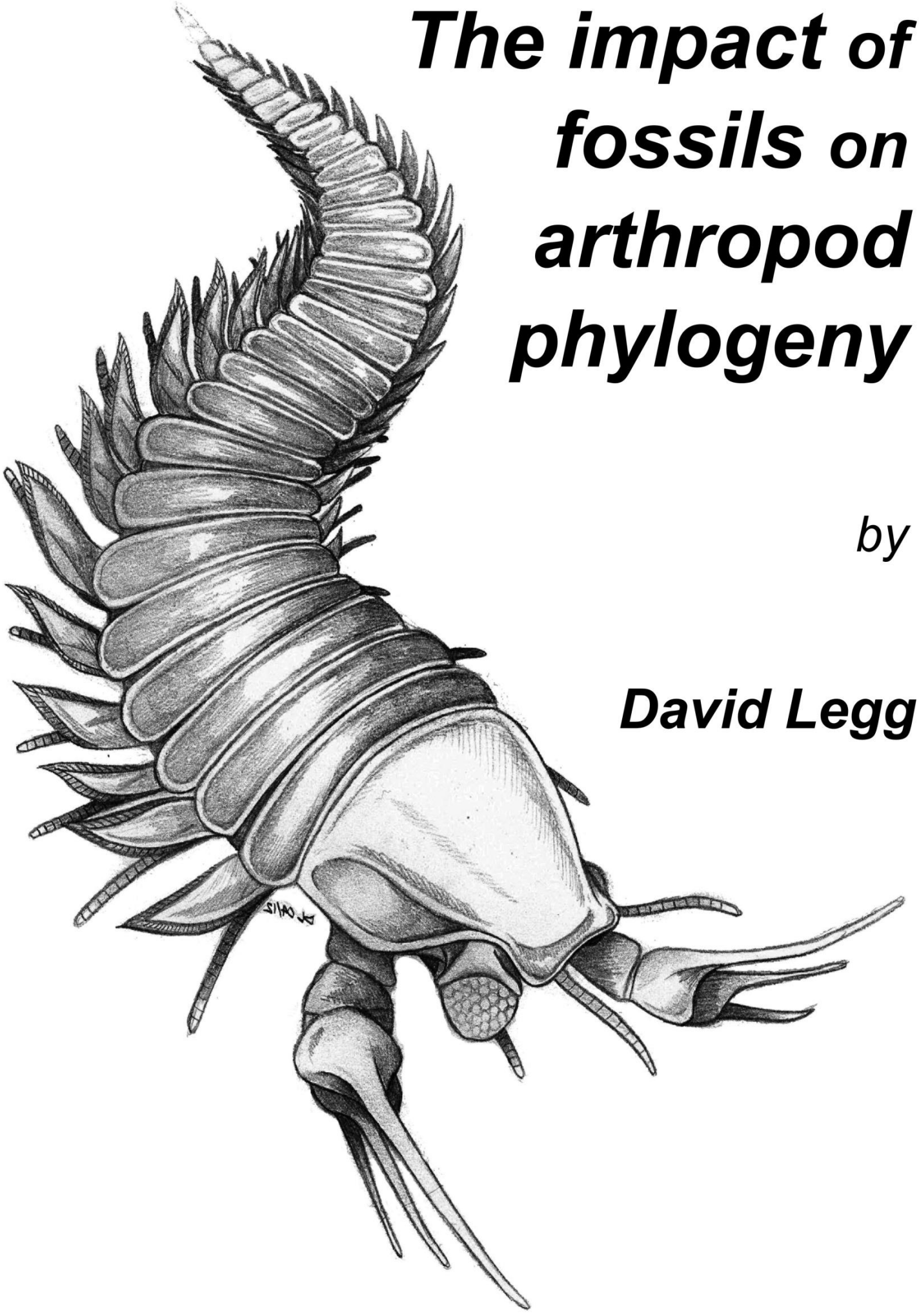


The impact of fossils on arthropod phylogeny

by

David Legg

Cover picture: A reconstruction of *Kootenichela deppi* Legg 2013, from the middle Cambrian Stephen Formation of British Columbia (Canada).

The impact of fossils on arthropod phylogeny

by

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A thesis submitted in partial fulfilment of the requirement for the degree of Doctor of philosophy and the Diploma of Imperial College London. This thesis is my own work except where explicitly indicated in the text.

Abstract

The arthropods are the most diverse, abundant and ubiquitous phylum on Earth. Five main extant groups (subphyla) can be recognized: Pycnogonida, Euchelicerata, Myriapoda, Hexapoda, and Crustacea. Each group displays a distinctive body plan and a suite of autapomorphies that makes determining their interrelationships difficult. Although a variety of hypotheses have been proposed regarding their interrelationships, just three have frequently been recovered in recent phylogenetic analyses. Rather than representing incongruent topologies these hypotheses represent variations of the position of the root on the same parent topology.

The long histories of the major arthropod subclades, which had begun to diverge by, at least, the early Cambrian, means that long-branch artefacts are highly probable. To alleviate potential long-branch attraction and provide a more accurate placement of the root, 214 fossil taxa were coded into an extensive phylogenetic data set of 753 discrete characters, which also includes 95 extant panarthropods and two cycloneuralian outgroups. Preference was given to those fossil taxa thought to occur during the cladogenesis of the major arthropod clades, i.e. the lower and middle Cambrian.

An extensive study of material from the middle Cambrian Burgess Shale Formation and the coeval Stephen Formation in British Columbia (Canada) was undertaken. This study focussed primarily on taxa thought to represent 'upper stem-group euarthropods', namely bivalved arthropods and megacheirans ('great-appendage' arthropods), as they will have the greatest utility in polarizing relationships within the arthropod crown-group [= Euarthropoda]. This study includes the description of three new genera and four new species: the bivalved arthropods *Nereocaris exilis*, *N. briggsi*, and *Loricicaris spinocaudatus*; and the megacheiran *Kootenichela deppi*; and a restudy selected material referred to the bivalved arthropod taxa *Isoxys*, *Canadaspis perfecta*, *Odaraia alata* and *Perspicaris dictynna*.

Results of the phylogenetic analysis and additional perturbation tests confirm the utility of these taxa for polarizing relationships within Euarthropoda and reducing long-branch artefacts. For example, the hexapods were recovered within a paraphyletic Crustacea, a result anticipated by molecular phylogenetic analyses but until now elusive in morphological phylogenies. Perturbation tests indicate that close affinities of myriapods and hexapods, a result common in morphological analyses, is the result of a long-branch artefact caused by the convergent adaptation to a terrestrial habit, which is broken by the addition of fossil material. The phylogeny provides a detailed picture of character acquisition in the arthropod stem group.

To my family

For their infinite patience and understanding.

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Institutional abbreviations

BGS	=	British Geological Survey, Keyworth, UK.
FMNH	=	Field Museum of Natural History, Chicago, USA.
NHM	=	Natural History Museum, London, UK.
NMNH	=	Smithsonian National Museum of Natural History, Washington D.C., USA.
OUMNH (SP)	=	Oxford University Museum of Natural History, Oxford, UK. [SP – indicates that examined specimens are available as SPIERS 'virtual reconstruction']
PMU	=	Palaeontological Museum of Uppsala University (Evolutionsmuseet), Uppsala, Sweden.
ROM	=	Royal Ontario Museum, Toronto, Canada.

1. Introduction

"There is something about writing on arthropod phylogeny that brings out the worst in people" – Hedgepeth *in* Schram, 1982:94.

1.1. General introduction

THE ARTHROPODS are a diverse, disparate, abundant and ubiquitous phylum (Figure 1.1). They outnumber all other phyla on Earth, both in terms of species, with over 1,214,295 described species (Zhang 2011b), and an estimated 10,000,000 yet to be described (Nielsen 2011, Basset *et al*. 2012), and biomass; the total biomass of Arctic krill alone has been estimated at around 500 million tonnes (Atkinson *et al*. 2009). They are found in all oceans and on all continents, from the depths of the Marianas Trench (Bartsch 2006), to the slopes of Mount Everest (Wanless 1975), and have colonised nearly every ecosystem including hot hydrothermal vents and subterranean caves, nearly 2000 m below sea level (Fabri *et al.* 2011, Jordana *et al*. 2012). They play a key role in many ecosystems as pollinators, decomposers, parasites, food sources, and disease vectors; mosquitoes are a common vector for over 15 human diseases including malaria, which kills over 1,000,000 people per year. Conversely Limulus amebocyte lysate, a coagulating agent extracted from the blue blood of horseshoe crabs is widely used in the pharmaceutical industry and it certainly saved numerous lives.

As well as dominating modern ecosystems, arthropods have been a key constituent of most habitats since their first appearance in the fossil record (Edgecombe and Legg 2013). The first unequivocal arthropod body fossils are bivalved arthropod carapaces from the Tommotian (lower Cambrian, c. 535 MYA), Hetang Formation of China (Braun *et al*. 2007), and potential arthropod trace fossils are known from immediately above the Neoproterozoic-Cambrian boundary (c. 542 MYA) of Estonia (Jensen and Mens 2001). The diversity of early arthropods is well documented by the abundant *Konservat-Lagerstätten* of the Cambrian Period, such as the lower Cambrian Chengjiang biota of China (Hou *et al*. 2004a), and the middle Cambrian Burgess Shale of Canada (Briggs *et al*. 1994). In these they represent over half of all recorded species, both in terms of species richness and overall abundance – and include a large variety of extinct body plans (Legg *et al*. 2012b, Edgecombe and Legg 2013).



Fig. 1.1 | The diversity of extant arthropods. A, the pycnogonid *Pycnogonum rickettsi* Schmitt 1934; **B**, the Monarch Butterfly *Danaus plexippus* (Linnaeus 1758); **C**, the Giant Centipede *Scolopendra gigantea* Linnaeus 1758; **D**, the American Horseshoe Crab *Limulus polyphemus* (Linnaeus 1758); **E**, the amblypygid *Damen* sp. (Koch 1850); **F**, the ostracod *Danielopolina* sp. (Kornicker and Sohn 1976); **G**, the Blue Bottle Fly *Calliphora vomitoria* (Linnaeus 1758); **H**, the Blue Crab *Callinectes sapidus* Rathbun 1896; **I**, the Common Wasp *Vespula vulgaris* (Linnaeus 1758); **J**, the European Tadpole Shrimp *Triops cancriformis* (Bosch 1801); the Gooseneck Barnacle *Pollicipes polymerus* (Sowerby 1883); **L**, the Peacock Mantis-Shrimp *Odontodactylus scyllarus* (Linnaeus 1758); and **M**, an unidentified symphylan.

Despite their riotous diversity, all extant arthropods possess a common suite of soft- and hard-part characteristics (Boudreaux 1979), the most prominent of which is the tough sclerotised exoskeleton composed primarily of chitin. This outer layer may have originally evolved to facilitate locomotion by providing a firm substrate for the attachment of muscles and by providing protection from the harsh external environment it may have also been an important exaptation for the colonisation of

new ecological niches (Labandiera and Beall 1990). The rigid nature of the exoskeleton impedes both growth and movement, thus accommodating mechanisms have evolved; arthropods grow via a series of incremental moult stages, wherein the older exoskeleton is shed (ecdysed), and replaced by a larger one. The exoskeleton is divided into distinct sclerotised plates (*sclerites*), separated by a soft arthrodial membrane. This arrangement is known as *arthrodization*, and allows for increased flexibility and movement of the main body axis. The segmentation of the appendages in this manner is known as *arthropodization* (from the Greek *arthros* meaning "jointed" and *podus*, "legs"), and is the namesake of the group (Siebold 1848). The grouping and specialisation of segments and appendages is known as *tagmosis* and is classically a primary criterion for recognising different groups of arthropods. At least five major groups of extant arthropods can be recognised, primarily based on their style of tagmosis (Figure 1.2). The composition and morphology of the five main extant groups of arthropods is outlined below. These subsections also contain a discussion of their monophyly and potential fossil representatives.

1.1.1. Pycnogonida

Pycnogonids, colloquially known as sea spiders due to their superficial resemblance to true spiders (Araneae; Fig. 1.1A), are an aberrant group of exclusively marine arthropods characterised by a wide suite of autapomorphies including an elongate anterior proboscis with a triradiate pharynx and a pair of modified egg-carrying limbs (ovigers), on the third cephalic segment (Fig. 1.2A). Although often treated as a "minor" clade of arthropods, current over 1300 species are recognised (Arango and Wheeler 2007). They have a cosmopolitan distribution in the world"s oceans, inhabiting all marine benthic environments, with most living in cryptic habitats (King 1973, Arnaud and Bamber 1987). The majority of pycnogonids are predatory, feeding predominantly on slow-moving or sessile soft-bodied animals such as cnidarians, sponges and molluscs (King 1973); juvenile instars of some taxa are parasitic (Staples and Watson 1987, Miyazaki 2002a).

As a consequence of their specialised morphology the monophyly of pycnogonids is little disputed, but deciphering their affinities has been an ongoing challenge (Dunlop and Arango 2004). Their body is broadly divided into two tagmata, an anterior limb-bearing cephalothorax or prosoma, and a diminutive posterior opisthosoma; this and the possession of chelate frontal appendages invite comparison with euchelicerates, although few other features support close affinities (Dunlop and Arango 2004). Unlike other arthropods their anterior tagma is not covered by an extensive cephalic shield (Waloszek and Dunlop 2002), and most organs have been reduced or incorporated into the appendages, with putative arthropod synapomorphies such as a labrum, nephridia and intersegmental tendons lacking (Edgecombe *et al*. 2000).

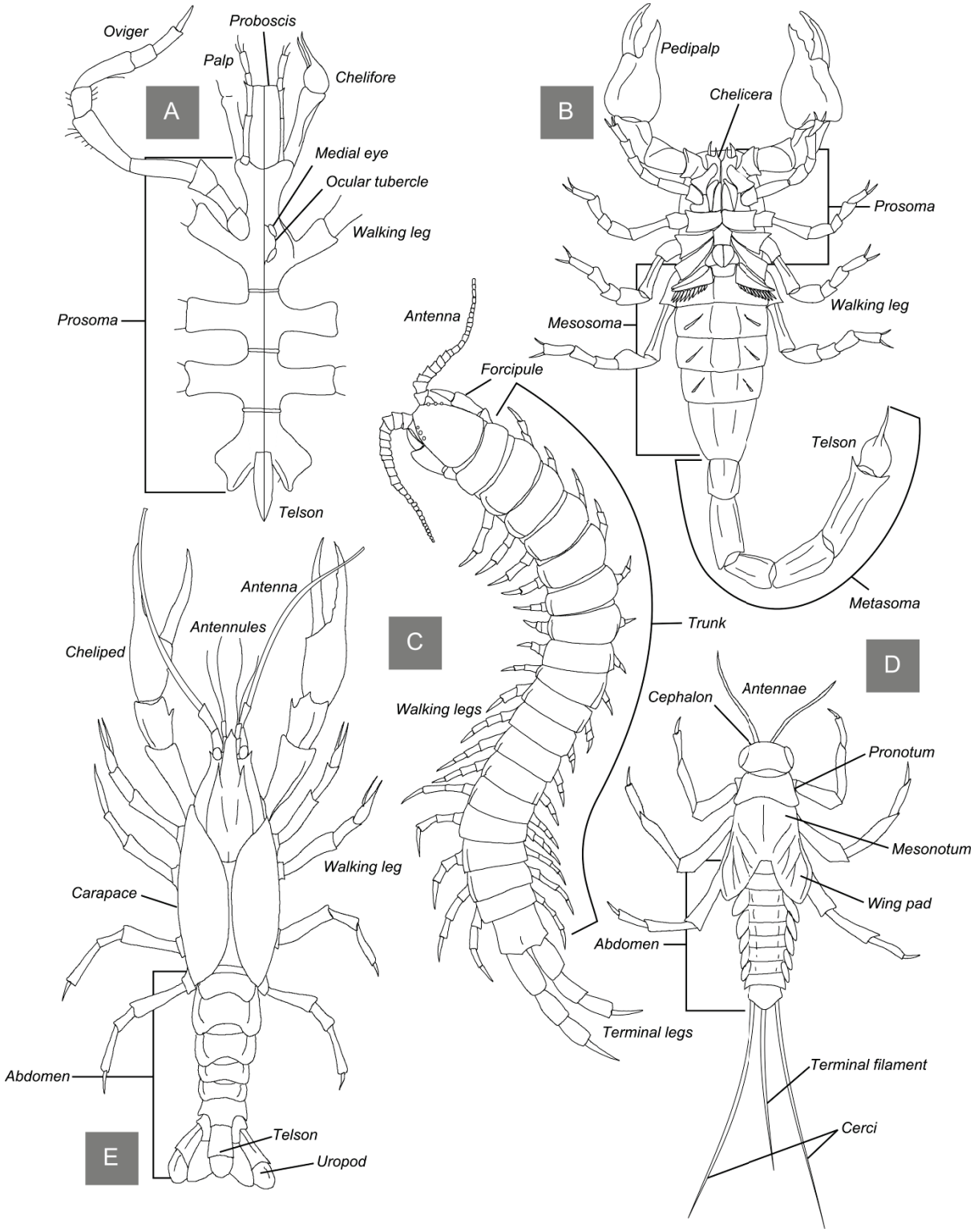


Fig. 1.2 | Basic arthropod body plans. Representatives of the five main groups of euarthropods demonstrating „typical" anatomical features. **A**, a partial reconstruction of the pycnogonid *Nymphon gracile* Leach 1814, with walking legs omitted (modified from King 1983, fig. 1a), ventral reconstruction on the left and dorsal reconstruction on the right; **B**, the Emperor Scorpion *Pandinus imperator* (Koch 1841); **C**, the Giant Centipede *Scolopendra gigantea* (Linnaeus 1758); **D**, a nymph of the mayfly *Baetis* sp. (Leach 1815); and **E**, the Common Lobster *Homarus gammarus* (Linnaeus 1758).

