

## Review Article

# Arthropod phylogeny: An overview from the perspectives of morphology, molecular data and the fossil record

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## ABSTRACT

Monophyly of Arthropoda is emphatically supported from both morphological and molecular perspectives. Recent work finds Onychophora rather than Tardigrada to be the closest relatives of arthropods. The status of tardigrades as panarthropods (rather than cycloneuralians) is contentious from the perspective of phylogenomic data. A grade of Cambrian taxa in the arthropod stem group includes gilled lobopodians, dinocaridids (e.g., anomalocaridids), fuxianhuiids and canadaspidids that inform on character acquisition between Onychophora and the arthropod crown group. A sister group relationship between Crustacea (itself likely paraphyletic) and Hexapoda is retrieved by diverse kinds of molecular data and is well supported by neuroanatomy. This clade, Tetraconata, can be dated to the early Cambrian by crown group-type mandibles. The rival Atelocerata hypothesis (Myriapoda + Hexapoda) has no molecular support. The basal node in the arthropod crown group is embroiled in a controversy over whether myriapods unite with chelicerates (Paradoxopoda or Myriochelata) or with crustaceans and hexapods (Mandibulata). Both groups find some molecular and morphological support, though Mandibulata is presently the stronger morphological hypothesis. Either hypothesis forces an unsampled ghost lineage for Myriapoda from the Cambrian to the mid Silurian.

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## 1. Introduction

Arthropods have been the dominant component of animal species diversity for all of the past 520 million years, since the main burst of the Cambrian radiation. The earliest arthropod body fossils are confidently dated to Stage 3 of the Cambrian (Fig. 1), though some records have been assigned to Stage 2 (Steiner et al., 1993, 2005). The trace fossil record of Arthropoda is generally regarded as predating the body fossil record, with *Monomorphichnus* and *Rusophycus* traces that are widely endorsed as being arthropodan extending back into Stage 2, from strata traditionally assigned to the Tommotian (Budd and Jensen, 2000).

For the purpose of this review, major competing hypotheses for the fundamental groupings in the Arthropoda are introduced by their proper names. I see little point in presenting “the” morphological perspective and (or versus) “the” molecular perspective because morphologists have advocated hypotheses as different from each other as any of them are to any molecular result (morphologists have supported either Tetraconata or Atelocerata, Mandibulata or Schizoramia, etc.). Likewise there is no singular

molecular tree for arthropods because different genes or different analyses have differed in the clades that they resolve. That said, certain recurring patterns can be recognised with different classes of evidence, e.g., molecular phylogenies are split between myriapods being most closely allied to chelicerates (Paradoxopoda/Myriochelata) or to hexapods and crustaceans (Mandibulata), but irrespective of what markers are employed, a hexapod–crustacean clade (Tetraconata) is emphatically favoured rather than a myriapod–hexapod clade (Atelocerata).

One region of the arthropod tree is the domain of a singular class of data, the resolution of the stem group. Fossils provide the only evidence for the sequence of branchings and character acquisition in the arthropod stem group. This field has advanced considerably in recent years, and a substantial degree of consensus has emerged with respect to such hypotheses as gilled lobopodians, anomalocaridids and other dinocaridids, and fuxianhuiids being positioned in the stem group of Arthropoda.

Arthropod phylogeny is sometimes presented as an almost hopeless puzzle wherein all possible competing hypotheses have support (“chaos” fide Bäcker et al., 2008, fig. 1). It is certainly the case that a great diversity of groupings has been advocated through the decades, and much of this diversity is seen even in contemporary work. However, it needs to be emphasised that the field of

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strongly supported competing theories has been winnowed down, and current debates focus on a few alternatives that each generally finds support from different kinds of evidence (Budd and Telford, 2009).

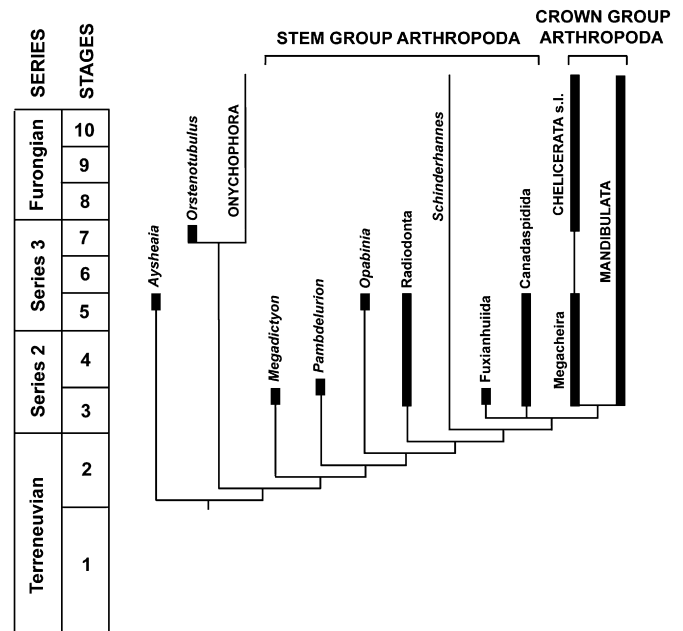
## 2. The sister group of Arthropoda: Onychophora or Tardigrada?

Arthropoda is here used in the sense of most English-language sources, that is, excluding Onychophora and thus corresponding to “Euarthropoda” in much European literature. Identifying the sister group of the arthropods has obvious importance for evaluating character polarity at the base of Arthropoda. Two competing theories are currently relevant to the arthropod sister group: either onychophorans or tardigrades are the closest relatives of arthropods. Both of these theories share a common basis in regarding moulting animals with paired, segmental ventrolateral appendages operated by intrinsic and extrinsic muscles to be a monophyletic group. The “legged” clade is often referred to as Panarthropoda (following Nielsen, 1995), though it has received a proper name, Aiolopoda Hou and Bergström, 2006, that has not yet received widespread usage.

Onychophora is traditionally recognised as the sister group of Arthropoda (and indeed is generally classified in Arthropoda in the German literature, i.e., Onychophora + Euarthropoda). The evidence in support of this relationship most obviously derives from the open, haemocoelic circulatory system, with a dorsal heart having segmental ostia in both groups. Arthropods and onychophorans share segmental leg musculature (versus distinct musculature of each leg in tardigrades; Schmidt-Rhaesa and Kulesa, 2007), have nephridia or nephridial derivatives that arise from the walls of coelomic cavities (Mayer, 2006a), and onychophorans have arthropod-type hemocyanin (Kusche et al., 2002). A sister group relationship between onychophorans and arthropods is strongly supported in broadly sampled analyses of expressed sequence tags (Roeding et al., 2007; Dunn et al., 2008), and when new embryological observations for tardigrades were incorporated into morphological datasets, the alliance of Onychophora and Arthropoda (to the exclusion of Tardigrada) was retrieved (Hejnol and Schnabel, 2006).

With its endorsement in Claus Nielsen’s “Animal Evolution” (Nielsen, 1995), a sister group relationship between tardigrades and arthropods – rather than onychophorans and arthropods – became increasingly discussed for several years. Nielsen (1995) cited three characters in favour of this hypothesis: 1) articulated limbs with intrinsic muscles; 2) a brain composed of three segments; 3) cross-striated musculature. The tardigrade–arthropod grouping was assigned the formal name Tactopoda (Budd, 2001) in recognition of the jointed leg structure. The homology of jointed limbs of arthrotardigrades and those of arthropods is undermined by the former being telescopic, rather than arthropodized. The brain argument for a tardigrade–arthropod alliance has come under fire from new studies of the tardigrade brain showing it to be unsegmented, with a circumesophageal morphology more closely resembling the brain of non-arthropod ecdysozoans – the Cycloneuralia – than the tripartite brain of arthropods (Zantke et al., 2008). In contrast, the central body of the brain of onychophorans shares detailed similarities with arthropods, indeed to the degree that possible relationships with Chelicerata have been considered (Strausfeld et al., 2006). Though I dispute the likelihood of an Onychophora + Chelicerata clade from the perspective of other morphological systems and molecular data, the similarities may instead be informative for the onychophoran–arthropod clade.

