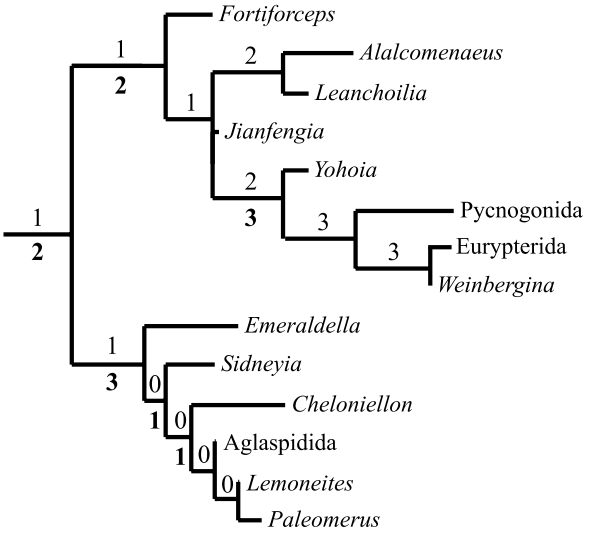

Figure 11 Bremer support values for clades within the 'chelicerate-allied' arachnomorphs (clade 3 of Fig. 8) when all taxa were included (normal weight font above nodes), and with *Lemoneites* and *Paleomerus* excluded (bold type below nodes).

The present study suggests that a shift from gnathobasic benthic feeding to a more vagrant lifestyle and raptorial appendage feeding occurred very early in the chelicerate lineage. Appendage feeding was clearly an important adaptation

for the terrestrialization of chelicerates (Dunlop 1997, p. 69; Dunlop & Webster 1999), but the model proposed here suggests that this considerably pre-dated terrestrialization. Gnathobasic feeding in xiphosurans and eurypterids may represent a reversal to a more primitve benthic arachnomorph lifestyle from a more pycnogonid-like ancestor.

3.2. Evolution of the arachnomorph head

The extant arthropod classes show highly conserved patterns of head segmentation (e.g. Wills *et al.* 1994). In contrast, there has been a near consensus amongst Cambrian arthropod workers (although rarely based on an explicit phylogenetic hypothesis) that patterns of head segmentation are highly homoplastic and hence of little systematic significance. Stürmer & Bergström (1978, pp. 78–9) suggested that 'even closely related forms may have different numbers of head segments and appendages', Bruton & Whittington (1983, pp. 576–7) that 'discussion on fossil arthropod relationships based on head segmentation . . . appears to be largely irrelevant and, at best, speculative' and Delle Cave & Simonetta (1991, p. 191) that 'there are no obvious phyletic affinities between genera having the same number of cephalized segments'. Most recently, Bergström & Hou (1997, p. 104) concluded that 'the segmental length of the head shield . . . seems to be of no relevance to the discussion and discrimination of evolutionary lineages'. It has been claimed that this view is supported by cladistic analyses in which patterns of tagmosis have been found to be rather poor at defining major arthropod clades (Briggs *et al.* 1992; Wills *et al.* 1994).

This suggestion is not only of relevance to systematics, but has featured prominently in recent debates surrounding the nature of the 'Cambrian explosion' (see Budd & Jensen 2000 for a recent review). Gould (1989, 1991) argued that the apparent plasticity of head segmentation in Cambrian compared to post-Cambrian arthropod evolution suggests that body-plan evolution was only constrained after the Cambrian explosion. According to this view, the origin of new higher taxa, with distinct body-plans, was only possible before the onset of these constraints (e.g. Valentine 1995). Taxa here recognised as arachnomorphs clearly played a major role in the development of Gould's hypothesis. This suggestion has previously been assessed in terms of overall morphological diversity, which is clearly rather distinct from Gould's concept of disparity. Wills *et al.* (1998b) showed that there was little correlation between overall morphological disparity and degree of limb specialisation, and that the latter was phylogenetically highly plastic. They remarked that (Wills *et al.* 1998b, p. 64) 'this finding has important implications for models of arthropod phylogeny and evolution that attribute overiding importance to head segmentation', but did not explicitly examine head segmentation, although it is likely to have been a major component of the index of tagmosis employed.