The pycnogonids have a sparse fossil record, with just eight named species reported from four Palaeozoic localities (Bergström *et al*. 1980, Kühl *et al*. 2013, Poschmann and Dunlop 2006, Siveter *et al*. 2004, Waloszek and Dunlop 2002, Rudkin *et al*. 2009, 2013), and a further three species reported from the Callovian (Lower Jurassic) of France (Charbonnier *et al*. 2007); the latter are almost certainly assignable to the crown-group and potentially even to extant families. The morphology of pycnogonids has remained remarkably conserved since their first documented appearance in the upper Cambrian (Waloszek and Dunlop 2002) however most Palaeozoic representatives possess a number of features, such as a telson and an elongate abdomen, which serve to distinguish them from crown-group representatives (Poschmann and Dunlop 2006). The exact affinities of these taxa remain equivocal (Arango and Wheeler 2007, Poschmann and Dunlop 2006, Siveter *et al*. 2004).

1.1.2. Euchelicerata

With over 111,937 described species, the euchelicerates represent one of the most species-rich clades on Earth today (Fig. 1.1D-E; Coddington *et al*. 2004, Zhang 2011b), second only to their primary food source, the hexapods. Like the pycnogonids, euchelicerates possess a differentiated anterior tagma, encompassing six pairs of appendages, the most anterior of which are chelate (Fig. 1.2B). Unlike pycnogonids however the anterior tagma, or prosoma, of euchelicerates is covered by an extensive dorsal cephalic shield. The posterior tagma, the opisthosoma, is subdivided into an anterior, usually respiratory, opercula-bearing mesosoma, and a posterior limb-less metasoma (Fig. 1.2B). The latter is often tipped with a highly modified telson, such as the aculeus of scorpions or the flagellum of palpigrades. Dunlop and Selden (1997) considered the presence of median eyes and/or a medial ocular tubercle a symplesiomorphic feature of Euchelicerata, but more recent work (Briggs *et al.* 2012, Lamsdell 2013) resolved taxa lacking these features, e.g. *Offacolus kingi* Orr *et al*. 2000, as the most basal euchelicerates.

Euchelicerate monophyly has been regarded as one of the least controversial issues in arthropod systematics (Dunlop 2005, Edgecombe 2010a). This clade is broadly split into two main groups: the marine xiphosurans, also referred to as „horseshoe crabs", and the predominantly terrestrial arachnids; the close affinities of the two groups were first recognised by Lankester (1881). The majority of extant euchelicerate diversity is attributed to the arachnids, with xiphosurans accounting for just four extant species (Shuster and Anderson 2004), although they have a diverse fossil record (Anderson and Shuster 2004, Lamsdell 2013). Dunlop (2010) recognised 16 orders of arachnids, four of which are now wholly extinct. Although arachnid monophyly is well established, their interordinal relationships remain equivocal (Shultz 2007), particularly with regards to the sister-taxon relationship of the scorpions (Dunlop and Braddy 2001). This controversy has been attributed to *a priori* assumptions of character importance (Wheeler and Hayashi 1998), with

neontologists favouring a sister-taxon relationship between scorpions and harvestmen (Shultz 1990, 2007) and palaeontologists advocating a close relationship with eurypterids (sea scorpions; Dunlop and Braddy 2001).

The euchelicerates have an extensive fossil record (Dunlop *et al*. 2008a) being particularly well represented in Westphalian (Upper Carboniferous) siderite nodules (Garwood *et al*. 2009, 2011, Legg *et al*. 2012a). The oldest euchelicerate body fossils are represented by undescribed „horseshoe crabs" from the Lower Ordovician (Tremadocian, 480 MYA) of Morocco (Van Roy *et al*. 2010). The oldest unequivocal euchelicerate trace fossils date from the latest Cambrian (Furongian, c. 501 MYA) of Texas and are attributed to chasmataspidids (Dunlop *et al*. 2004), a group that has been variously considered the sister-taxon of xiphosurans (Caster and Brooks 1956, Størmer 1972), the sister-taxon of eurypterids (Eldredge 1974, Legg *et al*. 2012b), or as sister-taxon to a eurypterid + arachnid clade (Dunlop and Selden 1997, Lamsdell 2013), formally designated Sclerophorata by Kamenz *et al*. (2011). The oldest arachnid is a mid Silurian (Llandovery, 436 MYA) scorpion, *Palaeophonus loudonensis* Laurie 1899 (Dunlop and Selden 2013), from the putative marine deposits of the Pentland Hills in Scotland (Anderson 2007). The ecology and phylogeny of the earliest scorpions is intimately linked to the issue of terrestrialisation, namely whether the arachnids colonised land once (Scholtz and Kamenz 2006), prior to the origination and diversification of the extant orders, or numerous times within different clades (Dunlop and Webster 1999). This issue remains to be resolved (Legg 2009), with many Palaeozoic scorpions previously thought to be aquatic now interpreted as terrestrial (Dunlop *et al*. 2008b, Kühl *et al*. 2012).

1.1.3. Myriapoda

The myriapods possess a relatively simple tagmosis consisting of a cephalic shield or head capsule, encompassing three or four pairs of differentiated appendages, and a long homonomous trunk with little or no limb specialisation apart from the fang-like forcipules of centipedes and the male gonopods of millipedes (Figs. 1.1C, M, 1.2C). Although perhaps most easily distinguished from other arthropods by their large number of trunk appendages, with some such as *Illacme plenipes* possessing as many as 750 pairs (Marek and Bond 2006), other groups more typically possess just eleven pairs (Scheller 2011, Szucsich and Scheller 2011), fewer than many other arthropod groups. Four distinct classes can be distinguished: Diplopoda (millipedes), Chilopoda (centipedes; Fig. 1.1C), pauropods and symphylans (Fig. 1.1M); however determining their interrelationships has been a contentious issue (Edgecombe 2011), with some even questioning the monophyly of Myriapoda.

The monophyly of myriapods has long been a contentious issue (Pocock 1893), with numerous studies considering them the paraphyletic outgroup to hexapods (Kraus 2001, Willmann 2003). Studies that resolved such topologies usually advocated absence characters in support of such relationships (Dohle 1980).

This is also true of neuroanatomical studies that have resolved myriapods as polyphyletic, with diplopods and chelicerates linked by the shared absence of a ml2 midline neuropil (Loesel *et al*. 2002, Strausfeld *et al*. 2006). Even molecular studies that have resolved myriapods as paraphyletic (e.g. Negrisolo *et al*. 2004, Gai *et al*. 2008) have retrieved strong support for myriapod monophyly when analysed using alternative methodologies (Reiger *et al*. 2008). Morphological characters supporting a monophyletic Myriapoda include the morphology of the "swinging tentorium" and its role in mandibular gnathal lobe abduction (Koch 2003); the arrangement of serotonin reactive neurons (Harzsch 2004); nuclear positioning in ommatidial eucones (Müller *et al*. 2007); structural similarities of the epidermal maxilla II-gland (Hilken *et al*. 2005); and the restriction of an *antennipedia* expression domain (Hughes and Kaufman 2002, Edgecombe 2004).

The nature of characters supporting myriapod affinities means that identifying potential fossil candidates for both the crown-group and stem-group has been particularly challenging (Edgecombe 2004). The oldest unequivocal myriapod fossils originate from the mid-late Silurian of Scotland and are readily assigned to crown-group Diplopoda (Wilson and Anderson 2004). Current phylogenetic hypotheses predict an early Cambrian origin for the myriapod stem-group, however no uncontroversial candidates have been identified to date (Edgecombe 2004), with potential candidates such as *Pseudoiulia cambriensis* Hou and Bergström 1998, more likely allied to other contemporaneous multi-segmented clades (*see* **Chapter 8**). The sparse nature of the myriapod fossil record may be due to their early terrestrialisation (Shear and Edgecombe 2010, Rota-Stabelli *et al*. 2013). All known extant myriapods are exclusively terrestrial, with many leaving in damp-leaf litter and humic habitats unsuited for fossil preservation. Currently trace fossil evidence indicates that terrestrialisation occurred by at least the Upper Ordovician, with subaerial *Diplichnites* and *Diplopodichnus* trackways attributed to a millipede-like arthropod (HW Wilson 2006) reported from the Borrowdale Volcanic Group in the English Lake District (Johnson *et al*. 1994).

1.1.4. Hexapoda

The hexapods are the dominated by the insects, and account for over 50 per cent of all described life on Earth (Grimaldi and Engel 2005). Despite their diversity, their morphology is remarkably conserved throughout the numerous flying and flightless orders (Fig. 1.1B, G, I); most hexapods have a body divided into three tagmata including an anterior cephalon bearing four differentiated appendage pairs and an intercalary segment, a posterior 10 or 11-segmented abdomen, and a three segmented thorax bearing the six pairs of appendages that provide the name of the clade (Fig. 1.2D). The vast majority of hexapods (98.5 per cent; Grimaldi 2010), also have wings on the thorax, and they were the first organisms to evolve powered flight, which they achieved by at least the Early Devonian (Engel and Grimaldi 2004). The monophyly of this clade is supported by the fusion of the second maxillae into a

labium, and the loss of mandibular palps (Klass and Kristensen 2001), although both features are also present in other arthropod groups, such a symphylans (Szucsich and Scheller 2011).

Despite the paucity of potential synapomorphies uniting hexapods (Klass and Kristensen 2001), their monophyly has rarely, if ever, been disputed on morphological grounds (Dohle 2001, Bitsch and Bitsch 2004, Grimaldi 2010). The only major challenge to hexapod monophyly came from mitochondrial evidence, which resolved springtails (Collembola) as sister-taxon to a paraphyletic assemblage of crustaceans containing a monophyletic Insecta (Nardi *et al*. 2003, Cook *et al*. 2005, Carapelli *et al*. 2005, 2007). A reanalysis of the Nardi *et al*. (2003) data set failed to retrieve hexapod polyphyly, instead finding weak support for a monophyletic Hexapoda with springtails as sister-taxon to insects (Delsuc *et al*. 2003). These studies were also criticised for excluding other basal flightless hexapod lineages, such as proturans (Meusemann *et al*. 2010), a deficiency shared by other molecular studies (e.g. Timmermans *et al*. 2008, Reiger *et al*. 2008, 2010). Hexapod monophyly was retrieved when these taxa were included in a large scale phylogenomic study including expressed sequence tags (ESTs; Meusemann *et al*. 2010).

Willmann (2002) estimated that over 25,000 species of fossil insect have been described, conceding that this was a very sparse fossil record considering the potential billion or more species that are likely to have lived throughout Earth‟s history. Molecular clock estimates indicate a possible Ordovician, or even latest Cambrian origin for crown-group hexapods (Rota-Stabelli *et al*. 2013), however, the first unequivocal fossil representatives, *Rhyniella praecursor* Hirst and Maulik 1926, and *Rhyniognatha hirsti* Tillyard 1928, are not found until the Early Devonian (Grimaldi 2010) in the Rynie Chert (c. 408 MYA) of Scotland. Both assignable to extant hexapod clades, *Rhyniella* possesses unequivocal collembolan features (Greenslade and Whalley 1986), and *Rhyniognatha* has dicondylic mandibles comparable to metapterygotans (Engel and Grimaldi 2004), a group that includes all winged insects except mayflies. *Leverhulmia mariae* Anderson and Trewin 2003, from the Windyfield Chert, the lateral equivalent of Rhynie Chert, was originally described as a myriapod (Anderson and Trewin 2003), however subsequent preparation of the type and only specimen revealed additional features indicative of stem-hexapod affinities (Fayers and Trewin 2005). Few other taxa have been advocated as potential stem-group hexapods. *Devonohexapodus bocksbergensis* Haas *et al*. 2003, from the Lower Devonian Hunsrück Slate, was originally considered a stem-group hexapod, with features of both myriapods and hexapods (Haas *et al*. 2003). A subsequent study (Willmann 2005) criticised the interpretation of supposed “hexapod features”, such as a three-segmented thorax, and later Kühl and Rust (2009) synonymised this genus with the more completely known *Wingertshellicus backesi* Briggs and Bartels 2001, concluding it represents a stem-group euarthropod and is therefore uninformative with regards to hexapod origins.

1.1.5. Crustacea

What the hexapods have in diversity, the crustaceans have in disparity (Fig. 1.1F, H, J-L). Crustaceans show a wide variety of body types and variations in tagmosis (Fig. 1.2E; Schram 1986), unfortunately this has made determining both their inter- and intrarelationships exceedingly difficult, with each new study proposing a different internal topology (Jenner 2010). The issue of crustacean paraphyly is no longer contentious and hexapods are now widely accepted as derived terrestrial crustaceans (see section 1.2.5. for discussion). The remaining crustaceans total approximately 67,000 described species (Zhang 2011b), divided into six major "classes" (Martin and Davis 2001). The long evolutionary history of these clades, which both molecular (Rota-Stabelli *et al*. 2013) and fossil evidence (Harvey *et al*. 2012) indicate diverged in the Cambrian, renders convincing synapomorphies of Crustacea extremely difficult to find (Schram and Koenemann 2004). Several characters have been suggested including the presence of a sternum resulting from the fusion of all post-oral cephalic sternites (Walossek and Müller 1998) and a proximal endite on the post-antennal limbs (Haug *et al*. 2010b); however Bitsch and Bitsch (2004) found only one consistent character supporting monophyly – the presence of second antennae - although the phylogenetic stability of this feature has also been queried (Schram and Koenemann 2004). Cladistic analyses of neuroanatomical characters such as optical neuropils and brain anatomy is congruent with molecular evidence for crustacean paraphyly with respect to hexapods (Strausfeld and Andrew 2011).

The crustaceans have a diverse fossil record, with approximately 2,600 genera reported from marine deposits (Sepkowski 2000). Unequivocal crustacean fossils are known from a number of Cambrian deposits and display a diversity of preservational styles. Fragmented masticatory apparatuses, preserved as carbonaceous cuticle, ("small carbonaceous fossils" or SCFs *sensu* Butterfield and Harvey 2012), are known from Middle to Late Cambrian mudstones of western Canada (Harvey *et al*. 2012), and a diverse phosphatised meiofauna, the so called "Orsten" fauna, has been reported from numerous sites across the globe including the benchmark locality in Sweden (Maas *et al*. 2006 and references therein), Australia (Maas *et al*. 2009) and China (Zhang *et al*. 2007). Surprisingly, unequivocal crustaceans are unknown from typical Burgess Shale-type (BST) deposits. Many bivalved arthropods, a common constituent of such deposits, have been allied to the crustaceans at some point (e.g. Briggs 1976, 1977, 1978, 1981, 1992, Wills *et al*. 1998), however this was often based on superficial resemblance and unreliable characters such as the presence of a bivalved carapace, a feature that has evolved many times amongst extant crustacean groups (Schram 1986), or the presence of multi-podomerous endopods (Hou 1999, Hou *et al*. 2004b, Fu and Zhang 2011), a feature also prevalent in stem-group arthropods (Legg 2013). Other purported Cambrian crustaceans, such as *Priscansemarinus barnetti* Collins and Rudkin 1981,

a supposed barnacle from the Burgess Shale, have almost certainly been misidentified and may not even be an arthropod (D. Rudkin pers, comm. 11/2010).