A tardigrade–arthropod sister group relationship is problematic from the perspective of phylogenomic evidence. Expressed



**Fig. 1.** Relationships of stem group arthropods (after Daley et al., 2009) plotted against Cambrian time scale. Assignment of Lagerstätten to stages follows Zhu et al. (2006). Stages 1 and 6–8 have been formalised as the Fortunian, Druman, Guzhangian and Paibian, respectively. In the arthropod crown group (see Fig. 2), crown group Chelicerata s.l. is minimally dated by *Cambropycnogon* (Waloszek and Dunlop, 2002) and Mandibulata by *Yicaris* (Zhang et al., 2007). Megacheirans are depicted as stem group chelicerates but their status in the arthropod crown group is contentious (see text).

sequence tag results noted above as favouring an onychophoran–arthropod alliance (Dunn et al., 2008) find that tardigrades are either sister group of onychophorans and arthropods or are instead nested within the Cycloneuralia, allied to nematodes and nematomorphs, depending on the taxonomic sampling used in the analyses. In the first instance, Panarthropoda is monophyletic whereas in the latter it is polyphyletic. A sister group relationship between Onychophora and Arthropoda with Tardigrada allied to Cycloneuralia was also found in EST analyses sampling a different onychophoran taxon (Roeding et al., 2007). Whether the tardigrade–nematoid clustering results from systematic error, e.g., long branch attraction (as seems likely from the perspective of morphology), remains to be determined.

Onychophora is depicted as sister group of Arthropoda in Fig. 1. Terrestrial onychophorans date to the Late Carboniferous (*Helenedora*: Thompson and Jones, 1980). No strong claims have been made that fossils of this antiquity are crown group onychophorans, but they are certainly better supported as at least stem group Onychophora than are any of Cambrian lobopodians (reviewed by Liu et al., 2008; Ma et al., 2009) that have sometimes been identified as stem group Onychophora (Ramsköld and Chen, 1998; Ma et al., 2009). Of Cambrian taxa, perhaps the most compelling candidate for assignment to the onychophoran stem group is *Ostenotubulus*, which shares a polygonal cuticular patterning with onychophorans, and has presumed sensory structures on the legs that are similar in detail to the dermal papillae of extant Onychophora (Maas et al., 2007).

## 3. Arthropod monophyly: no longer a controversy

The popular mid-20th Century theory that arthropods were polyphyletic (Tiegs and Manton, 1958; Anderson, 1973; Schram, 1978) had its critics even in its heyday (e.g., Lauterbach, 1974). The fundamental failure of arthropod polyphyly was that its advocates

never identified any real groups of organisms as the sister groups of the different arthropod branches. When imaginary worms are removed from trees depicting the ancestry of arthropod lineages (Fryer 1996, fig. 1), the branches converge on common ancestry, with no member of any other phylum being a part of the group. This is monophyly by any definition. On purely methodological grounds (an absence of any explicit rival hypotheses), morphologists thus reinstated arthropod monophyly on the basis of the unique features shared by all arthropods. Boudreaux (1979), for example, listed 17 putative autapomorphies of Arthropoda, though because this was done in the context of Articulata, several of the characters involving the cuticle and its moulting are now seen as apomorphies of Ecdysozoa rather than Arthropoda. Still, arthropod monophyly most conspicuously finds support from the sclerotized tergal exoskeleton, legs with sclerotized podomeres separated by arthrodial membrane, muscles attaching at intersegmental tendons, a reduced segmental complement of nephridial organs (Mayer, 2006a), compound eyes in which new eye elements are added in a proliferation zone at the sides of the developing eye field (Harzsch and Hafner, 2006; Mayer, 2006b), and the eyes being associated with two optic neuropils. Redescriptions of the onychophoran nerve cord allow that a “rope ladder” nerve cord with a pair of ganglia having commissures and connectives in each segment may additionally be autapomorphic for arthropods (Mayer and Harzsch, 2007, 2008). Segmentation gene characters can also be cited as autapomorphies for Arthropoda compared to Onychophora and Tardigrada, for example, Pax 3/7 proteins having pair-rule patterns (Gabriel and Goldstein, 2007).

The picture from molecular systematics strengthens arthropod monophyly to a degree that polyphyly is now a footnote in the history of systematics. Arthropods unite as a clade based on diverse sources of sequence data, such as nuclear ribosomal genes (Mallatt et al., 2004; Mallatt and Giribet, 2006), mitochondrial genomes (Hassanin, 2006), combinations of mitochondrial genomes and a large set of nuclear genes (Webster et al., 2006) or nuclear ribosomal and protein-coding genes with mitochondrial genomes (Bourelat et al., 2008), and Expressed Sequence Tags (Dunn et al., 2008).

#### 4. Chelicerata, Myriapoda, Crustacea and Hexapoda: monophyly and challenges

The deep relationships of arthropods amount to the arrangement of chelicerates, myriapods, crustaceans and hexapods. Of these four groups, the monophyly of each has been questioned at some point, though in current literature only Crustacea finds widespread recognition as probably being non-monophyletic. Because evidence for and against monophyly is appraised in detail in the chapters on each of these groups, only a brief summary is given here.

##### 4.1. Chelicerata

Chelicerata is here discussed in the sense of a group that is often called Eichelicerata (i.e., a clade composed of Xiphosura and Arachnida). The question of pycnogonid affinities is addressed below; when pycnogonids are identified as the sister group of chelicerates the formal name Chelicerata *sensu lato* is not uncommonly applied to that broader group (though the rarely used name Chelicerophora is available).

Chelicerate monophyly is generally regarded as one of the least controversial matters in arthropod systematics (e.g., the group is monophyletic across all explored analytical conditions in the combined morphology + nine gene analyses of Giribet et al. 2005), and among recent studies the view of Simonetta (2004) that Chelicerata could be polyphyletic may be unique. Simonetta's views

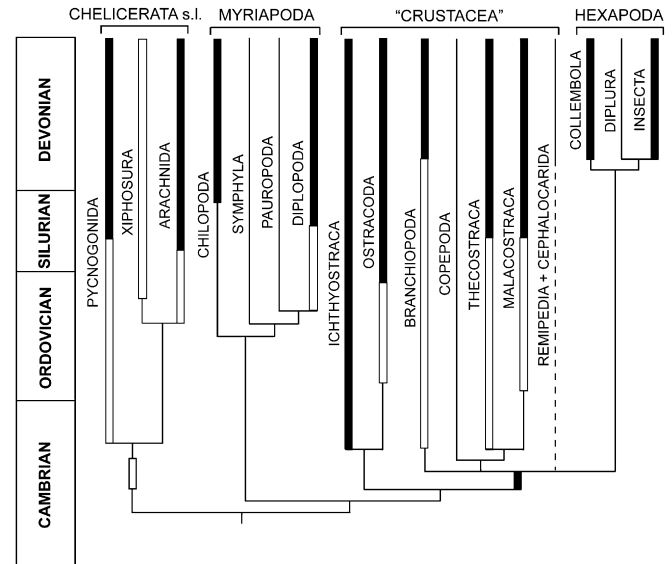


Fig. 2. Relationships in the arthropod crown group, with palaeontological calibration. Minimal dates for stem and crown groups (empty and filled vertical bars, respectively) are defended in the text. Remipedia + Cephalocarida is depicted with a doubtful pre-Devonian ghost lineage because some of the trees on which this summary is based (e.g., Regier et al., 2008, fig. 3) resolve the polytomy with remipedes and cephalocarids as sister group to Hexapoda. With that resolution a single ghost lineage applies to remipedes, cephalocarids and hexapods.

emphasised differences in respiratory structures between scorpions and other arachnids, but the case for arachnid monophyly has subsequently been reinforced by highly detailed similarities in the book lungs of scorpions and other arachnids (Scholtz and Kamenz, 2006). In addition to morphological autapomorphies, Chelicerata is one of the most stable and most strongly supported monophyletic groups in the entire Arthropoda across a range of analytical conditions for nuclear protein-coding genes (Regier et al., 2008). Fig. 2 depicts Chelicerata as monophyletic, with Xiphosura and Arachnida its constituent clades. Minimal divergence dates from fossil occurrences follow Dunlop and Selden (2009). Stem group Xiphosura date to the Late Ordovician, the arachnid stem group is dated by Middle Ordovician chasmataspidids, and the arachnid crown group by Early Silurian (Llandovery) scorpions.