The results of the present study suggest that arguments that arthropod head segmentation was unusually labile during the Cambrian are poorly founded. Rather, only four major patterns of euarthropod head segmentation are identified. The plesiomorphic euarthropod state, according to both Walossek & Müller (1997, 1998) and Scholtz (1997), which may more properly be the plesiomorphic state for the euarthropod crown group only (depending on the phylogenetic position of the Marrellomorpha), consists of four post-acronal segments, bearing the antennae and three pairs of biramous limbs. The present authors suggest that the term 'cephalon' be restricted to this kind of head, which is found in stem group mandibulates in addition to many arachnomorphs. Crown group mandibulates share a 'bimaxillary head', in which an additional pair of appendages, the labium or second maxillae, are

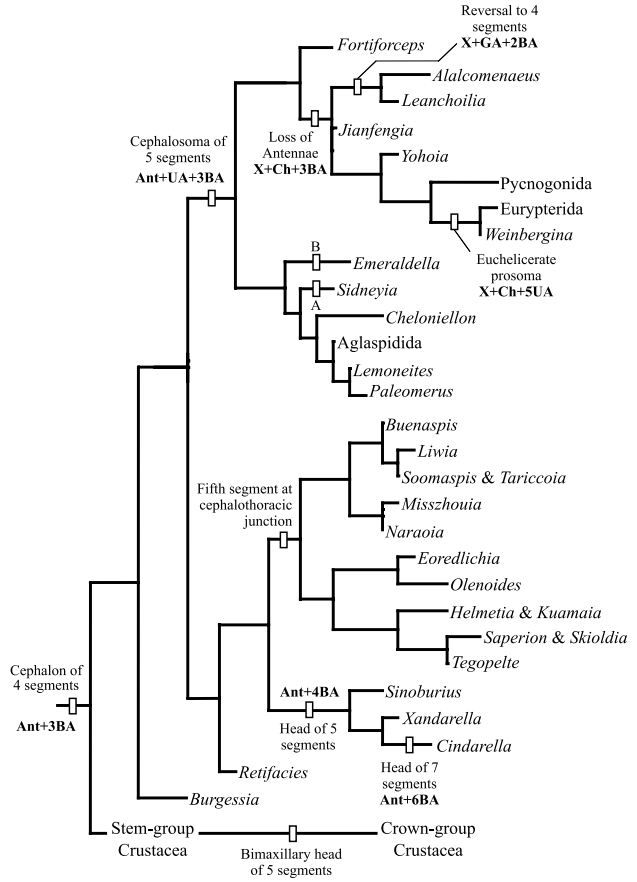

Figure 12 Cladogram from Fig. 10 showing changes in head segmentation. Bold type shows abbreviated head segmentation formula: Abbreviations: (Ant) antennae; (BA) biramous appendage pairs; (Ch) chelicerae; (GA) great appendages; (UA) uniramous appendage pairs; and (X) segment without appendages. Synapomorphy A is the autapomorphic reduction in head length to a single segment in *Sidneyia*. Alternatively, this may represent secondary division of the head shield. Synapomorphy B is the increase in the length of the head in *Emeraldella* to six segments.

incorporated into the head, but in crustaceans, these are not fused to the carapace (Scholtz 1997). Finally, two distinct forms of head tagmosis are found in chelicerates. A head with four pairs of appendages (but without antennae, giving a total of five segments incorporated into the head), which has been called the 'cephalosoma', is present in pycnogonids (Walossek & Dunlop 2002, pp. 434–5) and probably also in some euchelicerates (J. A. Dunlop, pers. comm. 2003). The 'prosoma' of most euchelicerates consists of this cephalosoma and two additional segments.

In general, these patterns of head segmentation are highly phylogenetically conserved (see Fig. 12). Only three homoplastic changes, namely reversal to a more primitive condition in the *Leanchoilia-Alalcomenaeus* clade, and the convergent origin of a five-segmented head in Clade 3 (of Fig. 8) and the Xandarellida, are necessary to optimise character 4 onto the most parsimonious cladogram. There are also transitions to autapomorphic states in *Emeraldella* and *Sidneyia.* In the case of *Sidneyia*, however, an argument could be made (following Bergström & Stürmer 1978, see discussion of Character 4) that the head consists of five segments, as in closely related taxa, but autapomorphically, each segment has a separate tergite. This would further increase the phylogenetic stability of head segmentation. Also following Bergström & Stürmer (1978), the head of *Cheloniellon* could be considered to consist of two tergites, making it more similar to the head of *Emeraldella* (with six pairs of appendages).

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TREVOR J. COTTON, Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK.
e-mail: trevor_cotton@hotmail.com.

SIMON J. BRADDY, Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol. BS8 1RJ, UK.
e-mail: S. J. Braddy@bris.ac.uk

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