1.2. Euarthropod interrelationships

This section will deal primarily with the interrelationships of the euarthropods, or crown-group arthropods, defined herein as the least inclusive clade including: the most recent common ancestor of pycnogonids, euchelicerates, myriapods, hexapods and crustaceans (i.e. "the big five" listed above) and all its descendants (*cf*. Weygoldt 1986). The extant content of this clade has remained stable since its inception (Lankester 1904), except for the occasional doubtful exclusion of pentastomids (e.g. Moore 1959), which are now recognised as derived crustaceans (Lavrov *et al*. 2004).

The definition and composition of Arthropoda Siebold 1848, is far more unstable (Fig. 1.3). The original contents were comparable to Lankester‟s Euarthropoda, with the exception of the inclusion of the tardigrades (water bears), which were considered arachnids and closely allied to pycnogonids. Later works expanded Arthropoda to include onychophorans (velvet worms) but left the position of tardigrades uncertain with regards to other members (e.g. Lankester 1904, Moore 1959). This clade is now generally referred to as Panarthropoda Nielsen 1995, with the onychophorans and tardigrades resolving as respective outgroups of Euarthropoda (Campbell *et al*. 2011, Nielsen 2011); under this scheme Arthropoda and Euarthropoda are effectively synonymous, except when we consider the euarthropod stem-group, the contents of which is discussed in **Chapter 4**.

Despite the stable composition of Euarthropoda the interrelationships of its major constituent clades remains controversial (Figure 1.4); indeed Bäcker *et al*. (2008:186) referred to the current state of knowledge as "chaos", attributing this to divergent sources of data and unjustified assumptions of homology. The main hypotheses of relationships are discussed below.

1.2.1. Cormogonida versus Chelicerata

The aberrant morphology of the pycnogonids has made determining their affinities particularly troublesome. Their tendency towards reduction of body segments and organ systems has made comparisons with other groups difficult (see Arango and Wheeler 2007). Early workers often compared them to crustacean larvae or considered them aquatic arachnids (Dunlop and Arango 2005 and references therein), however recent cladistic analyses have generally favoured two alternative hypotheses: a sister-taxon relationship between pycnogonids and euchelicerates (the Chelicerata or Chelicerophora hypothesis); or a sister-taxon relationship between pycnogonids and all other euarthropods (the Cormogonida hypothesis; Zrvarý *et al*. 1998).

A. SIEBOLD (1848)

Hauptgruppe 3. VERMES (inc. *Peripatus*)
Hauptgruppe 5. ARTHROPODA
- Classis 13. **CRUSTACEA**
  - Ordo V. POECILOPODA (inc. *Limulus*)
  - Ordo XI. **MYRIAPODA**
- Classis 14. ARACHNIDA
  - Ordo I. [unnamed]
    - Subordo 1. TARDIGRADA
    - Subordo 2. **PYCNOGONIDA**
  - Ordo II-IV (= **EUCHELICERATA** *in partim*)
- Classis 15. INSECTA (= **HEXAPODA**)

B. LANKESTER (1904)

Subphylum ARTHROPODA
- Grade A. HYPARTHROPODA
- Grade B. PROTOARTHROPODA
  - Class ONYCHOPHORA
- Grade C. EUARTHROPODA
  - Class 1. DIPLOPODA (= **MYRIAPODA** *in partim*)
  - Class 2. ARACHNIDA
    - Grade *a*. Anomomeristica (= TRILOBITA)
    - Grade *b*. Nomomeristica (= CHELICERATA)
      - (*a*) Pantopoda (= **PYCNOGONIDA**)
      - (*b*) Euarachnida (= **EUCHELICERATA**)
  - Class 3. **CRUSTACEA**
  - Class 4. CHILOPODA (= **MYRIAPODA** *in partim*)
  - Class 5. **HEXAPODA**

Incertae sedis: TARDIGRADA and PENTASTOMIDA

C. CURRENT VIEW

[unnamed rank] PANARTHROPODA
- Phylum TARDIGRADA
- [unnamed rank] ANTENNOPODA
  - Phylum ONYCHOPHORA
  - Phylum ARTHROPODA (= EUARTHROPODA)
    - Subphylum **PYCNOGONIDA**
    - Subphylum **EUCHELICERATA**
    - Subphylum **MYRIAPODA**
    - [unnamed rank] TETRACONATA
      - Subphylum **HEXAPODA**
      - Subphylum '**CRUSTACEA**'

Fig. 1.3 | Changing views on the composition of Arthropoda. A, The erection of Arthropoda by Siebold (1848). Note the horseshoe crab *Limulus* (pictured in figure 1.1D) was considered a crustacean at the time and the onychophoran *Peripatus* was placed with worm-like taxa (Vermes). The Tardigrades were considered the sister-taxon of pycnogonids. **B**, Lankester (1904) expanded his Arthropoda to include onychophorans but considered the position of tardigrades uncertain. Hyparthropoda was erected to encompass the hypothetical annelid-like ancestor of other arthropods. **C**, the current view of arthropod phylogeny (based primarily on Nielsen 2012).

The Chelicerata hypothesis was first expressed cladistically by Ax (1984). This relationship was supported by three synapomorphies: the presence of chelate chelicerae, the loss of antennae, and the division of the body into a prosoma and opisthosoma. Both the euchelicerate chelicerae and antennae of mandibulates arthropods (see section 1.2.3) innervate from the deutocerebral neuromere of the brain (Damen *et al*. 1998, Telford and Thomas 1998); meaning that if the chelifores of pycnogonids and the chelicerae of euchelicerates are homologous to the antennae of mandibulates then the presence of either chelicerae or antennae essentially represent alternative states of the same character. There has even been

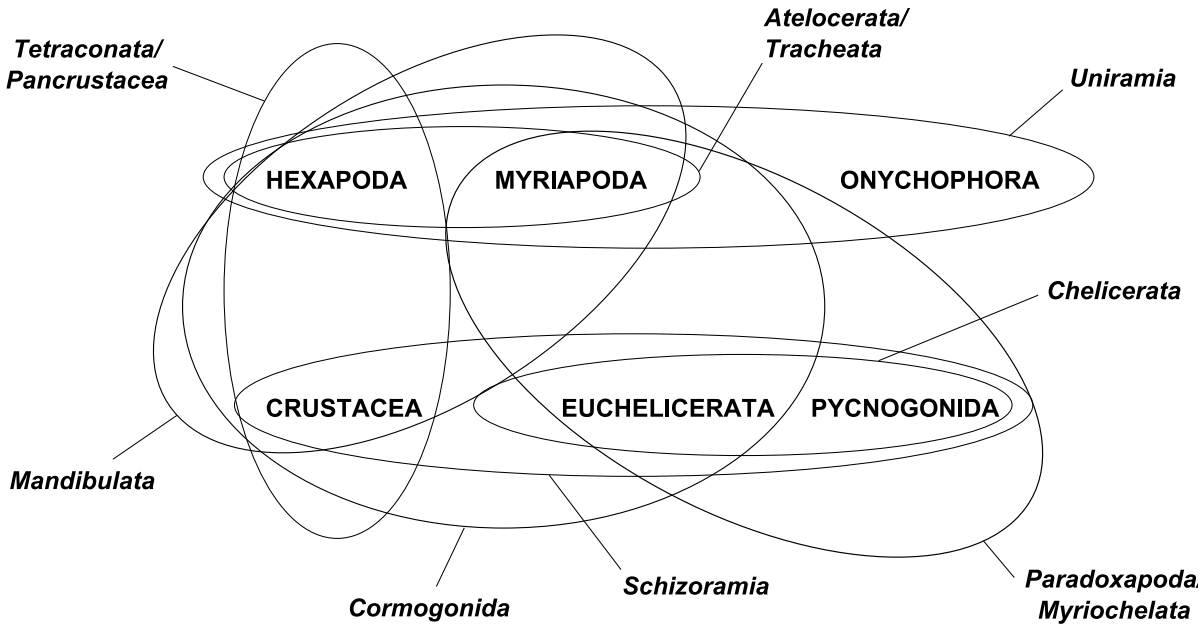


Fig. 1.4 | A Venn-diagram depicting the "chaos" of arthropod interrelationships. Modified from Bäcker *et al*. (2008, fig. 1) to include pycnogonids.

some debate regarding the homology of these appendages; a neuroanatomical study by Maxmen *et al*. (2005) considered the chelifores to innervate from the protocerebrum, although later neuroanatomical studies (Brenneis *et al*. 2008) and *Hox* gene expression indicate they are actually deutocerebral (Jager *et al*. 2006). Other studies have cast doubt on the segmental homology of the prosoma and opisthosoma of euchelicerates and pycnogonids (Vilpoux and Waloszek 2003, Manuel *et al*. 2006).

The alternative (Cormogonida) hypothesis is largely based on absence characters; specifically the absence of "typical" euarthropod characters (*sensu* Boudreaux 1979) such as the labrum, nephridia and intersegmental tendons. Subsequent studies have identified potentially homologous structure in pycnogonids such as excretory openings at the base of the chelifores (Fahrenbach and Arango 2007) and lobes on the developing proboscis which may correspond to the labral Anlage of other arthropods (Winter 1980, Scholtz and Edgecombe 2006, although see Macher and Scholtz 2010). The presence of a terminal mouth and a Y-shaped pharynx may be plesiomorphic features of pycnogonids shared with other panarthropods (Miyazaki 2002b) and thus potentially support the Cormogonida hypothesis.

Molecular analyses have been equivocal regarding pycnogonid affinities, with both Cormogonida (Zrvarý *et al*. 1998, Giribet *et al*. 2001) and Chelicerata (Giribet *et al*. 2005) finding support. Chelicerate affinities are also supported by EST data (Dunn *et al*. 2008) and nuclear coding genes (Reiger *et al*. 2010), although in the latter study a result including Cormogonida was only marginally less optimal.

Phylogenetic analyses including fossil data have generally resolved a monophyletic Chelicerata with the megacheirans, “great-appendage” arthropods, resolving either as sister-taxon or as their paraphyletic ancestor (Cotton and Braddy 2004, Chen *et al*. 2004, Dunlop 2005, Edgecombe *et al*. 2011). These studies have often rooted on putative mandibulate taxa however, such as marrellomorphs or trilobitomorphs, and would therefore inadvertently resolve a monophyletic Chelicerata. Increased sampling of the stem-group instead resolved megacheirans as the paraphyletic stem of Euarthropoda (Budd 2002, Daley *et al*. 2009).

1.2.2. Paradoxapoda (Myriochelata)

The onset of molecular phylogenetics in the mid 1990s had some unexpected outcomes not anticipated by morphological evidence. Notably, a sister-taxon relationship between chelicerates and myriapods was considered so surprising the resultant clade was named Paradoxapoda Mallatt *et al*. 2004 (alternatively Myriochelata Pisani *et al*. 2004). This grouping was first obtained in analyses of nuclear ribosomal 18S rRNA (Friedrich and Tautz 1995, Giribet *et al*. 1996) and later from a combination of 18S and 28S rRNA subunits (Mallet *et al*. 2004, Petrov and Vladychenskaya 2005, von Reumont *et al*. 2009), Hox gene sequences (Cook *et al*. 2001), hemocyanin sequences (Kusche and Burmester 2001), mitochondrial genomics (Hwang *et al*. 2001, Pisani *et al*. 2004, Hassanin 2006) and EST data (Dunn *et al*. 2008). However reanalyses of these data sets has not always recovered this grouping. Hemocyanin sequence studies that have resolved Paradoxapoda (e.g. Kusche and Burmester 2001) instead favour Mandibulata (Myriapoda + Hexapoda + Crustacea) when additional taxa were included (Kusche *et al*. 2003). When fast-evolving genes were excluded from analyses, Mandibulata was recovered (Regier *et al*. 2008). Likewise Rota-Stabelli and Telford (2008) emphasised the importance of outgroup choice in determining myriapod affinities (see also Rota-Stabelli *et al*. 2011). A monophyletic Mandibulata (rather than Paradoxopoda) has also been recovered using nuclear ribosomal genes (Giribet and Ribera 1998), nuclear protein-coding genes (Reiger *et al*. 2008, 2010), a combined data set of nuclear ribosomal, protein coding genes and mitochondrial genomics (Bourlat *et al*. 2008), and EST data (Campbell *et al*. 2011).

The repeated retrieval of Paradoxapoda in molecular studies stimulated the search for potential morphological synapomorphies. A number of studies have described potential neurogenetic characters (Dove and Stollewerk 2003, Kadner and Stollewerk 2004, Stollewerk and Chipman 2006, McGregor *et al*. 2008), although without outgroup comparisons the possibility remained that these features are symplesiomorphic for Euarthropoda. Mayer and Whitington (2009) emphasised similar patterns of neurogenesis in onychophorans and Tetraconata (Hexapoda + Crustacea), indicating the pattern observed in Paradoxapoda is potentially synapomorphic. These characters were subsequently employed in morphological cladistic analyses (e.g. Rota-Stabelli *et al*. 2011) but failed to resolve Paradoxapoda.

1.2.3. Mandibulata

Prior to the advent of molecular phylogenetics in the 1990s the myriapods were traditionally allied with hexapods and crustaceans, united by the possession of gnathobasic jaws, the mandibles, on the first post-tritocerebral somite. The homology of this feature across mandibulate groups is well established, on both morphological grounds (Wägele 1993, Bitsch 2001, Edgecombe *et al*. 2003) and gene expression patterns (Prpic and Tautz 2003), with some features recognized as potentially honologous for a long time (Crampton 1921, Snodgrass 1938, 1950). Rejection of mandibular homology featured prominently in mid 20th century arguments for arthropod polyphyly, with Manton (1964) rejecting the gnathobasic origins of myriapod and hexapod mandibles and instead suggested that the biting edge was formed by the tip of a whole limb; this theory was later refuted by studies of myriapod mandibular muscles (Lauterbach 1972, Bourdeaux 1979, Weygoldt 1979). Further gene expression studies have since demonstrated the gnathobasic nature of the mandibles of myriapods (Scholtz *et al*. 1998) and hexapods (Panganiban *et al*. 1995, Niwa *et al*. 1997, Popadiç *et al*. 1996, 1998, Scholtz *et al*. 1998, Prpic *et al*. 2001).

Other potential synapomorphies of Mandibulata include the specialisation of the first pair of post-mandibular appendages into maxillae (Edgecombe 2004), the presence of a crystalline cone in the ommatidium (Richter 2002, Müller *et al*. 2003, 2007), size differentiation in the somata supplying cerebral neuropils, the retention of a midline neuropil in the protocerebral matrix, a deutocerebrum containing olfactory lobes (Strausfeld *et al*. 2006), tritocerebral innovations of the stomatogastric and labral nerves (Scholtz and Edgecombe 2006), the development of paragnathal Anlagen and their role in the formation of a „chewing chamber" (Wolff and Scholtz 2006), and a fixed number of serotonergic neurons in the nerve cord (Harzsch 2004, Harzsch *et al*. 2005).

Despite the prevalence of morphological data supporting close affinities between mandibulate arthropods, results from molecular analyses have remained equivocal particularly with regards to the affinities of myriapods (see above: section 1.2.3.). It is possible that potential synapomorphies of Mandibulata actually represent symplesiomorphic characteristics of Euarthropoda which were subsequently lost or modified in chelicerates (Mayer and Whitington 2009). The large number of changes required makes this hypothesis unlikely, or at least unparsimonious.

The mandibulates have a rich fossil record, particularly from so called „Orsten" deposits (Edgecombe and Legg 2013). These fossils have rarely been treated in the context of Mandibulata, instead being placed on the eucrustacean (crown-group crustacean) stem-lineage (e.g. Haug *et al*. 2010b), Many of the features identified as eucrustacean synapomorphies in these studies, e.g. paragnathal Anlagen (Walossek and Müller 1998), are actually widespread amongst mandibulates (Wolff and Scholtz 2006). Under the hypotheses of Haug *et al*. (2010b), the phosphatocopids, a group of phosphatised Cambrian bivalved arthropods, were considered the plesion of eucrustaceans, a group with which they share paragnaths and a fleshy labrum

(Maas *et al*. 2003). However the lack of a true mandible in phosphatocopids may indicate a position outside of Mandibulata.