Recent discussions of the stem group of Chelicerata have singled out Megacheira (“great appendage” arthropods, including *Alalcomenaeus*, *Leancoilia*, *Jianfengia* and *Yohioia*) as derivatives from the chelicerate stem lineage, and if so, extending the record of total group Chelicerata s.l. into the early Cambrian (Chen et al., 2004; Cotton and Braddy, 2004; Dunlop, 2006). To date, this relationship has been defended based only on the morphology of so-called “short great appendages” in Cambrian taxa such as *Haikoucaris* (Chen et al., 2004) in comparison to chelifores and chelicerae. Alternatively megacheirans have been excluded from the arthropod crown group (Dewell and Dewell, 1997; Bergström and Hou, 1998; Dewell et al., 1999; Budd, 2002; Bergström et al., 2008), a position that can be reconciled with the elevated number of podomeres in the endopod (García-Bellido and Collins, 2007; Liu et al., 2007) compared to the inferred groundplan state in crown group Arthropoda (Boxshall, 2004). Figs. 1 and 2 depict Megacheira as a grade in the chelicerate stem group (cf. Chen et al., 2004, fig. 6) but their affinities are not well established.

##### 4.2. Myriapoda

Paraphyly of Myriapoda (relative to Hexapoda) was commonly advocated in light of the Atelocerata hypothesis. As discussed

below, a myriapod–hexapod alliance is strongly rejected in a broad range of molecular analyses (see discussion of *Tetraconata*), and the same analyses almost invariably retrieve Myriapoda as a clade with strong support (see, e.g., Regier et al., 2008). The dismissal of Ate-locerata means that no serious rival exists for monophyly of Myriapoda, apart from some investigations of brain anatomy that have isolated Diplopoda from other myriapods, and indeed from all other arthropods (Loesel et al., 2002; Strausfeld et al., 2006). Although morphological evidence for myriapod monophyly is often described as elusive, the details of the mobile cephalic endoskeleton (“swinging tentorium”) and its role in abduction of the mandibular gnathal lobe are unique to Myriapoda (Koch, 2003), and may be supplemented by arrangements of serotonin reactive neurons (Harzsch, 2004) and the position of the nuclei of eucone cells in the ommatidia (Müller et al., 2007) and the cuticle of intermediary cells in epidermal glandular organs (Hilken et al., 2005) that are shared by chilopods and diplopods and apparently apomorphic for Myriapoda. Accordingly, Fig. 2 shows Myriapoda as monophyletic, and its internal relationships are as discussed by Shear and Edgecombe (2010) elsewhere in this issue.

No convincing candidates for stem group Myriapoda have been found in any Cambrian Lagerstätte, or indeed from any early Palaeozoic marine rocks (Edgecombe, 2004). The body fossil record of myriapods is unsampled until the mid Silurian (ingroup chilog-nathan millipedes described by Wilson and Anderson, 2004 and Wilson, 2005), with crown group centipedes appearing at the end of the Silurian (Shear et al., 1998). This long ghost lineage appears to be partly filled by trace fossils. *Diplichnites* and *Diplopodichus* trackways from the late Middle or Upper Ordovician (Johnson et al., 1994) are consistent with a tracemaker having a millipede body-plan (Wilson, 2006). Using this to date the divergence of Diplopoda from Pauropoda sets a minimum age for Progoneata and Myriapoda as well. Early Cambrian records of the sister group, *Tetraconata* (Fig. 2), discussed below under *Crustacea*, emphasise an unsampled ghost lineage for Myriapoda of substantial duration.

#### 4.3. Crustacea

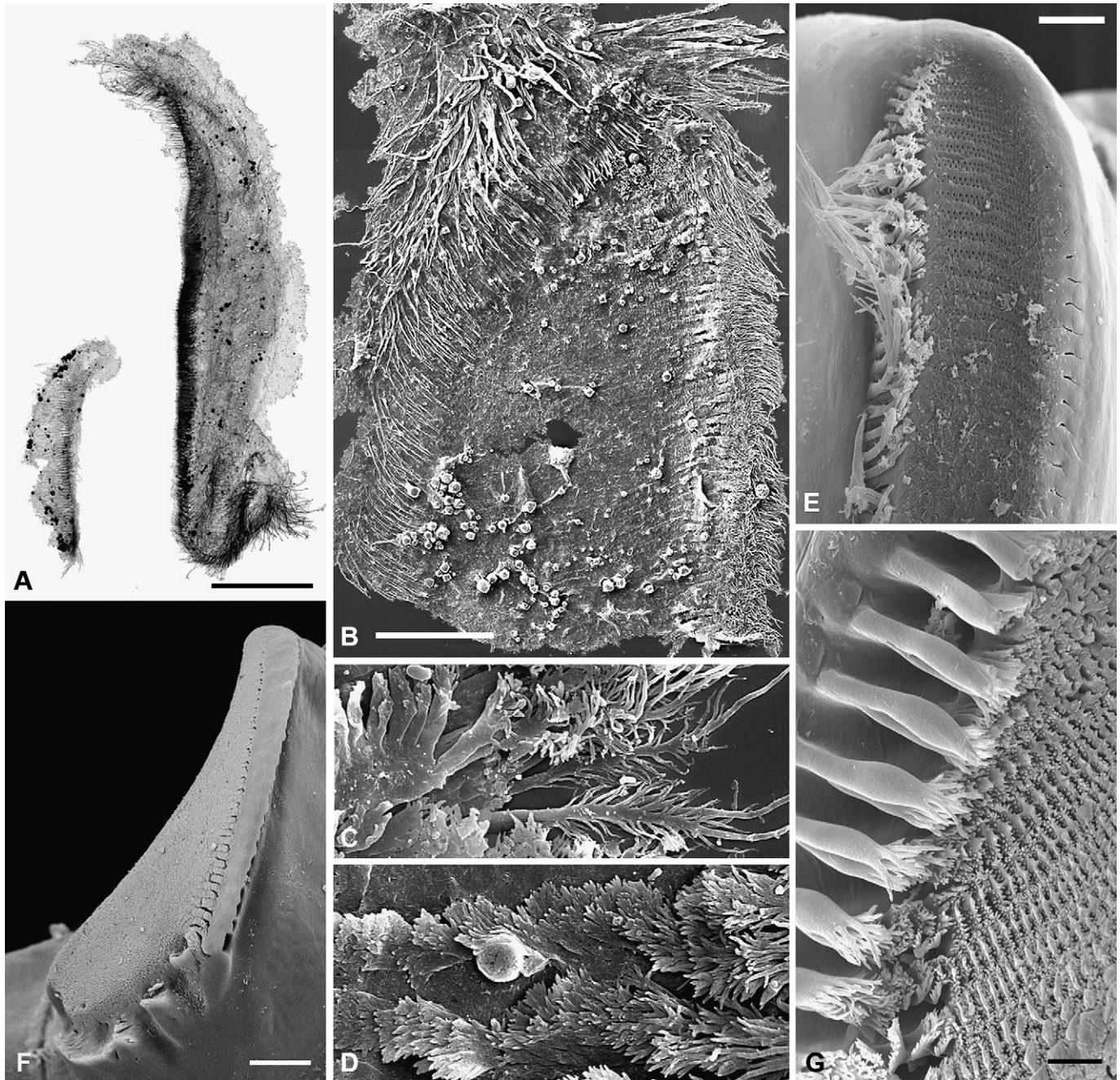
For at least 25 years it has been appreciated that few convincing apomorphies could be marshalled in support of Crustacea. Lauterbach (1983) concluded that the fusion of the naupliar eyes and a maximum of only two segmental organs (the antennal and maxillary glands) are the only convincing autapomorphies of Crustacea. Other workers add the nauplius larva (orthonauplius) as an additional crustacean autapomorphy (see discussion in Richter, 2002). An absence of pigment grains in the corneagenous cells of the ommatidium has been noted as another potential shared derived character of crustaceans (Müller et al., 2003), and crustacean monophyly (apart from the placement of pentastomid parasites) is typically retrieved in cladistic analyses of morphological data (Bitsch and Bitsch, 2004; Giribet et al., 2005). Monophyletic formulations of the crustacean total group (stem group and crown group Eucrustacea) have been proposed by Waloszek and colleagues (Waloszek et al., 2007 and papers cited therein), drawing heavily on Cambrian fossils from ‘Orsten’ preservation. Schram and Koenemann (2004) critiqued the traditional diagnostic features of Crustacea, concluded that none are straightforward (e.g., second antennae), and the group is likely to be non-monophyletic. Their morphology-based cladistic analysis (Schram and Koenemann, 2004, fig. 19.9) conforms to most molecular phylogenies in resolving insects within a paraphyletic crustacean grade, indeed being allied to Branchiopoda as in many sequence-based analyses (e.g., Babbett and Patel, 2005; Regier et al., 2005; Mallatt and Giribet, 2006; Dunn et al., 2008; Timmermans et al., 2008). Other morphologists who have judged crustaceans to be a grade relative

to insects have generally identified malacostracans as the most probable sister group of insects based on the anatomy of the optic neuropils (Harzsch, 2002; Sinakevitch et al., 2003) and other neuroanatomical characters (Strausfeld, 2009), or recognised a broader assemblage of remipedes, malacostracans, insects and cephalocarids based on brain characters that are not shared by branchiopods and maxillopodans (Fanenbruck and Harzsch, 2005; Harzsch, 2006).

Molecular analyses have typically found crustaceans to be non-monophyletic, almost invariably in the context of crustaceans and hexapods together forming a monophyletic group (see discussion of *Tetraconata* below). Paraphyly of Crustacea relative to Hexapoda is a recurring theme, but precisely which group(s) of Crustacea is sister to Hexapoda differs between analyses, as do most of the major groupings between well-established crustacean clades. Candidates for the sister group of Hexapoda are Branchiopoda (references cited above), Copepoda or Branchiopoda, based on nuclear ribosomal genes (Mallatt et al., 2004, Mallatt and Giribet, 2006, von Reumont et al., 2009), and a clade of Remipedia and Cephalocarida (using nuclear coding genes; Regier et al., 2008, fig. 3). Crustacean relationships in Fig. 2 follow the summary diagram of Regier et al. (2008), depicting a clade that unites malacostracans and branchiopods together with some “maxillopodans” (copepods and thecostracans), remipedes and cephalocarids as the closest relatives of hexapods. Crustacean paraphyly results from the exclusion of ostracodes and ichthyostracans (branchiurans and pentastomids; Møller et al., 2008) from this group.

Palaeontological calibration of crustacean divergences in Fig. 2 is provided by the following minimal dates: crown group Malacostraca, *Cinerocaris* (Briggs et al., 2004); stem group Malacostraca, Ordovician phyllocarids, including *Caryocaris*; crown group Thecostraca, *Rhamphoverritor* (Briggs et al., 2005); stem group Thecostraca, *Bredocaris* (Waloszek and Müller, 1988, 1998); crown group Branchiopoda, *Lepidocaris* (Olesen, 2004); stem group Branchiopoda, *Rehbachella* (Waloszek, 1993; Olesen, 2004); crown group Ichthyostraca, late Cambrian stem group pentastomids (Waloszek et al., 2006); crown group Ostracoda, *Myodoprimigenia* (Gabbott et al., 2003); stem group Ostracoda, *Eopilla*, *Nanopsis* and *Kimsella* (Williams et al., 2008).

“Crustacean spotting” has a long history in palaeontology, but most of the candidates for Cambrian crown group crustaceans (e.g., bradoriids, *Canadaspis*, *Ercaia*, *Pectocaris*) have been rejected by subsequent investigators. Currently only two strong candidates for early or middle Cambrian crustaceans are known, *Yicaris* from Cambrian Stage 3 of China (Zhang et al., 2007; Maas et al., 2009) and an unnamed taxon described by Harvey and Butterfield (2008) from isolated cuticular fragments, including well-preserved mouthparts, from Cambrian Stage 4 in Canada. *Yicaris* was assigned to Eucrustacea and, more specifically, allied to branchiopods, cephalocarids and maxillopodans (the traditional Entomostraca). Although the monophyly of Entomostraca (Boxshall, 2007) and the ingroup eucrustacean status of *Yicaris* have been questioned (Harvey and Butterfield, 2008), affinities to cephalocarids and nesting in the eucrustacean crown group have been retrieved in morphological analyses (Edgecombe, in press). The “Mount Cap crustacean” of Harvey and Butterfield (2008), known from organic preservation, has a mandibular pars molaris (Fig. 3A–D) that is so similar in detail to that of crown group crustaceans (branchiopods and malacostracans; Fig. 3E, G, respectively) and hexapods (Fig. 3F) (see Edgecombe et al., 2003) that I accept the interpretation that this fossil is nested within *Tetraconata* (Harvey and Butterfield, 2008). In the tree used for Fig. 2, this type of mandible is not known in the ostracod–ichthyostracan group, and it is conservatively used to provide a minimal age for the clade that includes hexapods and the remaining crustaceans.



**Fig. 3.** Mandibular pars molaris in Cambrian and extant Tetraconata. (A–D) Early Cambrian crustacean from the Mount Cap biota, northwestern Canada. Images courtesy of T. H. J. Harvey and N. J. Butterfield. (A) Light micrographs, scale 100  $\mu\text{m}$ . (B–D) Scanning electron micrographs; scale in B applies to C–D. (B) scale 50  $\mu\text{m}$ . (C) Marginal setal fringe, outer margin to right, scale 6  $\mu\text{m}$ . (D) Transition between marginal fringe (at right) and rows on branching spines on molar surface; scale 8  $\mu\text{m}$ . (E) *Cyclestheria hislopi* (Branchiopoda: Cyclestherida), scale 10  $\mu\text{m}$ . (F) *Nesomachilis howensis* (Insecta: Archaeognatha), scale 30  $\mu\text{m}$ . (G) *Meganictyphanes norvegica* (Malacostraca: Euphausiacea), scale 10  $\mu\text{m}$ . Images E and G courtesy of S. Richter.

#### 4.4. Hexapoda

Though the tagmosis pattern of hexapods appears to provide a rather straightforward autapomorphy of the group, attempts to compile strictly apomorphic characters of the Hexapoda have routinely observed that the list is surprisingly short (Klass and Kristensen, 2001). That said, apart from some literature emphasising the peculiarities of proturan sperm (but without identifying an alternative sister group that is not a hexapod), morphology must be regarded as indicative of hexapod monophyly. The situation has

been somewhat strengthened by new evidence from embryology, notably from proturan embryos (Machida, 2006).

Retrieval of hexapod monophyly was a challenge for early molecular analyses, which routinely placed certain hexapods in morphologically anomalous positions. Notably, mitochondrial genomic data presented a controversial resolution of Hexapoda as paraphyletic, with Collembola resolved basal to a group uniting other hexapods with crustaceans (Nardi et al., 2003). Some subsequent analyses amplified this pattern of hexapod paraphyly when Diplura were placed even more basally than Collembola

(Carapelli et al., 2007), with both Crustacea and Hexapoda resolved as mutually paraphyletic (as in Cook et al., 2004). However, reanalyses of mitogenomic data have found that the evidence against hexapod monophyly is inconclusive (Cameron et al., 2004; Hassanin, 2006). Evidence from nuclear genes contrasts with the mitogenomic picture in that recent analyses instead retrieve hexapod monophyly, notably a “standard”, morphologically supported resolution of Collembola as primitively flightless hexapods (Regier et al., 2004, 2008; Mallatt and Giribet, 2006; Timmermans et al., 2008; von Reumont et al., 2009).

On the basis of morphology and nuclear genes, Hexapoda is depicted as a clade in Fig. 2. Its known fossil record commences in the Early Devonian cherts of Rhynie, Scotland, represented by the collembolan *Rhyniella* (Greenslade and Whalley, 1986), the likely pterygote *Rhyniognatha* (Engel and Grimaldi, 2004), and the archaeognathan-like *Leverhulmia* (Fayers and Trewin, 2005). The putative marine stem group hexapod *Devonohexapodus*, from the Early Devonian, has been convincingly shown to be neither a hexapod nor even a crown group mandibulate (Kühl and Rust, 2009). Stem group Hexapoda remain unsampled.

## 5. The fundamental clades of Arthropoda

### 5.1. Mandibulata

A clade of arthropods in which the post-tritocerebral appendage assumes the form of a jaw or mandible (Fig. 4A) has provided the traditional basis for uniting myriapods, crustaceans and hexapods as Mandibulata. The homology of the mandible has been defended on morphological (Bitsch, 2001; Edgecombe et al., 2003) as well as gene expression (Prpic and Tautz, 2003) grounds. Additional anatomical evidence for the monophyly of Mandibulata has been summarised by Wägele (1993) and Harzsch et al. (2005). It is, in total, a substantial sum of data from diverse anatomical systems. Among them are the following shared (apparently apomorphic) characters of myriapods, crustaceans and hexapods: the brain having a conserved midline neuropil embedded in the proto-cerebral matrix (Fig. 4E and F), the somata that supply cerebral neuropils being variable in size, and the deutocerebrum containing the olfactory lobe (Fig. 4B) (Strausfeld et al., 2006); the stomatogastric and labral nerves being connected to the tritocerebrum rather than to the deutocerebrum (Scholtz and Edgecombe, 2006); sternal Anlagen on the posterior stomodaeal region (Fig. 4D) (Wolff and Scholtz, 2006); a crystalline cone being developed in the dioptric apparatus (Müller et al., 2003, 2007), with the ommatidia having identifiable cells (e.g., cone cells and proximal reticular cells) (Fig. 4C); interommatidial pigment cells (Müller et al., 2003) (Fig. 4C); and a low and fixed number of serotonergic neurons in the nerve cord, in which cells are individually identifiable (Harzsch, 2004; Harzsch et al., 2005).