1.2.4. Tetraconata (Pancrustacea)

Close affinities between crustaceans and hexapods have long been deduced from on ocular morphology (Grenacher 1879, Parker 1891, Hesse 1901) and neurological evidence (Hanström 1926) although a close link between these groups was generally dismissed in favour of the Atelocerata hypotheses (see below). The clade name Tetraconata Dohle 2001 (= Pancrustacea Zrvarý and Štys 1997), refers to the shared presence of four crystalline cones in the ommatidia. Additional shared ophthalmic characteristics include variability in the number of accessory pigment cells surrounding the ommatidium (Paulus 1979, 2000), cone cell process arrangement (Melzer *et al*. 1997, Dohle 2001), cell recruitment patterns in ommatidial development (Hafner and Tokarski 1998, Melzer *et al*. 2000), and the mode of growth of visual surfaces, the so called “morphological front type” (*sensu* Harzsch and Hafner 2006). Shared neurological characteristics include the morphology of the optic neuropils and chiasmata (Harzsch 2002, Strausfeld 2005), similarities in protocerebral construction (Loesel *et al*. 2002), the arrangement of serotonergic neurons in the thoracic hemiganglion (Harzsch 2004), the role of neuroectoderm in epidermal and neural cell generation (Stollewerk and Chipman 2006) and the expression of identical markers by pioneer neurons (Ungerer and Scholtz 2008). Whether these characters represent synapomorphies of Tetraconata as a whole or a more exclusive clade within it depends on the position of Hexapoda in relation to other crustacean subgroups.

Although molecular phylogenies consistently recover close affinities of hexapods and crustaceans, determining the sister-taxon relationship of hexapods has been an ongoing endeavour (Jenner 2010). Generally studies that have resolved hexapods as sister-taxon to a monophyletic Crustacea have had a limited taxon sampling, being too depauperate to adequately test crustacean paraphyly (e.g. Friedrich and Tautz 1995). Sequence-based analyses and nuclear ribosomal gene studies have tended to ally hexapods with copepods or branchiopods (Mallet *et al*. 2004, Babbett and Patel 2005, Regier *et al*. 2005, Mallatt and Giribet 2006, Dunn *et al*. 2008, Timmermans *et al*. 2008, von Reumont *et al*. 2009), although some studies recovering similar topologies have not sampled cephalocarids and/or remipedes (Roeding *et al*. 2009, Meuesemann *et al*. 2010, Campbell *et al*. 2011, Rota-Stabelli *et al*. 2011). Cephalocarids and remipedes are collectively known as xenocarids (*sensu* Regier *et al*. 2010) and tend to resolve as sister-taxon to hexapods in studies including nuclear coding genes (Giribet *et al*. 2001, Reiger *et al*. 2008, 2010). In these studies branchiopods tended to resolve close to malacostracans, although malacostracans group with hexapods based on neurological characters (Strausfeld 2009, Strausfeld and Andrews 2011). Similar topologies were also recovered using EST data (Meuesemann *et al*. 2010, Andrew 2011), and the first EST study to

include remipedes resolved them as sister-taxon to Hexapoda (von Reumont *et al*. 2012). Additional support for this grouping comes from haemocyanin structure (Ertas *et al*. 2009), ovarian morphology (Kubrakiewicz *et al*. 2012) and was recently recovered in a study combining molecular and morphological data (Oakley *et al*. 2013).

1.2.5. Atelocerata (Tracheata) and Schizoramia

Two oppositional clades have been proposed based exclusively on morphological evidence: a grouping of uniramous arthropods, the Atelocerata, and their antipode, the Schizoramia, a clade containing arthropods which symplesiomorphically possess biramous appendages. These clades have rarely been given consideration in recent analyses, although prior to the proliferation of molecular studies a sister-taxon relationship between myriapods and hexapods, as Atelocerata or Tracheata, was considered one of the most stable relationships in arthropod phylogenetics (Snodgrass 1938, 1950, 1951, Hennig 1969, 1981, Manton 1977, Boudreaux 1979, Kristensen 1991, Wheeler *et al*. 1993). Some more recent studies have continued to uphold Atelocerata, but these are either based on singular character systems (Bäcker *et al*. 2008) or inadequate character sampling (Wills *et al*. 1998, Bitsch and Bitsch 2004). Many of the features supporting monophyly of this clade, such as Malpighian tubules, a limbless intercalary segment, uniramous appendages and respiratory tracheae, are arguably convergent adaptations to a terrestrial habit (Harzsch 2006, Garwood and Edgecombe 2011). The expression pattern of the *Drosophila collier* gene in the intercalary segment of the chilopod *Lithobius* (Janssen *et al*. 2011) may indicate a conserved genetic mechanism rather than a putative synapomorphy of Atelocerata (Giribet and Edgecombe 2013).

The grouping of biramous arthropods under the Schizoramia concept is intimately linked to palaeontological data (Edgecombe 1998). The original content of this group was just trilobites and chelicerates (Bergström 1976, 1979) and was later expanded to include crustaceans (Bergström 1992, Hou and Bergström 1997), making it equivalent to the TCC (= trilobite, chelicerate, crustacean) group of earlier workers (Tiegs 1947, Cisne 1974). The majority of extant chelicerates actually possess uniramous appendages and their placement in Schizoramia is due to an inferred plesiomorphic condition based on supposed homology of the xiphosuran flabellum and book-gills with the exopods of trilobites and crustaceans. This is potentially refuted by gene expression data (Damen *et al*. 2002) and clonal analysis of crustacean appendages (Wolff and Scholtz 2008) which may indicate the outer rami of chelicerates represent exites rather than exopods, which are restricted to crown-group crustaceans.

1.2.6. Resolution

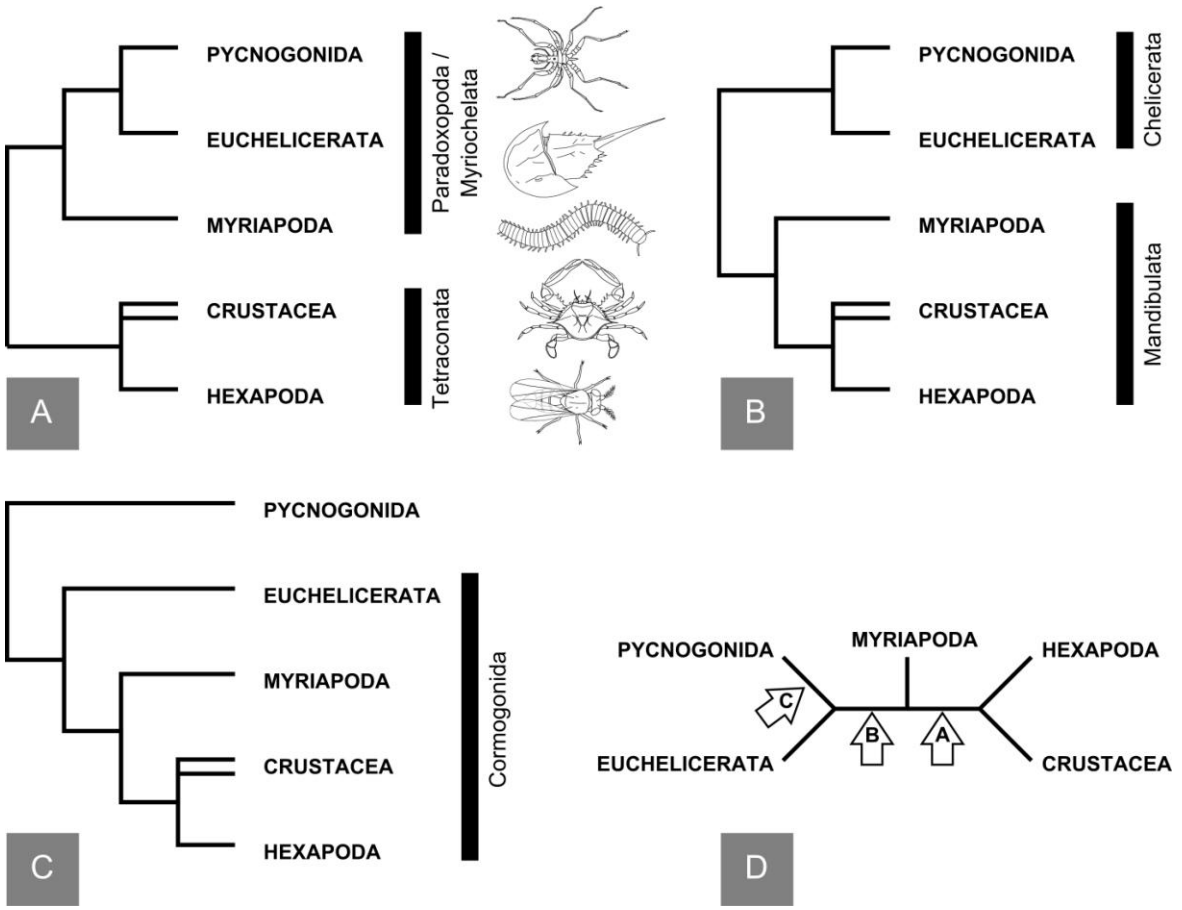


Fig. 1.5 | Arthropod phylogeny – a rooting issue. A summary of current hypothese of arthropod relationships. Note the overall topology does nt change but the position of the root does. **A**, the Paradoxapoda (Myriochelata) hypothesis with myriapods as sister-taxon to Chelicerata; **B**, the Chelicerata/Mandibulata hypothesis with a clade composed of euchelicerates and pycnogonids (= Chelicerata) as sister-taxon to mandible-bearing arthropods (= Mandibulata); **C**, the Cormogonida hypothesis with pycnogonids as sister-taxon to all other euarthropods (= Cormogonida); and **D**, arthropod phylogeny expressed as an unrooted network. Arrows represent different rooting points and the hypotheses they support.

Contrary to Bäcker *et al.*"s (2008) contention, arthropod phylogenetics is not chaotic. Although various lines of evidence seemingly support different sister-taxon relationships, overall topologies remain relatively stable and our current view of arthropod relationships can be visualised as an unrooted network (Figure 1.5; Giribet *et al*. 2005, Caravas and Friedrich 2010, Giribet and Edgecombe 2012, 2013). The deep divergence times of extant arthropod clades, which recent molecular clock evidence suggests lie in the latest Neoproterozoic or earliest Cambrian (Rota-Stabelli *et al.* 2013), increases the likelihood of long-branch attraction effects in phylogenetic analyses of extant taxa, both in morphological (Gauthier *et al*. 1988) and molecular studies (Rota-Stabelli and Telford 2008). Fossils have been empirically shown to mitigate long-branch attraction effects in phylogenies of extant taxa (Gauthier *et al*. 1998, Edgecombe 2010b), however to date few analyses

combining extinct and extant arthropods have been undertaken (see **Chapter 2** for details), and recent advances in arthropod biology have yet to be incorporated into rigorous phylogenetic analyses.

1.3. Thesis aims and structure

The aim of this thesis is to determine the impact of fossil data on large scale morphological phylogenies of arthropods. There are eleven chapters in this thesis. The following chapter is a literature review detailing the utility of fossils in phylogenetic analyses and provides an overview of previous works incorporating fossil data in phylogenetic analyses of arthropods. **Chapter 3** contains details of the phylogenetic methodology utilized in this study. **Chapter 4** introduces stem-group arthropods and demonstrates their utility in rooting the arthropod tree of life. **Chapters 5** to **8** contains descriptions of new fossil data, particularly from Cambrian *Konservat-Lagerstätten*. **Chapters 9**-**11** contain results, discussion of findings and overall conclusion, respectively. A complete list of included taxa, along with data sources, and phylogenetic characters are described in the appendices.

2. Fossils *in* arthropod phylogeny

"The mere fact that some species happen to be contemporaries of man does not make them phylogenetically more interesting" – Bergström, 1979:3-4.

2.1. Introduction

Although the inclusion of fossil data seems like a logical solution to the problem of determining deep-splits in arthropod interrelationships, some workers have dismissed their importance, instead treating fossils as unnecessary data to be included in analyses *a posteriori* (Nelson 1987, Ax 1987, Patterson 1981). This sentiment was particularly rife during the 1970s and 80s with the advent and proliferation of both cladistic and molecular phylogenetic techniques (*see* Patterson 1981 *and references therein*). Prior to this, evolution was generally regarded as a historical event and as such fossil data were integral to its understanding (Simpson 1961, Bergström 1979, 1980, 1992, Patterson 1981). Opponents of this philosophy argued that fossils must be a poor source of data, as the interpretation of their biology relies on comparisons to extant organisms (Kitts 1974), and criticised speculation resulting from the incompleteness of fossil data (Hennig 1965, 1966, 1969, 1981). 'Missing-data' still appear to be the primary criticism of the use of fossils in phylogenetic analyses, with numerous studies still excluding fossils *a priori* due to their incompleteness. This chapter reviews the philosophical and empirical implications of including highly-incomplete taxa in phylogenetic analyses, and discusses the reasons why the inclusion of fossil data in phylogenetic analyses is actually highly desirable.

2.2. A 'missing-data' problem

Hennig's (1965, 1966, 1969, 1981) rationale for excluding fossils from phylogenetic analyses, i.e. that their incompleteness made determining relationships speculative, asserted that because fossil taxa were so incomplete it was not possible to make reliable homology statements, thus rendering the determination of relationships speculative at best. The underlying assumption here is that determining homology among extant taxa is an objective undertaking with little inherent speculation or error. This is obviously not the case, and even among extant taxa there is considerable disagreement about what constitutes a homologous structure. Edgecombe (2010b) provided an example from the arthropods whereby the femur-tibia joint in hexapods could not be homologised across Arthropoda due to the uncertainty regarding the correspondence of podomeres in other arthropod groups. Should a similar joint be found on the appendages of another arthropod group, e.g. chelicerates, then due to the additional uncertainties regarding homologies we would necessarily have to code the presence of this structure as uncertain in the latter taxa. Gauthier *et al*. (1988) noted a similar problem when coding the monotremes (the duck-billed platypus and echidnas) into his phylogeny of amniotes. These aberrant taxa have undergone such extensive modification of their skeletons that identifying the original identity of particular elements, thus enabling them to be homologised with elements in other mammals, is nearly impossible. In both cases the uncertain homologies would be coded as missing data. This would be an example of uncertainty coding, whereby all (or at least more than one) character coding is theoretically possible.

Missing data can also arise from inapplicable characters. The identity of a character may be dependent on the coding of another character. For example, in a blind taxon any characters pertaining to the morphology of the eyes would be treated as inapplicable. This is different from uncertainty coding as neither character state can possibly exist.

More recent discussions regarding the impact of missing data on phylogenetic hypotheses have focussed on the computational implications (Kearney and Clark 2003). It is a widely held assumption that increasing the amount of missing data in phylogenetic analyses will result in the production of more trees and increase computational time (Nixon and Wheeler 1992, Novacek 1992). This is based on the misconception that an increased number of trees implies phylogenetic instability, thereby weakening conclusions that can be drawn from the data. Kearney and Clark (2003) reanalysed a number of phylogenetic data sets with varying percentages of missing data and found no correlation between the amount of missing data and the number of optimal trees. This study also showed that in some instances the inclusion of fossil data can increase the stability of topologies produced using extant taxa alone, a result also found in simulations by Wiens (2005). A similar study was undertaken by Cobbett *et al*. (2007), who demonstrated using first-order jackknifing that there was little difference in the behaviour of extinct and extant terminals within phylogenetic analyses.

Taxa with very labile placement in phylogenetic analyses are often referred to as Wildcard taxa (Nixon and Wheeler 1992, Wilkinson 2003). This labile placement results from an inability to decide between equally parsimonious tree topologies. Although often linked to missing data (Nixon and Wheeler 1992), this phenomenon is not limited to incomplete taxa and is a function of character conflicts rather than taxon completeness (Kearney and Clark 2003). Wildcard taxa can be easily identified and removed using agreement subtree methods, thereby revealing underlying topologies.

These studies demonstrate empirically that there is no missing data problem, however, many workers insist on *a priori* exclusion of incomplete taxa. This may inadvertently create a different type of missing data problem, which, to distinguish it from the former, is herein termed the 'excluded data problem'. That is, by excluding taxa with a lot of uncertain character codings, character combinations are removed which might resolve conflicts among more complete exemplars.

If 99 per cent of all life that has ever existed is now extinct (Nee and May 1997) then any analysis based solely on extant taxa will already be excluding a considerable diversity of organisms before undertaking secondary taxon selection. Depending on the group this may mean ignoring over 500 million years of evolution, during which ancestral characteristics have almost certainly been overprinted. This concept highlights the real importance of fossils when it comes to determine evolutionary relationships, that is, as samples of extinct and intermediate morphologies with unique combinations of character states.

2.3. Fossils as examples of intermediate morphologies

Fossils are important first and foremost as representatives of extinct morphologies. Without them we could only infer potential ancestral states of extant clades. For instance, whilst we might be able to predict the basic arthropod body plan based on extant arthropods and onychophorans, I doubt we could ever envision anything quite as fanciful as the stem-arthropod *Opabinia* (Fig. 2.1). In this regard we see the real potential of fossils. They provide samples of morphology close to the divergence points of major clades. They may thus demonstrate primitive morphologies that have otherwise been lost in extant members. In this way fossils may offer advantages over extant taxa when determining relationships among deep diverging nodes (Edgecombe 2010b).