Mandibulata has been retrieved as monophyletic in some analyses of nuclear ribosomal genes (Giribet and Ribera, 1998), hemocyanin sequences (Kusche et al., 2003), under diverse analytical conditions for a broad sampling of nuclear protein-coding genes (Regier et al., 2008), and a combination of nuclear ribosomal and coding genes and mitochondrial genomes (Bourlat et al., 2008). In each case, Myriapoda is sister to a crustacean–hexapod clade.

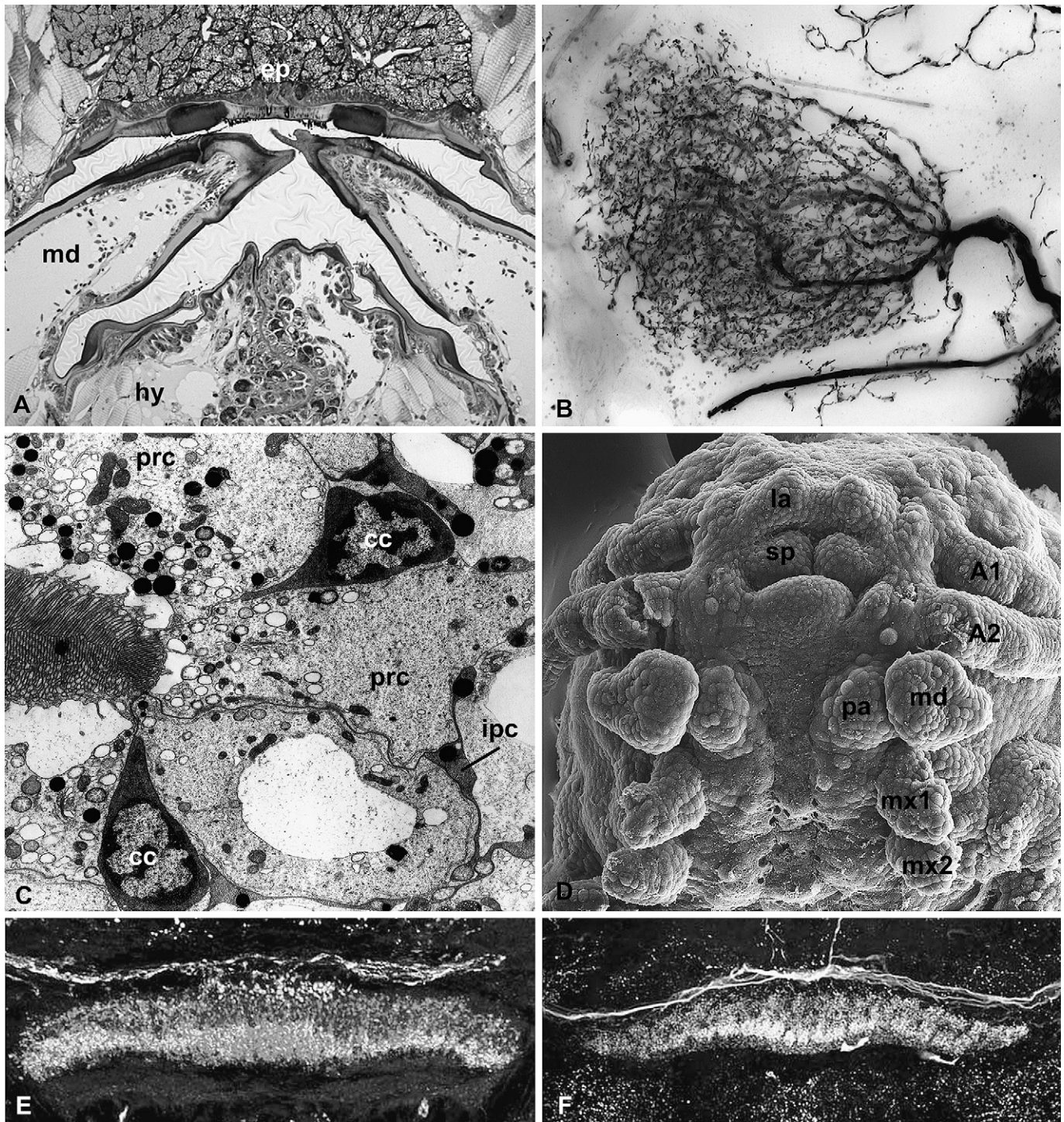
Mandibulata can be accommodated by palaeontological data. Cambrian ‘Orsten’ fossils (including *Martinsonia*, *Oelandicaris*, *Cambrocaris*, *Cambropachycope*, *Goticaris*, *Henningsmoenicaris* and *Phosphatocopina*) that have been assigned to the crustacean stem group by Waloszek and colleagues (see Waloszek et al., 2007; Stein et al., 2008 for recent accounts) have alternatively been identified as stem group mandibulates (Lauterbach, 1988; Moura and

Christoffersen, 1996; Richter and Wirkner, 2004). The third cephalic appendage is not encapsulated in the head and is less differentiated from other biramous cephalic limbs than is the case in mandibles in the mandibulate crown group. However, taxa such as *Martinsonia* and *Henningsmoenicaris* have a modification that can be identified as a precursor of a mandibular coxal gnathobase in that a proximal endite (an apomorphy of the mandibulate total group fide Waloszek; e.g., Zhang et al., 2007, fig. 3) is elaborated relative to the condition on adjacent limbs. Zhang et al. (2007, their fig. 3) depicted these “stem group crustaceans” in the stem group of Mandibulata as a whole (i.e., their scope of “Crustacea” is equivalent to total group Mandibulata). As such, fossils can be seen to provide evidence for the origin of the mandible, and indicate a crustacean-like habitus for stem group mandibulates. Other fossil taxa exhibit a mix of crustacean and myriapod- or hexapod-like characters, in particular the Silurian *Tanazios*. Originally referred to the crustacean stem group (Siveter et al., 2007), the head appendages were subsequently reinterpreted as including frontal filaments rather than first antennae and a possibly limbless intercalary segment (Boxshall, 2007) that would be alternatively favour myriapod or hexapod affinities. The position of *Tanazios* in the Mandibulata is ambiguous, but its combination of crustacean and myriapod-like characters (e.g., tagmosis into a head and homonomous trunk) suggests its relevance to tracking the basal splits between crown group mandibulate lineages.

### 5.2. Paradoxopoda/Myriochelata

An alliance between chelicerates and myriapods emerged in the mid 1990s with analyses of the small nuclear ribosomal 18S rRNA (Friedrich and Tautz, 1995; Giribet et al., 1996), and has been found in some later analyses that combined complete 18S sequences with the large ribosomal (28SrRNA) subunit (Mallatt et al., 2004; Petrov and Vladychenskaya, 2005; von Reumont et al., 2009). Several subsequent analyses using different kinds of molecular data, including Hox gene sequences (Cook et al., 2001), hemocyanin sequences (Kusche and Burmester, 2001), mitochondrial genomics (Hwang et al., 2001; Hassanin, 2006), and Expressed Sequence Tags (Dunn et al., 2008), likewise found a myriapod–chelicerate group, which was almost simultaneously named Paradoxopoda (Mallatt et al., 2004) and Myriochelata (Pisani et al., 2004) in two studies that retrieved that grouping in molecular analyses. The “Paradox-“ prefix of the former name refers to the inability to find morphological support for this assemblage. For several years the sole indication for the potential monophyly of Paradoxopoda came from a similar, detailed pattern of neurogenesis seen in spiders, millipedes and centipedes (reviewed by Stollewerk and Chipman, 2006) that contrasts with the neuroblasts that give rise to neural tissue in insects and crustaceans (Ungerer and Scholtz, 2008). Studies of onychophoran embryogenesis by Mayer and Whittington (2009) with a particular focus on nervous system development amplify the case for Paradoxopoda/Myriochelata. Onychophorans, sampled from both extant families, share three characters with hexapods and crustaceans, providing evidence that an alternative state shared by myriapods and chelicerates is apomorphic. The putative apomorphies of Paradoxopoda/Myriochelata involve immigrating clusters of post-mitotic cells noted above, segmental invaginations of the neuroectoderm in each hemisegment that lead to the formation of so-called ventral organs, and the exclusive generation of neurons in the central neuroectoderm (versus a dual role of the neuroectoderm giving rise to both neurons and epidermis in Onychophora and Tetracoelata).

Paradoxopoda is a rival to Mandibulata on the basis of its retrieval from so many different markers. After several years of accumulating molecular support for a myriapod–chelicerate clade,



**Fig. 4.** Anatomical characters shared by Mandibulata. (A) Mandibles (*md*) embedded in chewing chamber between the epipharynx (*ep*) and hypopharynx (*hy*) (*Scolopendra oraniensis*: Chilopoda: Scolopendromorpha). (B) Olfactory glomerulus in deutocerebral/antennal segment (*Bombus*: Insecta: Hymenoptera). (C) Ommatidium showing nuclear region of crystalline cone cells (*cc*), proximal reticular cells (*prc*), interommatidial pigment cells (*ipc*) (*Scutigera coleoptrata*: Chilopoda: Scutigeromorpha). (D) Sternal Anlagen on posterior stomodaeal region, forming paragnaths (*pa*) in crustaceans (*Orchestia cavimana*: Crustacea: Amphipoda). Labrum (*la*), stomodaeal projections (*sp*), first (*A1*) and second (*A2*) antennae, mandible (*md*), first (*mx1*) and second (*mx2*) maxillae. (E and F) Central body of brain with midline neuropil embedded in protocerebral matrix. (E) *Machilis germanica* (Insecta: Archaeognatha). (F) *Lebbeus groenlandicus* (Crustacea: Decapoda). Images courtesy of M. Koch (A), N. J. Strausfeld (B, E, F), C. H. G. Müller (C), C. Wolff (D).

a few studies that have attempted data exploration have found that Mandibulata emerges as the stronger signal in some datasets that had been identified as pro-Paradoxopoda. For example, hemocyanin sequence data that provided support for Paradoxopoda/Myriochelata (Kusche and Burmester 2001) instead favoured Mandibulata with the addition of more taxa (Kusche et al. 2003).

Exploration of mitochondrial genomic data by Rota-Stabelli and Telford (2008) found that the resolution of either Mandibulata or Paradoxopoda was sensitive to the choice of outgroup, whereas for nuclear coding genes Mandibulata is better supported than Paradoxopoda under varied analytical conditions, notably when fast-evolving genes are excluded (Regier et al., 2008).

### 5.3. *Schizoramia/TCC*

From the perspective of extant arthropods – drawing on either morphology or molecular evidence – the deepest split in the arthropod crown group is described by one of the two hypotheses just discussed, Mandibulata or Paradoxopoda (see discussion of the Cormogonida hypothesis below for arguments why pycnogonids are allied to chelicerates). A third alternative has a long tradition in the palaeontological literature (Edgecombe, 1998), a grouping of crustaceans and chelicerates as “TCC” (=trilobites, crustaceans, chelicerates) or Schizoramia. The latter name refers to the shared presence of biramous appendages. The placement of chelicerates in Schizoramia (when most chelicerates have uniramous limbs) is based on biramous limbs in fossils such as trilobites that have been allied to Chelicerata under the Arachnomorpha concept, and the view that Xiphosura retain rami homologous with prosomal exopods (the flabellum) or opisthosomal endopods (the inner flap on the book gills) (Waloszek and Müller, 1998, fig. 5.6D,E). Schizoramia was generally seen by palaeontologists in opposition to Atelocerata or Uniramia (which have uniramous limbs).

The Schizoramia hypothesis suffers on several grounds. The Arachnomorpha hypothesis has been questioned as a plausible basis for classifying trilobites (Scholtz and Edgecombe, 2005), though even if trilobites are instead allied to mandibulates, other “arachnomorphs” with biramous appendages may still be stem group chelicerates (e.g., if megacheiran “great appendage” arthropods like *Haikoucaris* are stem group Chelicerata; Chen et al. 2004; Cotton and Braddy, 2004). More problematic is the fact that biramy itself has come under serious fire as a homology between crustaceans and any chelicerate-allied taxa or stem group arthropods. The clonal analyses of crustacean limbs by Wolff and Scholtz (2008) suggest that “biramy” in Crustacea is uniquely produced by splitting of a single developmental axis, such that the exopod of crustaceans would not be homologous with the outer branch of fossil “biramous limbs”, which is instead an exite possibly homologous with an epipodite.

A chelicerate–crustacean group is refuted by all well sampled molecular analyses; crustaceans are invariably grouped with hexapods rather than with chelicerates. Schizoramia cannot be saved by special pleading for the inclusion of fossils because when fossil taxa with “biramous” limbs are included in morphological analyses, Mandibulata rather than Schizoramia is retrieved (Scholtz and Edgecombe, 2006). Schizoramia would be expected to fare even worse with the addition of molecular data to the character sample because they are even more strongly conflicting with Schizoramia. Schizoramia/TCC is an artefact of palaeontologists carving arthropods into a group that is marine and known from the Early Palaeozoic (“Schizoramia”) and another group that is terrestrial and not known until the Siluro–Devonian (“Atelocerata”).

### 5.4. *Tetraconata/Panrustacea*

As noted in the introduction, a relationship between crustaceans and hexapods (exclusive of myriapods) has been a recurring theme of molecular systematic analyses of Arthropoda as far back as the pioneering total evidence analysis by Wheeler et al. (1993). The hexapod–crustacean clade is variably referred to as Panrustacea or Tetraconata. From the perspective of morphology, most of the arguments in favour of the monophyly of this group come from studies of the nervous system, comprehensively reviewed by Strausfeld (1998), Dohle (2001), Richter (2002), Harzsch (2006), and Strausfeld et al. (2006). Putative apomorphic characters for the Tetraconata involve detailed similarities in compound eye ultrastructure, mode of growth of visual elements (Harzsch and Hafner, 2006), the optic neuropils and chiasmata (Harzsch, 2002;

Strausfeld, 2005), midline neuropils in the brain (Loesel et al., 2002), serotonin immunoreactivity in the nerve cord (Harzsch, 2004), a role of the neuroectoderm in generating epidermal and neural cells (Stollewerk and Chipman, 2006), and neuroblasts that express the same markers and produce homologous neurons (Ungerer and Scholtz, 2008).

Molecular evidence amplifies the neuroanatomical similarities of hexapods and crustaceans, not just because of the strength of support found in analyses of any particular kind of sequence data but also because Tetraconata is independently retrieved by so many kinds of molecular information. Among these are nuclear ribosomal genes (Mallatt et al., 2004; Petrov and Vladychenskaya, 2005; Mallatt and Giribet, 2006, and many earlier studies cited therein), nuclear protein-coding genes (Regier et al., 2005, 2008, and earlier papers by the same authors), mitochondrial genomics (Hassanin, 2006; Gai et al., 2008), Hox gene sequences (Cook et al., 2001), hemocyanin sequences (Kusche et al., 2003), mitochondrial gene order (Boore et al., 1998), combination of many different markers (Bourlat et al., 2008), and Expressed Sequence Tags (Dunn et al., 2008).

### 5.5. *Atelocerata/Tracheata*

An alliance between hexapods and myriapods, the Atelocerata (=Tracheata and Antennata), has a long history, and can accurately be described as the orthodox perspective on hexapod affinities. That said, theories compatible with the rival Tetraconata hypothesis date back at least to the neuroanatomical work of Holmgren and Hanström (e.g., Hanström, 1926), emphasising characters of the optic lobes and midline neuropils of the brain shared by insects and crustaceans that have come back to the discussion in the past 15 years. I make this point to emphasise that Atelocerata cannot be claimed to be “the” morphological solution to arthropod phylogeny. Indeed, some morphological cladistic analyses resolve Tetraconata in favour of Atelocerata (Giribet et al. 2005, fig. 1).