Gauthier *et al.*'s (1988) study of amniote phylogeny was able to demonstrate the importance of intermediate morphologies, present in fossil taxa, for overturning hypotheses of relationships based on extant taxa alone. When the extant taxa were analysed separately, mammals resolved as sister-taxon to the archosaurs, a group containing crocodiles and birds, within a paraphyetic assemblage of extant reptiles. However, when fossils were added to the analyses the mammals resolved outside of Reptilia, with the lepidosaurs (snakes and lizards) instead resolving as sister-taxon

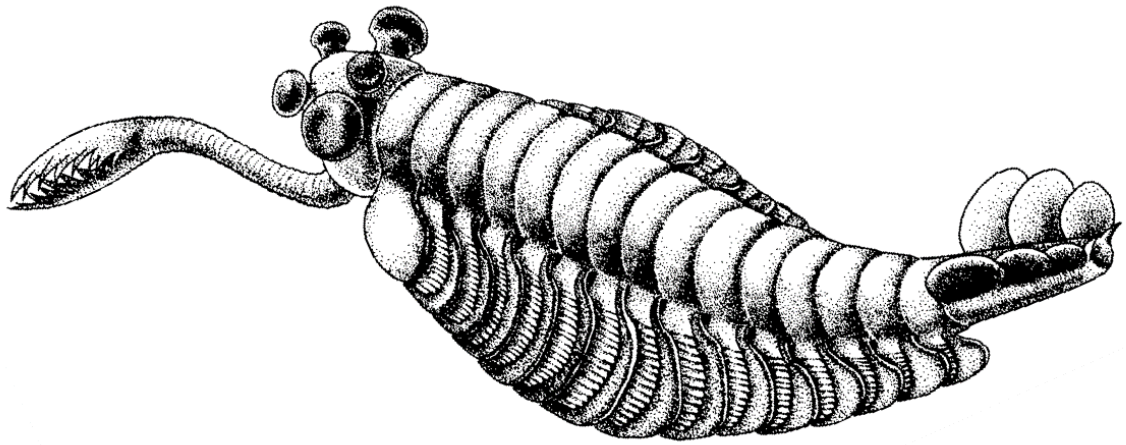


Fig. 2.1 | Reconstruction of the aberrant stem-arthropod *Opabinia regalis* Walcott, 1911a. Drawn by Marianne Collins © 2011.

to the archosaurs. The important taxa in these analyses were the wholly extinct mammal-like reptiles (synapsids). These taxa resolved as the paraphyletic stem group of mammals and demonstrated the convergent acquisition of characters linking mammals and archosaurs. This study was one of the first to empirically demonstrate the importance of fossils for identifying convergence among extant clades and also provided a clear example of fossils overturning hypotheses of relationships based on extant taxa alone. Patterson (1981) considered this possibility to be rare, if not nonexistent.

2.4. Previous work – fossils in arthropod phylogeny

This section is details the role fossil taxa have played on our understanding of arthropod interrelationships, the advances in our understanding of their morphology, and methodological techniques that have prompted new hypotheses regarding their relationships.

Fossil taxa were afforded little significance in early discussion of arthropod relationships, often just treated as another branch on the tree of life (e.g. Haeckel 1866, 1896) or 'shoehorned' into existing groups (e.g. Walcott 1912). The eurypterids and trilobites were notable exceptions to this rule however, discussed in particular with regard to the affinities of *Limulus* (e.g. Woodward 1872). In his pioneering monograph on the affinities of *Limulus*, Lankester (1881) provided detailed arguments for allying this genus with arachnids, essentially proposing the formation of what would be later known as Euchelicerata. A close relationship between xiphosurans and eurypterids had previously been recognised (Dohrn 1871, Owen 1873), although these taxa were regarded as crustaceans at the time (Siebold 1848). Key characters supporting this placement were the aquatic mode of respiration and the possession of compound eyes. Lankester (1881) dismissed these

characters as convergent adaptations to a similar mode of life, he also listed an extensive set of characters shared by xiphosurans, eurypterids and arachnids, particularly emphasising similarities between eurypterids and scorpions. In this way the eurypterid body plan served as an intermediate morphology between that of xiphosurans and arachnids. This study provides one of the earlier examples of fossils overturning hypotheses of relationships regarding extant taxa and led to the establishment of one of the most stable clades in modern arthropod systematic, the Euchelicerata.

Many of the early studies that recognised close affinities of xiphosurans and eurypterids also emphasised similarities between *Limulus* and trilobites (e.g. Dohrn 1871). Key characters included the morphology of the dorsal cephalic shield, the presence of trilobation and similarities between juvenile trilobites and the so-called 'trilobite-larva' of xiphosurans (Fig. 2.2; Packard 1872). Close affinities of trilobites and xiphosurans were generally accepted prior to the discovery of trilobite appendages (Walcott 1881), however, the discovery of antennae in *Triathrus eatoni* (Hall 1838) from the Ordovician of New York (Beecher 1893), prompted some to reassign trilobites to the Crustacea (Walcott 1894, Bernard 1894, Carpenter 1903).

Others maintained chelicerate affinities for trilobites, with Lankester (1904) adding the fusion of the posterior tagma as an additional character supporting this relationship, and Fedotov (1924) discussing similarities in tagmosis, limb morphology and cuticular architecture. Størmer (1933, 1939, 1942, 1944) in extensive reviews of arthropod relationships emphasised differences between crustaceans and trilobites, particularly focussing on absent characteristics such as a lack of trilobation, a styliform telson or extensive intestinal diverticulae, in crustaceans. He also argued that the outer rami of the biramous limbs of crustaceans and trilobites originated from different podomeres, with the crustacean exopod arising from the basis, and the 'pre-epipodite' of trilobites arising from a segment proximal to the coxa (Fig. 2.3; Størmer 1939).

Størmer was criticised for dismissing crustacean affinities in his studies (Heegaard 1945, Linder 1945, Tiegs 1947, Vandel 1949), with some arguing that the two hypotheses, i.e. crustacean vs. chelicerate affinities for trilobites, were not mutually exclusive (Raymond 1920, 1935, Tiegs 1947). Around this time many studies had argued for a polyphyletic origin of Arthropoda (Tiegs 1947, Tiegs and Manton 1958, Manton 1969, 1972). The latter authors considered the main arthropod lineages to have evolved independently from separate polychaete-like ancestors. The isolation of Crustacea by Størmer was used as support for a polyphyletic origin of arthropods (Manton 1963, 1964, 1969). In response to this Cisne (1974), and Hessler and Newman (1975) deduced that Arthropoda could not possibly be polyphyletic, and were at most diphyletic, as, in their opinion, trilobites represent the 'primitive' arthropod condition and were ancestral to both chelicerates and crustaceans. Hessler and Newman (1975) reasoned that the primitive morphology of Crustacea resembled a trilobite, whilst continuing to follow Størmer's arguments for chelicerate-trilobite affinities. Bergström (1979, 1980) expanded upon this idea and

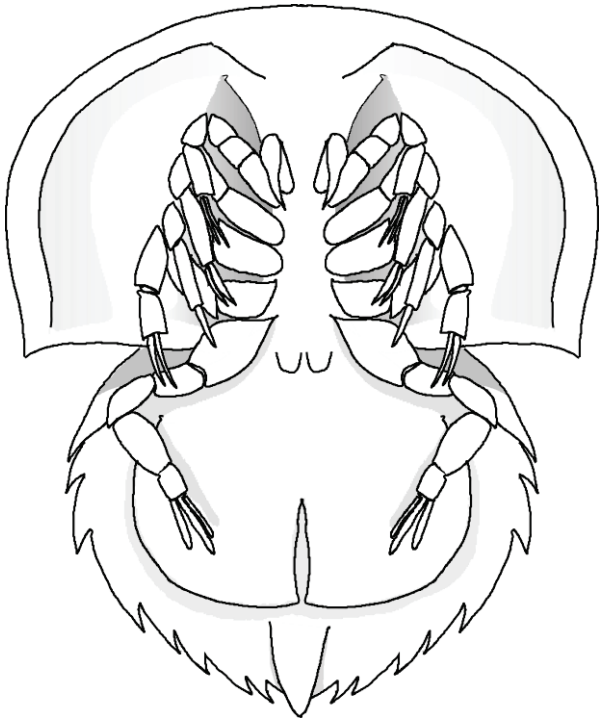


Fig. 2.2 | Reconstruction of the 'trilobite-larva' of the horseshoe crab *Limulus polyphemus* (Linnaeus 1758). Redrawn from Shuster and Sekiguchi (2003, Fig. 5.2).

argued fervently for the importance of fossils in determining interrelationships; he also proposed the name Schizoramia (Bergström 1976) for a clade including trilobites and chelicerates, and later expanded the concept to include all biramous arthropods (Bergström 1992; see section 1.2.5).

Many of the arguments in favour of arthropod polyphyly relied on structural differences, i.e. these structure are too different to have a common origin, however with the conception and adoption of phylogenetic systematics in the 1960s and 70s (Hennig 1965, 1966, 1969, Jeffries 1979), workers began to appreciate the importance of shared derived similarities in determining relationships. This methodology replaced more intuitive methodologies, and prompted a search for potential synapomorphies of proposed arthropod clades (e.g. Lauterbach 1980, 1983). Many of the concepts proposed by Hennig (1965, 1966) were first applied to fossil arthropods by Walossek and Müller (1990). The relationships of fossil taxa could be determined via construction of a hypothetical ground pattern for extant clades (Walossek and Müller 1998). Fossils were then used as means to construct scenarios for the evolution of selected features and trees were constructed by hand. In their view (Walossek and Müller 1998) this approach conformed to more strictly to Hennigian principles which served to explain evolutionary change and was therefore superior to numerical cladistic methodologies, which were considered phenetic rather phylogenetic (*see also* Haug *et al*. 2012c). This methodology however, places undue importance on selected morphological characters, relies on the construction of *ad hoc* and *a priori* scenarios of character evolution, and it fails to account for all implied character transformations (i.e., reversals and losses).. For instance, in order for their model of 'great-appendage' evolution to work, Haug *et al*. (2012a, c) postulated the existence of two additional podomeres in the appendages of

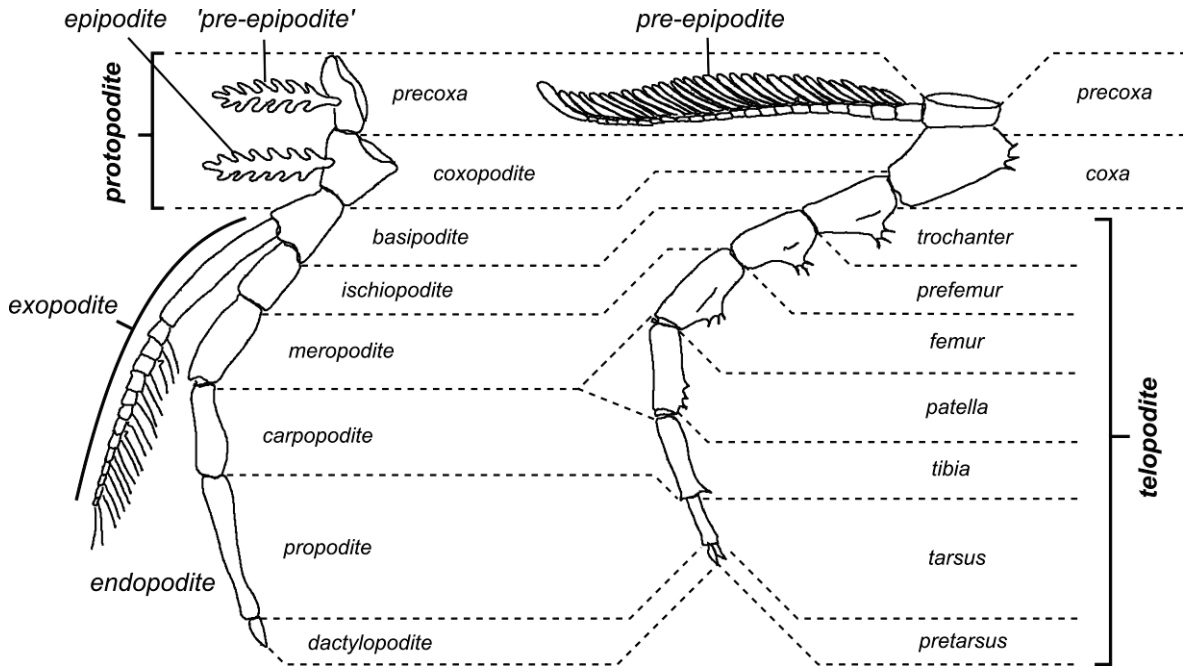


Fig. 2.3 | Hypothetical homology of crustacean and trilobite limb elements. Modified from Størmer (1944, fig. 22).

anomalocaridids, an *ad hoc* inference that is not supported by fossil evidence (Daley *et al*. 2009, Daley and Budd 2010).

The question of arthropod poly- or diphyly remained until the advent of computer-based cladistics in the early 1990s (Briggs and Fortey 1989, 1992, Briggs 1990, Briggs *et al*. 1992, Wills *et al*. 1995, 1998). This work was, in part, prompted by a wealth of new information emerging from lower Palaeozoic *Konservat-Lagerstätten*, particularly the Middle Cambrian Burgess Shale (Briggs *et al*. 1994), and the Upper Cambrian 'Orsten' fauna (Walossek and Müller 1998). Gould (1989) had previously emphasised the high levels of disparity among early arthropods and emphasised their uniqueness, and coined the term 'weird wonder'. The analyses of Briggs (1990, Briggs and Fortey 1989, 1992), however, demonstrated that anatomical novelties in Cambrian did not prevent them from being understood in a phylogenetic framework. Perhaps the most significant finding of these early analyses was the paraphyly of crustaceans with regard to chelicerates and trilobites. However, these early analyses had flaws from a modern perspective. For example,,trees were rooted using the Burgess Shale taxon *Marrella*, assumed to be primitive as it has a low number of head segments; this view has not stood up to scrutiny (Siveter *et al*. 2007a).

Although the issue of arthropod polyphyly was addressed, the exclusion of uniramous arthropods (onychophorans, myriapods and hexapods) from the early numerical cladistic analyses meant that polyphyly could not be fully tested. Later analyses (Briggs *et al*. 1992, Wills *et al*. 1995, 1998) included a much larger range of taxa, including uniramous arthropods and more extant crustaceans. These trees were also rooted on non-arthropod taxa such as the lobopodian *Aysheaia* (Briggs *et*

al. 1992) or representative annelids and molluscs (Wills *et al*. 1995, 1998). In these analyses, Crustacea resolved as sister-taxon to a monophyletic group containing chelicerates, trilobites and a number of Cambrian 'arachnomorphs'. They also resolved a monophyletic Arthropoda, although there was a fundamental divide between uniramous and biramous arthropods. Both of those groups were overturned in later phylogenetic analyses that included a small sample of fossils amidst a larger set of extant arthropods (Edgecombe 2010b; Rota-Stabelli *et al*. 2011). Instead, uniramous arthropods were resolved with myriapods as sister group to crustaceans and hexapods, according to the Mandibulata and Tetraconata hypotheses (see sections 1.2.3 and 1.2.4, respectively), The main difference from the earlier analyses was the inclusion of new characters, mostly from ultrastructure, that support the monophyly of Tetraconata, and the correction of erroneous character codings for 'Uniramia', e.g., a supposed difference between gnathobasic and 'whole limb' mandibles (refuted by Scholtz *et al.* 1998).

Others have argued that cladistics using parsimony is not an adequate means for determining relationships among extinct and extant arthropods (Delle Cave and Simonetta 1991, Simonetta 1999, 2004). In particular, some (Bergström and Hou 2003, Simonetta 2004) considered convergent and parallel evolution to be so prevalent amongst extant arthropods that identifying homologous structure is impossible. The tracheae of terrestrial arthropods were given as an example of convergent adaptations to a similar habitat; the implication being that a cladistic analysis including these structures would assume they were homologous. This demonstrates a fundamental misunderstanding of parsimony-based phylogenetic analyses – the purpose of which is to test hypotheses of homology via congruence with other characters (Farris 1983). Simonetta (2004) also failed to recognise the pivotal role fossils play in identifying homologous structures. Analyses that have rejected cladistics have also produced very unorthodox hypotheses of relationships, rarely supported by other lines of evidence, such as molecular phylogenetics. A notable exception is the study by Bousfield (1995) which utilized an intuitive, non-quantitative approach to resolving arthropod relationships. Many of the groupings he proposed are consistent with more recent cladistic analyses.

More recent studies have emphasised a 'total evidence' approach including data from morphological and molecular sources, some of them using a combination of extinct and extant taxa (Wheeler *et al*. 1993, 2004, Edgecombe *et al*. 2000, Giribet *et al*. 2001, 2005, Rota-Stabelli *et al*. 2011). This later stage of study was brought about by advances in genetic studies, such as the utilisation of microRNAs (Sperling and Peterson 2009), new gene expression data (Damen *et al*. 1998), developmental data (Liu *et al*. 2010), and new fossil data from lower Palaeozoic Lagerstätten, such as the Silurian Herefordshire Lagerstätte (Siveter 2008). This has led to a better understanding of structural and molecular homologies among arthropod clades (Richter *et al*. 2013) and provided us with a better framework for understanding arthropod interrelationships.

2.5. Summary

Reservations regarding the inclusion of fossil data in phylogenetic analyses are both empirically and philosophically unfounded, particularly when studying deeply divergent nodes. In such instances fossils can be invaluable for demonstrating extinct morphologies that serve to link clades that might have otherwise possessed shared characteristics overprinted by subsequent evolution. Despite early advocacy of the use of fossils in arthropod phylogeny, recent analyses have only included a limited sample of fossil taxa and, critically, many recently described fossil species and new ideas about character homologies revealed by fossils have not been included in the analyses. In order to understand the divergence of the five main extant arthropod clades, which diverged more than 500 million years ago, the inclusion of fossil data is integral.

3. Phylogenetic methods

"Nothing in biology makes any sense except in the light of evolution" – Dobzhansky, 1973:127.

"Nothing in evolution makes sense without a phylogeny" – Gould *and* MacFadden, 2004:219.

3.1. Introduction

In order to explore the potential significance that fossils have for our understanding of arthropod phylogeny, an extensive dataset of extinct and extant exemplars was coded into a large-scale cladistic analysis. The details of the included taxa are given in **chapter 4**. The aim of the current chapter is to give details and justification of the methodologies included in this study. A brief discussion of alternative methodologies not employed here will also be given. Section 3.5.2.1. was published in part in Legg *et al*. (2012b, suppl.) and Legg and Caron (in press).

3.2. A justification for parsimony analysis

A number of models have been proposed for inferring evolutionary relationships, i.e. phylogenies. The most commonly used for discrete character matrices, such as the one utilised in this study, is maximum parsimony. Parsimony is a non-parametric statistical method based on Occam's principles; it considers the preferred phylogenetic result to be the one requiring the fewest character changes, i.e. least assumptions of evolution (Kluge and Farris 1969, Farris 1970, Fitch 1971). Farris (1983) equated parsimony with explanatory power, considering other models to rely more heavily on speculative reasoning and *ad hoc* assumptions about evolutionary mechanisms. In this way parsimony follows general Hennigian principles, which, although conceived prior to the advent of computational cladistics, equate with non-

explicit *general parsimony* (*see* section 3.5.2). These Hennigian principles follow three basic rules: (1) *the grouping rule*; (2) *the inclusion/exclusion rule*; and (3) *the homoplasy rule* (Wiley and Lieberman 2011).

The grouping rules posits that character states deduced as synapomorphies, i.e. shared derived characteristics, are the only evidence of unique common ancestry (Hennig 1966). In computational cladistics the apomorphic character state is usually determined with reference to an apparent outgroup (*see* section 3.3.1).

Under the inclusion/exclusion rule, congruent information from divergent sources, i.e. additional synapomorphies, are combined into a single hypothesis of relationship, thereby providing stronger support for the inclusion and/or exclusion groups based on other (conflicting) potential synapomorphies. In other words, the best supported topology is that based on the greatest number of independent lines of evidence. If, however, potential evidence supports divergent topologies then the homoplasy rule applies; this states that if two or more characters imply different relationships then at least one of the character states must be homoplastic, thereby producing a false topology. The identification of the offending character state often relies on congruence with other character states and is therefore intimately associated with the inclusion/exclusion rule. The formulation of these rules represented an empirical leap forward in determining evolutionary relationships, which was until then based on an intuitive approach in which particular character states were afforded more significance than others with little justification. These rules also represent one of the greatest strengths of parsimony, whereby convergent characters, which may be informative with regards to the relationships of particular taxa, may be identified and used to produce tree topologies, albeit with reference to other, non-homoplastic, characters (Källersjö *et al*. 1999).

Other researchers have argued that probabilistic approaches to phylogenetics, e.g. maximum likelihood and Bayesian inference, are superior to parsimony-based approaches (e.g. Huelsenbeck and Hillis 1993, Huelsenbeck 1995, Swofford *et al*. 2001, Felsenstein 2004, Huelsenbeck *et al*. 2001, Lee and Worthy 2012). These methods differ from parsimony in assigning each branch of the tree a 'length', which is calculated based on an assumed rate of evolution under a specified model. Each character change is then compared to this proposed length to determine its probability of change. A gamma distribution is applied to account for variations in rates of character change (Yang 1996), ensuring a homogenous rate of evolution and consistent branch lengths. This length is optimized in maximum likelihood methodologies, whereas in Bayesian analyses it is changed during a Monte Carlo Markov Chain (Lewis 2001). For morphological data, both methods assume a Markov (Mk) model of a homogenous evolutionary rate (Lewis 2001). A homogenous rate of evolution throughout geological history seems unlikely especially given observations of modern organisms (Chang 1996, Gingerich 2009). In simulations incorporating heterogeneous character changes parsimony has been shown to perform better than probabilistic approaches (Kolaczkowski and Thornton 2004, Goloboff and Pol 2005, Simmons *et al*. 2006), especially when there is abundant missing data in the dataset (Goloboff and Pol 2005, Lemmon *et al.* 2009,

Simmons 2011, 2012). For these reasons the current data set was analysed under maximum parsimony.

3.3. Taxon selection

A total of 311 taxa were used in this study, 96 of which are extant and 215 extinct (**Appendix 1**). Although it has been argued that a smaller data set is sufficient for addressing specific problems in phylogeny (e.g. Vermeij 1999, Carpenter 2001), such an approach does not allow for a clear identification of apomorphies, and thus provides undue support for clades based on characters that might otherwise resolve as plesiomorphic or convergent in larger analyses (Zwickl and Hillis 2002).

Extant exemplars were selected to provide broad taxonomic coverage and included a diverse range of morphologies from the five major arthropod groups (*see* section 1.1.1); including three pycnogonids, 21 euchelicerates, 13 myriapods, 13 hexapods, and 40 crustaceans. For ease of comparison between morphological and molecular analyses, extant taxa that have been included in large-scale molecular studies (e.g. Regier *et al*. 2010) were preferentially selected, using the same species where possible.

No *a priori* exclusion of fossil taxa, based on percentage of missing data, was undertaken (*see* section 2.2 for a justification of this approach). In fact, no taxon in the data set could be reliably coded for all characters, and even the most incomplete taxon, *Furca bohemica* Fritsch 1908, whose fossil record comprises just isolated cephalic shields (Rak *et al*. in press), could nonetheless be coded for over ten percent of characters. Preference was given to taxa thought to lie outside of the five extant crown-groups (*see* **Chapter 4** for a detailed discussion), although fossil taxa referable to extant groups, e.g. the Carboniferous scorpion *Compsoscorpius buthiformis* (Pocock 1911), were also included to provide a clearer picture of character polarity within extant clades (Gauthier *et al*. 1988).

3.3.1. Outgroup selection

In order to determine character polarity within the group of interest, i.e., the operational ingroup, Euarthropoda, outgroup criteria were utilised (Maddison *et al*. 1984, Nixon and Carpenter 1993). This method relies upon the comparison of ingroup taxa with other taxa, extinct or extant, thought to lie outside of the ingroup, i.e. outgroups (de Jong 1980, Ax 1987, Nixon and Carpenter 1993). Character states shared between the outgroup and ingroup taxa are then assumed to represent the primitive condition (plesiomorphic state) of the ingroup clade (Watrous and Wheeler 1981). Outgroups should ideally display sufficient characters to enable comparison with ingroup taxa, yet display others that indicate a position outside of the operational outgroup (Gauthier *et al*. 1988). The uncertain relationships of many fossil arthropods make outgroup selection problematic for Euarthropoda. For

example, the 'great-appendage' arthropods have variously resolved as either stem-chelicerates, stem-euchelicerates, or stem-euarthropods (*see* section 4.6); using them to polarise relationships within Euarthropoda could therefore lead to unreliable topologies. For this reason a wide selection of non-arthropod outgroups were utilised in this study. This included dinocaridids (section 4.3), lobopodians (section 4.2), and the extant onychophorans and tardigrades (section 4.1), although even relationships amongst these taxa are uncertain (**Chapter 4**). For this reason the non-panarthropod ecdysozoans *Caenorhabditis elegans* Maupas 1900, and *Priapulus caudatus* Lamarck 1816, were used as prime outgroups (*sensu* Barriel and Tassy 1998).

3.4. Character choice

A total of 753 phylogenetic characters were utilised in this study (**Appendix 2**); the majority of these characters (702 characters) pertain to variations in morphology, with additional characters from development (29 characters), behaviour (6 characters) and gene order and gene expression (16 characters).

The aim of any character based study, such as this one, is to accurately identify those structures thought to diagnose relationships (Kitching *et al*. 1998). Character states represent assumptions of homology however, because of convergent evolution, similar structures may evolve numerous times. This led some workers (e.g. Delle Cave and Simonetta 1991, Simonetta 1999, 2004, Haug *et al*. 2012c) to reject parsimony as a means for determining relationships, instead favour the more Hennigian philosophy that relationships should be based on well-studied characters whose homology can be little disputed. This ignores one of the greatest strengths of parsimony analysis, that is, the ability to distinguish between *„primary"* and *„secondary" homology* (de Pinna 1991), i.e. those characters that pass an initial test of morphological similarity (*primary homologies*) and those that pass a test of character congruence under rigorous cladistic analysis (*secondary homologies*).

Characters were generally based on comparative anatomy, i.e. those features seemingly shared by two or more taxa, regardless of inferred relationship. All character states were coded as discrete variables, and include both binary, e.g. absence (0) / presence (1), and multi-state formulations. To avoid inappropriate character linkage, multi-state characters were generally avoided and instead contingent characters were employed (Forey and Kitching 2000). Although continuous characters can be incorporated into discrete character matrices using certain phylogenetic programs (Goloboff *et al*. 2006), e.g. TNT (*see* section 3.5.1), none were used in this study.

3.5. Phylogenetic methodology

3.5.1. Phylogenetic software

The phylogenetic matrix was converted to NEXUS file format (Maddison *et al*. 1997) and analysed using the program TNT v.1.1. (Tree analysis using New Technology; Goloboff *et al*. 2008b). Although a large number of programs have been created which can analyze data sets using parsimony, e.g. Hennig86 (Farris 1988, 1989a), PAUP* (Swofford 2003), PHYLIP (Felsenstein 2007), and NONA (Goloboff 1999a), only TNT is sufficient for analyzing large (100 + taxa) data sets (Goloboff 1999b, Goloboff *et al*. 2009), such as the one in this study. The graphic user interface version of TNT was used, although commands for the command line version are also provided in the text below using the following format: (**<< *command* >>**).

3.5.2. Character settings

Characters can be optimized according to different models of parsimony. The most commonly used are Fitch parsimony (Fitch 1971) and Wagner optimization (Farris 1970). Under Fitch parsimony all character state transformations are treated as unordered with no additional cost between multi-state character transformations, i.e. under equal character weighting a change from state zero to one, or a change from zero to two, both count as a single character transformation. In contrast, under Wagner optimization multi-state characters are treated as ordered such that a change from zero to two would be treated as two character transformations, from zero to one to two. Most phylogenetic programs, TNT included, allow the use of both kinds of character optimization, i.e. some multi-state characters may be ordered and others not. This is referred to as '*general*" *parsimony* (Swofford and Olsen 1990).

Other, more uncommon, forms of character optimization include Camin-Sokal parsimony (Camin and Sokal 1965) and Dollo parsimony (Farris 1977). Both are implemented on rooted trees only. Camin and Sokal (1965) considered evolution irreversible so under their model character state reversals were not allowed. Dollo parsimony allows reversals, but only under the establishment of an initial apomorphic state; therefore under this model secondary character loss is considered more likely that convergence through parallel evolution.

Although earlier versions of the analysed data set were analysed using general parsimony, whereby some multi-state characters were ordered (e.g. Rota-Stabelli *et al*. 2011), Fitch optimization was used in the current study to avoid *a priori* assumptions of character transformation.

3.5.2.1. Character weighting

Character weighting is arguably one of the most important aspects of any character based phylogenetic analysis, second only to the initial choice of characters and character states. Character weighting is fundamental to any phylogenetic analysis as a character with no weight will have no effect on a tree's topology. Most, if not all,

phylogenetic programs weight all characters equally, by default; equally weighted characters are often erroneously described as unweighted (e.g. Wood and Lonergan 2008). Equal weighting, however, is only appropriate in an ideal analysis that includes no homoplastic characters. A complete lack of homoplastic characters rarely, if ever, occurs as convergence appears to be the rule rather than the exception in evolution (Sanderson and Hufford 1996). Differential character weighting was employed in this study for that reason.

Most methods of character weighting apply *ad hoc* assumptions of character importance either *a priori* or *a posteriori*. This seems illogical and liable to lead to circular reasoning, as under these schemes levels of homoplasy are determined with reference to a branching pattern which, in turn, is determined by the character state distribution. For instance, in successive weighting, characters are weighted *a posteriori* according to their fit, which in turn is determined by distribution on a tree topology. Changing the character weight may affect tree topology however, and result in longer trees.

Implied weighting (**<< *piwe* >>**) has been proposed as a method to overcome the logical impasse imposed by either *a priori* or *a posteriori* character weighting methods (Goloboff 1993). With this method, characters are weighted during analyses, and the resultant trees are compared to determine maximum total character fit, with individual character fits defined as a function of homoplasy (Fig. 3.1). Using this technique, the most-parsimonious trees will be those that maximize character informativeness, i.e., they are not necessarily the shortest trees but those that imply the highest sum of implied weights for all characters. This means that unlike other methods of differential character weighting, e.g. successive approximations weighting, this method is self-consistent, i.e. it will only produce trees that are shorter under the weights they imply. Conversely, other weighting options may inadvertently produce longer trees than those produced using weighting options, e.g., equal weighting, i.e., they are not self-consistent.

Character fit can be adjusted using a concavity constant (*k*). In TNT the default concavity constant is 3 (**<< *piwe* = *3***), which defines a near linear decreasing function (Fig. 3.1). Under this parameter, character fit will decrease proportionately with increased homoplasy. Goloboff (1993) argued that a more concave decreasing function (k = > 3) was more reliable as it would resolve relationships in favour of those with less homoplasy, whereas a more convex decreasing function (k = < 3) would resolve in favour of more homoplasy but increase character usage; this may explain why other phylogenetic programs, e.g. PAUP* v. 4.0b10 (Swofford 2003) use a default concavity constant of 2. In the present study concavity constants of 2, 3 and 10 were used to determine what effect, if any, weighting against homoplasy had on the final topology.

3.5.3. Searching tree space

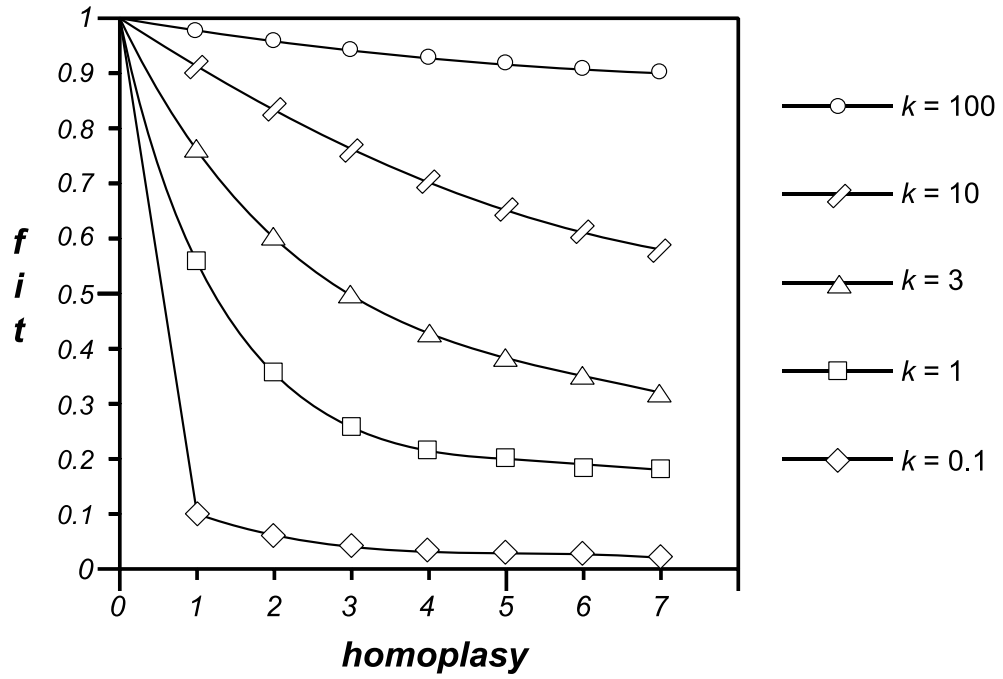


Fig. 3.1 | The hyperbolic weighting function for different values of *k*. The hyperbolic weighting function is defined as *k / (k + homoplasy)*. Redrawn from De Laet (1997, fig. 3.3).