That said, it is indisputable that Atelocerata does have a solid body of morphological support, reviewed by Klass and Kristensen (2001) and Bitsch and Bitsch (2004), including the limbless intercalary segment, tentorial endoskeleton, postantennal organs, Malpighian tubules, and the single pretarsal (depressor) muscle. Bäcker et al. (2008) provide an additional argument from a restatement of classical “subcoxal theory”, reconstructing concentric pleural sclerites around the leg base as an apomorphy in the myriapod/hexapod groundpattern.

Atelocerata is a “morphology-only” hypothesis. No molecular data of any kind favour an alliance of myriapods and hexapods exclusive of crustaceans or chelicerates (apart from an alignment experiment conducted with a small fragment of 12S rRNA to debunk the placement of onychophorans within the Arthropoda; Wägele and Stanjek, 1995). This is a serious defect of the Atelocerata hypothesis. Because Tetraconata accommodates a large body of genetic information from diverse sources as well as numerous highly detailed features of the nervous system, it is depicted in favour of Atelocerata in Fig. 2.

### 5.6. *Chelicerata s.l. versus Cormogonida: the pycnogonid problem*

The history of research on the affinities of pycnogonids has been reviewed by Dunlop and Arango (2004). Currently only two hypotheses merit serious consideration: either pycnogonids are sister group of chelicerates (the Chelicerata *sensu lato* or Chelicerophora hypothesis), or they are sister group of all other crown group arthropods (the Cormogonida hypothesis, the name referring to gonopores situated on the trunk, as opposed to on the legs). The Chelicerata *sensu lato* hypothesis largely relies upon a homology



between the chelifores of pycnogonids and the chelicerae of chelicerates. The Cormogonida hypothesis was originally formalised based on combined analyses of morphological and molecular data (Zrzavý et al., 1997), but finds morphological support from features shared by non-pycnogonid arthropods (including chelicerates) that are lacking in Pycnogonida, such as segmental organs (nephridial derivatives), intersegmental tendons, and a labrum. The discovery of an excretory gland opening at the base of the chelifore in one pycnogonid species (Fahrenbach and Arango, 2007) weakens the first character, and likewise the absence of a labrum is possibly refuted by lobes on the developing proboscis of pycnogonids that may correspond to the labral Anlage of other arthropods (Winter, 1980; Scholtz and Edgecombe, 2006). The suggestion that pycnogonid neuroanatomy indicates that chelifores are innervated by the protocerebrum (Maxmen et al., 2005) rather than the deutocerebrum as in chelicerae was consistent with theories about protocerebral appendages having been present in the arthropod stem group (Budd, 2002; Scholtz and Edgecombe, 2006). Subsequent observations on Hox gene expression (Jager et al., 2006) and neuroanatomical studies of additional pycnogonid species (Brenneis et al., 2008) reinforced the segmental homology of chelifores and chelicerae as deutocerebral appendages. There is thus no compelling challenge to the traditional hypothesis that the pycnogonid anterior appendages are homologous with those of chelicerates.

Combined molecular and morphological analyses have variably supported either Cormogonida (Zrzavý et al., 1997; Giribet et al., 2001) or Chelicerata *sensu lato* (Giribet et al., 2005). Because the latter result was obtained in analyses with an updated and expanded character sample, pycnogonids are depicted as sister group to Chelicerata in Fig. 2. This result is also the better supported alternative in analyses based on EST data (Dunn et al., 2008).

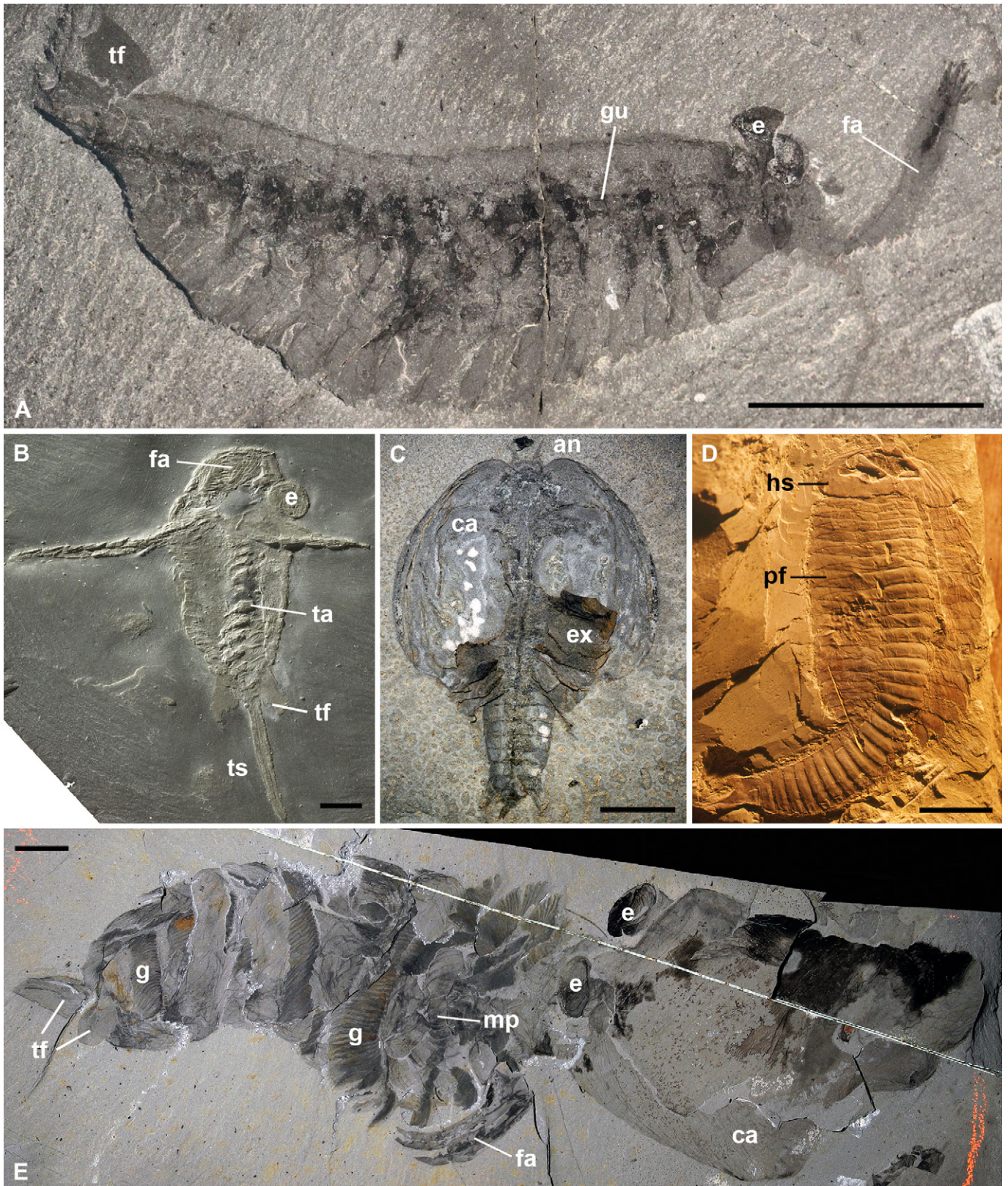
The first record of Pycnogonida in Fig. 2 (and Chelicerata *s.l.* in Fig. 1) is based on the late Cambrian *Cambropycnogon* (Waloszek and Dunlop, 2002). The pycnogonid identity of this fossil has been questioned (Bamber, 2007), but the purported differences are in part erroneous (i.e., *Cambropycnogon* does not possess biramous limbs, though they are gnathobasic, as would be expected in the pycnogonid stem group under the Chelicerata *s.l.* hypothesis). The mid Silurian *Haliestes* (Siveter et al., 2004) provides an uncontested record of remarkably modern pycnogonids in the Palaeozoic, and a resolution of *Haliestes* in the pycnogonid crown group is obtained in combined analyses of morphological and molecular data that include fossil pycnogonids (Arango and Wheeler, 2007).