The potential results of any phylogenetic analysis can be visualised as a three-dimensional landscape, or tree space (Fig. 3.2). The surface of this landscape represents every possible combination of character states and taxa. The topology of this landscape represents potential tree length, with optimal trees represented by peaks, as measured using tree length or character fit, and the troughs representing less parsimonious trees. The lowest potential point in any analysis is one in which all characters are maximally homoplastic. A number of algorithms have been devised for exploring tree space.

3.5.3.1. Implicit enumeration

Ideally we would perform an exhaustive search (implicit enumeration) (**<< *ienum* >>**) of all tree space (Fig. 3.3), as this is the only method guaranteed to find the most optimal trees. However, computational time increases exponentially with the addition of taxa and characters (Felsenstein 1978). For a cladogram of n – 1 taxa, there are $2n$ – 5 possible positions for the n^{th} taxon. This means that for six taxa there are 105 potential trees, for 20 taxa there are 2×10^{20} potential trees and for 63 taxa there are 10^{100} potential trees (Kitching *et al.* 1998). Implicit enumeration is therefore only feasible for data sets with fewer than 25 taxa.

3.5.3.2. Traditional searches

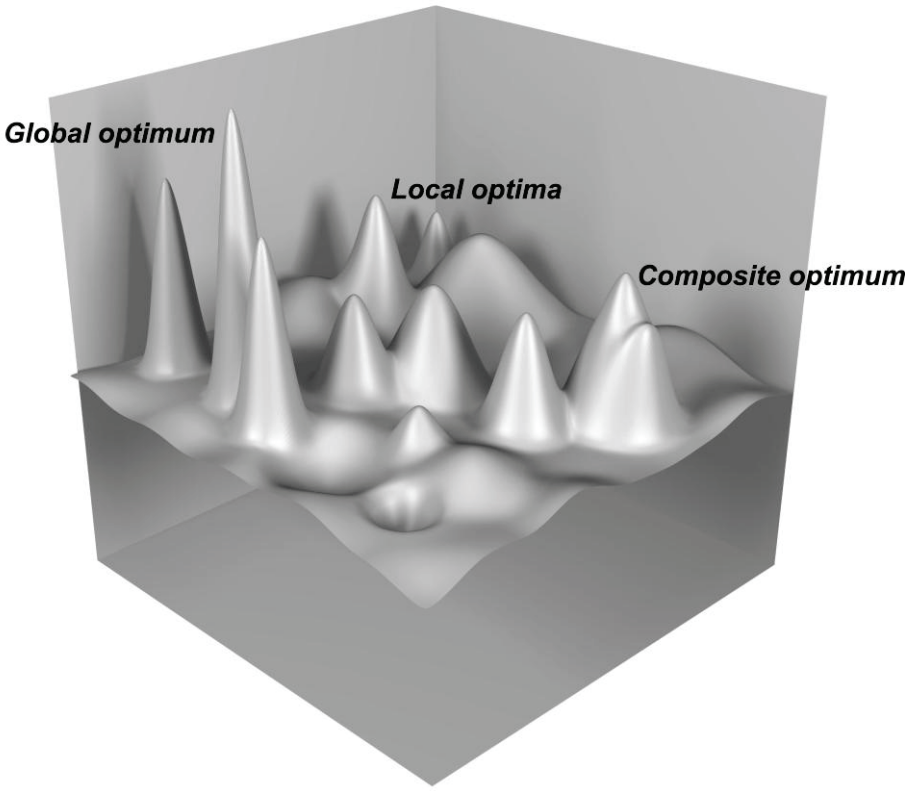


Fig. 3.2 | The hypothetical tree space landscape. The landscape represents potential trees for any given data set. Peaks represent the shortest, i.e. most-parsimonious, and troughs represent the least parsimonious trees. Image produced by Russell J. Garwood (University of Manchester).

For larger data sets, heuristic methods of tree searching must be employed. Traditional search options (**<< *mult* >>**) utilize two basic heuristic methodologies, *Wagner tree* construction and *branch-swapping*. Wagner trees are constructed by the sequential addition of taxa to their most-parsimonious branching point. It is possible to randomize the insertion sequence of taxa by using the command (**<< *rseed* >>**), which initialises the pseudo-random number generator. The command is usually followed by an integral seed value, e.g. (**<< *rseed 0* >>**); analyses performed with the same seed will produce the same topology as they will use the same sequence of pseudo-random numbers. Due to their method of construction, Wagner trees may only find local optima. With the subsequent addition of taxa to the tree the position of other taxa may become more unparsimonious. For this reason the construction of Wagner trees is followed by branch-swapping algorithms.

Traditional search options in TNT use two types of global branch swapping (Fig. 3.4), TBR (*Tree Bisection and Reconnection*) (Farris 1988) (**<< *mult tbr* >>**) and SPR (*Subtree Pruning and Regrafting*) (Felsenstein 2007) (**<< *mult spr* >>**). A third type of 'local' branch-swapping (Fig. 3.4A), NNI (*Nearest-Neighbour*

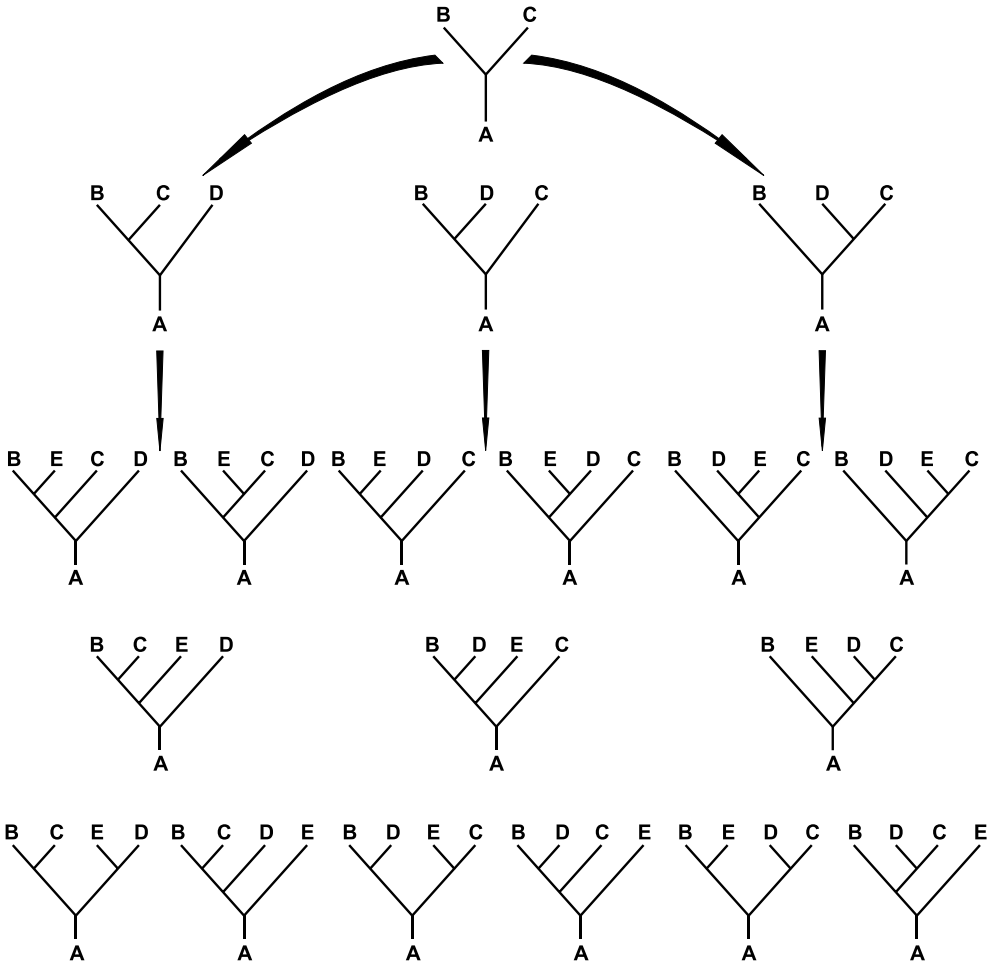


Fig. 3.3 | Tree determination using implicit enumeration. Diagram demonstrating the exponential increase in possible relationships with the addition of taxa. Redrawn from Kitching *et al*. (1998, fig. 3.2).

Interchange) is not implemented in TNT. Both TBR (Fig. 3.4C) and SPR (Fig. 3.4B) clip trees into two subtrees and then rejoin them in a number of possible ways, much like in Wagner tree construction. The secondary topology is then compared to the original tree and discarded, added or replaces the previous tree, depending on its tree length. In SPR branch-swapping the pruned subtrees are rooted (Fig. 3.4B), so they retain the original topology amongst terminal taxa, whereas in TBR branch-swapping the subtrees may also be rerooted (Fig. 3.4C). Arguably TBR will also test topologies recovered by SPR and is therefore a more rigorous method of searching tree space. Obviously this also increases computational time; the number of possible rearrangements needed to complete a replicate of TBR increases with the cube of the number of taxa, therefore a data set with twice the taxa will take more than twice the time to complete a replicate. TNT is able to assess the consequence of branch-swapping without making unnecessary calculations, thereby decreasing computational time (Moilanen 1999).

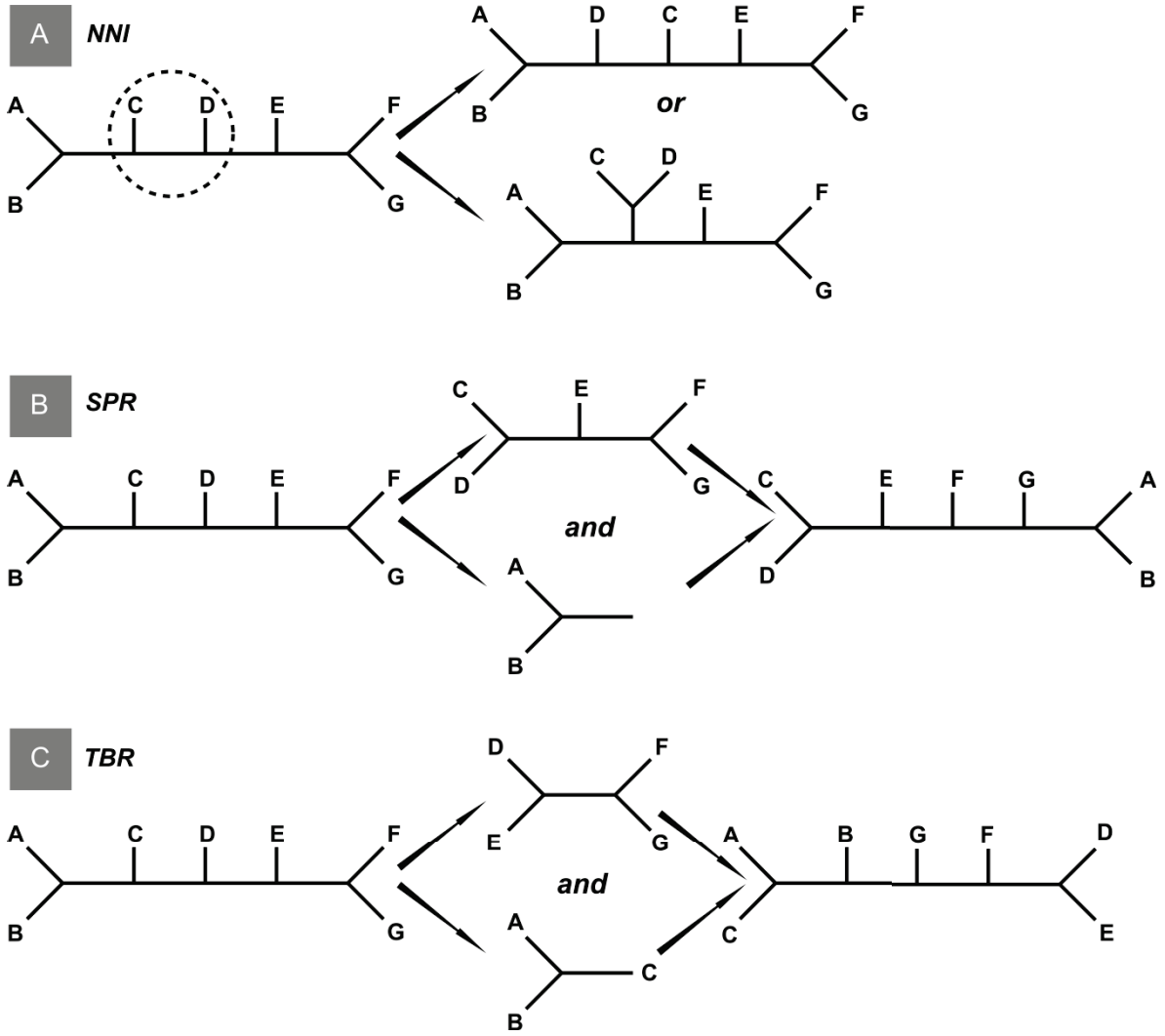


Fig. 3.4 | Methods of branch-swapping. A, Nearest Neighbor Interjoining (NNI), **B**, Subtree Pruning and Regrafting, and **C**, Tree Bisection and Reconnection (TBR). See text for explanation. Modified from Wiley and Lieberman (2011, fig. 6.12).

TBR branch-swapping becomes more liable to find local optima, or 'islands' (*sensu* Maddison 1991), under increased data set size. By virtue of its design, the algorithm will not allow the descent of peaks in the tree space landscape. Methods to compensate for this include using multiple starting points for TBR and the retention of suboptimal trees during swapping. The latter is computationally expensive and is unlikely to search far beyond the local optima. The former approach is implemented using random addition sequences (RAS) (**<< *mult*** *[number of RAS]* **>>**), which produce divergent Wagner trees and ensure a greater spread of the tree space landscape is explored. This method is useful for data sets of between 50 and 150 taxa, but larger data sets require additional, more aggressive search methods.

3.5.3.3. 'New Technology' searches

When applied to large data sets, traditional search options can exhibit a phenomenon termed *composite optima* (Goloboff 1999b), whereby subsets of a large data set may have their own 'local' or 'global' optima (Fig. 3.2). The likelihood of finding a global optimum for the entire data set then falls exponentially when analyses use RAS and TBR. A number of perturbation methods, collectively termed New Technology Search options (Goloboff *et al*. 2008b) (**<< *xmult* >>**), have been devised to overcome this obstruction, including the Ratchet (Nixon 1999), Sectorial searches, tree-fusing and tree-drifting (Goloboff 1999b).

Ratchet

The Parsimony Ratchet was developed by Nixon (1999). This technique escapes local optima by selectively reweighting or deleting a selection of characters, typically 5-15 per cent. Topologies are then produced using RAS and TBR that favour these characters. Topologies are evaluated using the entire data set with all characters weighted according to their original, pre-ratchet, weights and the shorter trees are retained. The command for ratcheting is (**<< *xmult = ratchet [number of perturbation cycles]* >>**). Each perturbation cycle consists of: original weighting > TBR > upweighting > TBR > downweighting > TBR > repeat.

Sectorial searches

Sankoff *et al*. (1994) posited that analyzing subclades of a large data set in isolation was the best way of resolving relationships within subclades and reducing computational time. This method was developed, and formalized as Sectorial searches (**<< *secsch* >>**), by Goloboff (1999b), applying TBR to analyzed subclades. After each round of TBR the resultant topologies are compared to the original topologies and shorter trees retained. Another round of TBR is then performed on the next subclade, or sector. For small subclades, each round of sectorial searches consists of an initial round of three RAS and TBR searches. If no difference in tree length is detected then three more rounds of RAS and TBR are undertaken. For large subclades a preliminary cycle of tree-drifting is also undertaken (*see below*). Three type of sectors can be defined – constraint-based, random, and combination.