## 6. Stem group Arthropoda

Comparison of crown group arthropods and their extant sister group, Onychophora, is the morphological equivalent of a long branch problem, and it is not a surprise that the controversy over Mandibulata versus Paradoxopoda has been described as a rooting problem (Giribet et al., 2005, fig. 1). Given that no additional extant taxa can be added to the sample to try and break up the long branches that separate (crown group) arthropods and onychophorans, fossils have a unique opportunity to inform on this region of the tree, the arthropod stem group. This question has been the subject of considerable attention in recent years, and although the interpretation of certain features in key fossils is intensely debated (e.g., appendicular versus gut structures in *Fuxianhuia*; Waloszek et al., 2005; Bergström et al., 2008; Budd, 2008), and the precise sequence of taxa in the stem group differs in different studies, it is accurate to say that broad consensus has been reached concerning the membership of several taxa in the arthropod stem group. Major points of consensus about the arthropod stem group include the

following (listed in more or less increasing distance from the arthropod crown group):

- 1) *Fuxianhuia* (Fig. 5D) and related taxa from the Chengjiang Lagerstätte (*Chengjiangocaris* and *Shankouia*) are upper stem group arthropods (Hou and Bergström, 1997; Dewell et al., 1999; Waloszek et al., 2005, 2007; Bergström et al., 2008; Budd, 2008). These taxa most conspicuously unite with the arthropod crown group on the basis of hardened tergites with paratergal folds, the association of two rami in the trunk limbs (a pediform limb stem and an outer flap), and the posterior orientation of the mouth, opening at the back of a hypostome;
- 2) *Canadaspis* (Fig. 5C) and allied bivalved arthropods are likewise upper stem group arthropods. They are variably resolved either in a clade with fuxianhuiids (Budd, 2002) or instead as more closely allied to the arthropod crown group than are fuxianhuiids (Bergström and Hou, 1998; Waloszek et al., 2007). Like fuxianhuiids they have a substantially greater number of articles in their pediform limb ramus than is observed in the arthropod crown group, and the limb stem does not have a clearly differentiated protopodite (*sensu* Boxshall, 2004);
- 3) Anomalocaridids (=Radiodonta) (Fig. 5E) are positioned lower in the arthropod stem group than are fuxianhuiids or canadaspids. Their most evident synapomorphy with the arthropod crown group (and upper stem group) is the shared presence of at least one fully arthropodized appendage, i.e., with sclerotized regions separated by arthroal membranes;
- 4) *Opabinia* (Fig. 5A) is either most closely allied to anomalocaridids (as reflected by their classification together as Dinocarida) or is positioned in the arthropod stem group a node more stemward (Budd, 1996; Cotton and Braddy, 2004; Zhang and Briggs, 2007; Kühl et al., 2009). Apomorphies shared by *Opabinia*, anomalocaridids and crown group arthropods include stalked, compound eyes and a non-annulated trunk;
- 5) “Gilled lobopodians”, represented by *Kerygmachela* (Budd, 1999) and *Pambdelurion* (Budd, 1997), both from the early Cambrian Sirius Passet Lagerstätte, either branch lower in the arthropod stem group than do anomalocaridids and *Opabinia* (Budd, 1996, 1997, 1999, 2002; Dewell and Dewell, 1997; Cotton and Braddy, 2004; Kühl et al., 2009; Daley et al., 2009) or form part of a clade with them (Chen et al., 1994; Hou and Bergström, 2006; Ma et al., 2009; see discussion below). *Pambdelurion* more closely resembles anomalocaridids than does *Kerygmachela* in having a ventrally situated mouth circling of overlapping, medially dentate plates (Budd, 1997 and pers. obs.) and the “gilled lobopodians” have accordingly been regarded as a paraphylum with *Pambdelurion* positioned more crownward in the arthropod stem group (Budd, 1997, 1998, 1999; Dewell et al., 1999; Daley et al., 2009);
- 6) The basal part of the arthropod stem group is represented by taxa that are consigned to the Cambrian lobopodian assemblage (see Liu et al., 2008, Ma et al., 2009, for overviews). Although a few of these lobopodians have been singled out as showing characters that are putatively synapomorphic with arthropods, some of the arguments are unconvincing (e.g., that the body regionalisation of *Luolishania* is homologous with arthropod tagmosis; Liu et al., 2004). The most plausible candidates for membership in the arthropod stem group among described Cambrian lobopodians are the Chengjiang taxa *Jianshanopodia* (Liu et al., 2006) and *Megadictyon* (Liu et al., 2007). These resemble the Greenland “gilled lobopodians” in having robust, spine-bearing, annulated frontal appendages, and resemble these and other stem group arthropods in having metameric, reniform midgut glands with an internal structure of submillimetric lamellae (see Butterfield, 2002, for sections of



**Fig. 5.** Stem group Arthropoda from the Cambrian (A, C–E) and Lower Devonian (B). (A) *Opabinia regalis* from the Burgess Shale, in lateral aspect. (B) *Schinderhannes bartelsi* from the Hunsrück Slate, in ventral aspect. (C) *Canadaspis perfecta* from the Burgess Shale, in dorsal aspect, with bivalved carapace “butterflied”. (D) *Fuxianhuia protensa* from the Chengjiang biota. (E) The radiodontan (“anomalocaridid”) *Hurdia victoria* from the Burgess Shale, in dorsolateral aspect. Abbreviations: *an*, antenna; *ca*, carapace; *e*, eye; *ex*, exopod of thoracic appendage; *fa*, frontal appendage; *g*, gill; *gu*, gut; *hs*, head shield; *mp*, ‘Peytoia’ mouth part; *pf*, paratergal fold; *ta*, trunk appendage; *tf*, tail fan; *ts*, tail spine. Images A, C and E courtesy of A. Daley; B courtesy of D. E. G. Briggs. All scales 1 cm.

*Leanchoilia* and literature citations for homologous structures in other Cambrian arthropods).

Hou and Bergström (2006) have repeatedly (Bergström and Hou, 2003; Hou et al., 2005; Bergström et al., 2008) stressed that the part of the arthropod stem group characterised by lateral appendage flaps, radial mouths, and spinose frontal appendages (i.e., *Opabinia*, anomalocaridids and the “gilled lobopodians”) could most parsimoniously be identified as a monophyletic group (equivalent to the “giant predator” group of Chen et al., 1994). Monophyly has the advantage of lessening the number of character reversals that are forced by a scheme in which these taxa are instead a grade in the arthropod stem group as was resolved by Budd (1996, 1997, 1998, 1999), Dewell and Dewell (1997), Dewell et al. (1999), Cotton and Braddy (2004), Zhang and Briggs (2007), and Kühl et al. (2009). Characters cited by Hou and Bergström in support of a broader “dinocaridid” clade have been included in cladistic analyses, and although reversals are indeed demanded, the grade (rather than clade) resolution has been found to be more parsimonious (Daley et al., 2009; Kühl et al., 2009). The alternative favoured by Hou and Bergström carries its own set of homoplasies, notably convergent gain of compound eyes and arthropodized appendages in anomalocaridids and arthropods. Interrelationships in the arthropod stem group shown in Fig. 1 follow the cladistic analysis of Daley et al. (2009), updated for inclusion of the Devonian *Schinderhannes* (Fig. 5B), which is positioned as by Kühl et al. (2009).

## 7. Closing “open questions”

Throughout this review I have attempted to differentiate between hypotheses that have fallen by the wayside in the face of conflicting evidence and hypotheses that continue to merit serious attention. In my opinion, too many summaries of arthropod phylogeny have been too quick to treat all nodes of the tree as an “open question” because some class of data (sometimes a single character) may support a group and that result was published. Often it turns out that those data were few and flawed. A page of competing cladograms showing all published trees for the Arthropoda or Venn diagrams that depict complete incongruence (Bäcker et al., 2008, fig. 1) perpetuate the notion that “anything goes”, which is simply not an accurate depiction of the field in 2009. Figs. 1 and 2 depict explicit resolutions of several of the main questions that have been widely debated in recent literature because they represent nodes that have strong support from diverse sources of molecular data and are also based on a suite of complex anatomical characters. Among these are pycnogonids as sister group of Chelicerata (rather than as basal arthropods), Myriapoda as a clade (rather than a grade), and crustaceans as a paraphyletic group, some of which are the closest relatives of Hexapoda. An alliance between myriapods and hexapods (“Atelocerata”) can be dismissed, but the affinities of myriapods to either chelicerates or to Tetraconata – the Paradoxopoda/Myriochelata versus Mandibulata debate – can rightly be identified as the most fundamental open question in deep arthropod phylogeny. This controversy is enhanced by the proposal that several characters of nervous system development may be synapomorphic for myriapods and chelicerates (Mayer and Whittington, 2009). Figs. 1 and 2 resolve the cladogram in favour of Mandibulata based on its larger body of morphological support in the face of comparable molecular support for the two hypotheses.

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