In constraint-based searches (**<< *css* >>**), nodes are resolved as polytomies connecting to no less than *n* branches (where *n* is defined by the user). Each polytomy is then analyzed using TBR. As each sectorial search may affect tree topology this process is repeated three times for the entire data set. During random searches (**<< *rss* >>**), sectors are chosen at random, regardless of resolution, although sector size is user defined. Both methods are used in the combined searches.

Tree-fusing

Tree-fusing (**<< *tfuse* >>**) involves the exchange of common taxa between trees. This method is based on the assumption that resolved subclades may be optimal but relationships within them may not be. As with the other methods, the sorter topology is retained.

Tree-drifting

Tree drifting (**<< *drift* >>**) is similar to ratcheting except rather than reweighting characters, perturbation topologies are accepted based on a probability that depends on both the relative fit difference and the absolute fit difference (Goloboff 1999b, Goloboff and Farris 2001).

Combined approach

The methods described above are unlikely to find the global optimum when used in isolation, with the possible exception of ratcheting (Nixon 1999). Instead these methods are used as part of a combined approach. In TNT, RAS and TBR are followed by sectorial searches, which utilize both ratcheting and drifting, and then the resulting trees are fused. The non-exact nature of New Technology searches means that predicting an appropriate number of replicates is not always possible. Fewer replicates may adequately explore the data set and therefore increasing replicates will unnecessarily increase computational time.

3.5.4. Measures of character fit

A number of different metrics exist for determining cladogram 'quality'. The most commonly used is tree length. Other common metrics include consistency indices, retention indices and weighted character fit.

3.5.4.1. Tree length

The most commonly used assessment of cladogram quality is tree length. One of the basic assumptions of parsimony is that fewest changes equates with explanatory power (Farris 1983), therefore the shortest tree is considered the best explanation of the data. For equally weighted trees, tree length correlates to the number of character transformations (synapomorphies), however, the length of an implied weighted tree does not. Also tree length alone is not informative with regard to the levels of homoplasy implied by the tree topology.

3.5.4.2. Weighted character fit

Tree lengths for analyses using character weighting functions are often much lower than those reported for equally weighted trees. For instance, Liu *et al.* (2011) reported a suspiciously high tree length of 130 steps for an implied weighted tree (*k* = 2) for 28 taxa. Even under equal weighting a tree length this high is unexpected for a small number of taxa. Reanalyses of this data set (Legg *et al*. 2011, Mounce and Wills 2011) using both implied weighting (*k* = 2), and equal weighting produced trees of 16.4 steps and 89 steps, respectively. This is obviously a significant difference in tree length between methodologies, but just because the tree length is shorter for the implied weighted trees does this mean they represent a better explanation of the data, or a higher quality tree?

The reason tree lengths for implied weighted tree topologies differ from those under equal weights is because the number of steps does not correlate with the number of character transformations, as it does for equally weighted topologies, but rather represents the sum of all implied character weights. We can compare lengths of equal and implied weighted trees by calculating the total character fit (**<< *fit* >>**) for an implied weighted tree, defined as $f = e / (e + k)$, where k is the concavity constant (*see* section 3.5.2.1) and e is the number of extra steps implied by the topology.

3.5.4.3. Consistency index (ci) and ensemble consistency index (CI)

Consistency indices and retention indices (*see below*) are metrics that designed to report levels of homoplasy in a singular character, or all characters within a data set. The assumption is that a topology with high levels of character inconsistency, i.e. high levels of homoplasy, is less reliable that those with lower levels. The consistency index (ci) is defined as, m / s, where s is the minimum number of steps a character exhibits on a given tree, and m is the minimum number of steps a character can have on any tree. For an equally weighted character the minimum number of steps a character can have on any tree is logically one. This means that a character with no homoplasy, i.e. one that appears just once on a tree, will have a ci of 1, a character that appears twice will have a ci of 0.5, and so on. A character with a low ci is therefore considered inappropriate for determining relationships. When applied to the entire data set, as an ensemble consistency index (CI), we get an idea of how prevalent homoplasy is across the entire data set. The equation M / S is still applied, but instead M represents the sum of minimum steps for all characters, so for an equally weighted data set of 20 characters this value is 20, and S is the sum of all minimum character steps on a given tree, i.e. its tree length.

The inclusion of autapomorphies can unduly inflate consistency indices. An autapomorphy by its very nature will have a consistency index (ci) of 1. Ensemble

consistency indices will therefore be raised by these characters and give a false impression of levels of homoplasy across a given tree.

3.5.4.4. Retention index (ri) and ensemble retention index (RI)

Farris (1989b) recognised that consistency indices measure levels of homoplasy rather than character fit (synapomorphies), and so he proposed the retention index (ri) and ensemble retention index (RI) as alternatives. The retention index (ri) is defined as, *(g –s) / (g – m)*, where *g* is the greatest possible number a character can have on any tree. Thus, if the character is present in state 1 in 5 taxa then *g* equals 5. Like consistency indices, this metric can be applied to the entire data set, as an ensemble retention index (RI). The same principles applied as for the consistency indices, i.e. each value represents a sum total for the entire data set. There is currently no command in TNT for calculating consistency indices and retention indices but a script (*Stats.run*) is available from the TNT wiki website (tnt.insectmuseum.org/index.php/Scripts).

3.5.5. Consensus trees

For any given data set there may be more than one maximally parsimonious tree. In such instances congruence is often seen as a measure of accuracy or stabiliy (Nelson and Platnick 1981, Penny and Hendy 1986, Swofford 1991). In other words, if a particular clade is present across all, or the majority of trees produced by the data set then it is more stable and likely to represent a more accurate view of evolutionary history. This congruence is summarised using consensus methodologies.

The most commonly used types of consensus methodologies are Strict (Schuh and Polhemus 1981) (**<< *nelsen* >>**) and Majority-rule (Swofford 1991) (**<< *majority* >>**). These methods are both based on a simple count of the frequency of 'informative' groups (*sensu* Nelson and Platnick 1981) in component trees. Strict-consensus trees only include those relationships recovered in all trees (Sokal and Rohlf 1981), whereas majority-rule trees can be constrained to include relationships recovered in over 50 per cent of the component trees. Nixon and Carpenter (1996) argued that only strict-consensus trees represent an accurate depiction of the component data and other consensus methods should be considered 'compromise trees'.

The nature of consensus methodologies means that compromise trees may contain clades that are not present in any of the constituent trees. For this reason some have rejected this methodology (Miyamoto 1985, Carpenter 1988), although it has been argued that a consensus is still reliable as it provides a reasonable summary of information provided by the data set (Anderberg and Tehler 1990, Bremer 1990, Nixon and Carpenter 1996).

Incongruent component tree topologies may result in a lack of resolution in strict and majority-rule consensus trees. This lack of resolution may be the result of a limited number of topologically labile taxa, termed 'wildcard taxa'; these taxa aside there may still be a well-resolved underlying topology. In such instances an agreement subtree can be produced.

3.5.5.1. Agreement subtrees

Agreement subtrees (**<< *prunnelsen* >>**) show only the components common to all constituent trees. In this method, sometimes called the greatest agreement subtree (GAS) method, terminals are pruned from each of the constituent trees until all topologies agree. The agreement topology with the least number of taxa pruned is taken as the agreement subtree.

3.5.6. Nodal support

As well as methods for determining the reliability of characters and the overall topology of the tree (*see* section 3.5.4), a number of support metrics exist to determine the support of individual clades. These metrics are all based on the principles that the clades with either (a) the highest number of synapomorphies; and/or (b) least affected by data perturbations, such as data deletion or reweighting, are the most accurate. The most commonly applied methods of nodal support are decay analysis, bootstrapping and jackknifing.

3.5.6.1. Decay analysis

Decay analysis (Bremer 1988, Donoghue *et al*. 1992), also known as 'Bremer support' (Källersjö *et al*. 1992), 'branch support' (Bremer 1994), 'length difference' (Faith 1991), 'clade stability' (Davis 1993), or 'Bremers support index' (Davis 1993), posits that a precise measure of character support is the number of extra steps required to remove that clade from the strict consensus. The decay index is calculated by producing consensus trees of successively suboptimal trees and comparing them to the original consensus. Clades recovered in more suboptimal trees are more stable and assigned the highest nodal support. For instance, if a clade is present in the strict consensus of a tree five steps suboptimal to the original consensus then the node is assigned a value of five. There is no command in TNT for obtaining Bremer support values however a script (*bremer.run*) is available from the TNT website (tnt.insectmuseum.org/index.php/Scripts).

3.5.6.2. Bootstrapping

Bootstrapping (**<< *resampling boot* >>**) is a form of model-independent Monte Carlo randomization process (Efron 1979), whereby randomly sampled characters are deleted and replaced to form a pseudoreplicate data set of the same dimensions as the original (Felsenstein 1985). During this process some characters are randomly weighted and others are randomly deleted with the net effect that the sum of all weights is equal to that of the original data set. A set number of pseudoreplicates are produced, typically 100 or 1000 (**<< *resampling boot replications 1000* >>**). Each pseudoreplicate is then analysed and the resultant consensus compared to the strict-consensus of the original data set. The frequency of common clades in the pseudoreplicates is then taken as the nodal support for that clade. What constitutes a well-supported clade has been hotly debated (*see* Felsenstein 2004), with Hillis and Bull (1993) suggesting values as low as 70 per cent can be considered well-supported.

One of the main limitations of bootstrapping is the size of the sample required for it to be statistically valid. Values for any form of resampling, jackknifing and symmetric resampling included, can only be considered approximations for data sets below 1000 taxa (Kitching *et al*. 1998). Like consistency indices, bootstrap values can be greatly inflated by autapomorphic character states (Carpenter 1996), despite claims to the contrary (Harshman 1994).

3.5.6.3. Jackknifing and symmetric resampling

Like bootstrapping, jackknifing (**<< *resampling jak* >>**) relies on the production of pseudoreplicates, however there is no compensation for deleted characters or taxa and hence the pseudoreplicates are always smaller than the original data set. During first-order jackknifing (Mueller and Ayala 1982, Lanyon 1985), either one character (Farris *et al*. 1996) or taxon (Lanyon 1985, Siddal 1995) is removed. After analysis the resultant consensus trees, from a set of pseudoreplicates, is compared to the original data set and the frequency of common clades taken as the nodal support value. Higher-order jackknifing follows the same procedure except a larger subset of *n* (typically no more than 10) observations is removed to produce a pseudoreplicate.

Both forms of jackknifing are liable to underestimate nodal support for clades based on few apomorphies, regardless of character consistency. In the case of higher-order jacknifing, only clades supported by at least as many characters as there are taxa are likely to be supported (Kitching *et al*. 1998). Both jackknifing and bootstrapping are extensively affected by character weighting and transformation costs (Goloboff *et al*. 2003), whereas symmetric resampling (**<< *resampling sym* >>**) is not. In symmetric resampling each character has a change probability of 2*P*, and can be duplicated or deleted with equal probability. Unlike bootstrapping and jackknifing, in which the absolute frequency of a clade (F) is taken as nodal support, symmetric resampling uses GC values (Goloboff *et al*. 2003). GC, shorthand for 'group present/contradicted', represents the difference in frequency between a group and its most frequent contradicted group. This method has been shown to produce

more realistic measures of support than those obtained using traditional jackknifing and bootstrapping (Goloboff *et al*. 2003).

3.6. Applied methodology

A data set of 311 taxa and 753 characters was constructed and converted to NEXUS file format (Maddison *et al*. 1997) (available on the CD attached to this document). This data set was analysed in TNT v.1.1. (Goloboff *et al*. 2008b) (**<< *proc [File location]* >>**). Memory was increased to allow for 10000 trees to be retained (**<< *hold 10000* >>**). All characters were non-additive (unordered) and active (**<< *ccode –[* >>**). The data set was analysed with both equal character weighting and a variety of concavity constants for implied weights [*k* = 2, 3 and 10 (**<< *piwe = [k]* >>**). There were no continuous characters. Analysis involved New Technology Search options including 100 random addition sequences (RAS), combined sectorial searches, drifting, ratcheting and tree-fusing (**<< *xmult rss 10 css drift 3 ratchet 10 fuse 2* >>**). Character fit was calculated using CI and RI (*Stats.run*) and nodal support measure using symmetric resampling (Goloboff *et al*. 2003) with 100 replicates, each of which applied a New Technology search (i.e. sectorial searches, drifting, ratcheting and tree-fusing) with a change probability of 33 per cent (**<< *resampling sym replicates 100 probability 33* >>**).

4. Taxon sampling (stem- and non-arthropods)

4.1. Introduction

In **Chapter 1** the problem of euarthropod interrelationships was identified as a rooting issue, and the need for fossils in resolving this issue was discussed in **Chapter 2**. The current chapter contains an overview of key arthropod and non-arthropod taxa, and their potential utility in resolving relationships within Euarthropoda. Although the five major extant clades of euarthropods possess an extensive fossil record (*see* section 1.1) their content is not covered here as this chapter is primarily concerned with polarising relationships between rather than within euarthropod clades. Each section contains a justification for the inclusion of certain taxa in the phylogenetic analysis. A complete list of included taxa, including those referable to extant groups, and source of phylogenetic coding is presented in **Appendix 1**. Taxa included in the analysis are given in bold in the text below.

Section 4.4. was published, in part, in the journal *Palaeontology* (Legg and Caron in press). The reconstruction of *Diania cactiformis* Liu *et al*. 2011, appeared in Ma *et al*. (in press, fig. 4), in the *Journal of Systematic Palaeontology*.

4.1.1. The extant sister-taxon of Arthropoda

Before dealing with the fossil record of arthropods it is necessary to consider the putative extant sister-taxa of arthropods and the role they play in understanding the plesiomorphic condition of Arthropoda. Two extant phyla are most commonly identified as the sister-taxon of Arthropoda – the tardigrades (water bears) and the onychophorans (velvet worms).

4.1.1.1. Tardigrades

The tardigrades are a phylum characterised by diminutive size (Schmidt-Rhaesa 2001) and the possession of a bilaterally symmetrical, usually ventrally flattened and dorsally convex, body composed of five segments (Fig. 4.1A), a head and four trunk segments (Ramazzotti and Maucci 1983). The posterior of the body is divided into three trunk segments and a caudal segment, each bearing a pair of short, latero-ventral, lobopodous limbs tipped with either claws, toes or adhesive discs (Fig. 4.1A). Their small size, and their tendency to contract during fixing, makes them hard to study (Nelson 1991, Mayer *et al*. 2013). The smallest recorded specimens measured just 50 µm, and the largest are specimens of *Milnesium tardigradum* Doyère 1840, which can measure over 1200 µm; 250-500 µm is a more typical size for other tardigrades (Ramazzotti and Maucci 1983).

Tardigrades have colonized a wide variety of ecological niches from the extreme pressures of deep-marine trenches (Seki and Toyoshima 1998) to the heights of the Himalayas, where they dwell within glaciers (Dastych 2004). Their tolerance to such extreme environments is renowned; they can survive extremely high doses of radiation, more than 1000 times that of a human (Horikawa *et al*. 2006), and repeated tests have demonstrated they can live in the near-vacuum and near-absolute zero conditions of Earth‟s orbit (Jönsson *et al*. 2008). Their diet can consist of other micrometazoans, such as rotifers and nematodes, algae and lichens, or bacteria and detritus. Despite this, their internal anatomy remains remarkably conserved (Fig. 4.1B), with their digestive system consisting of a complex buccal-pharyngeal apparatus and a simple gut with an oesophagus, midgut and hindgut (Guidetti *et al*. 2012).

Tardigrades were first discovered by Goeze (1773), who called them „*Kleiner Wasserbär*‟, meaning „little water bear‟, hence their vernacular name. Three years later Spallanzani (1776) coined the term tardigrade, meaning „lumbering gait‟, although it was Doyère (1840) who first formalised the taxon, and it is common to see the name Arctisconia Haeckel 1866, meaning „bear worms‟, in older literature. Close affinities with arthropods have long been recognised (Siebold 1848, Claus 1868, Thorell 1876, Plate 1889), although early workers sometimes allied them with vermiform taxa, such as annelids (e.g. Bronn 1850, Graff, 1877, Haeckel 1896). Cuénot (1932) considered tardigrades a link between onychophorans and euarthropods, a view also followed by Ramazzotti (1962), who granted tardigrades phylum status.

A sister-taxon relationship between tardigrades and euarthropods has been advocated many times (Marcus 1929, Riggin 1962, Bussers and Jeuniaux 1973, Kristensen 1981, Brusca and Brusca 1990, Kitchin 1994, Nielsen 1995, 2001, Monge-Nájera 1995, Wills *et al*. 1995, 1997, 1998, Budd 1996, 2001, Dewel and Dewel 1996, 1997, Dewel *et al*. 1999), and has been given the formal clade name, Tactopoda Budd 2001a. Schmidt-Rhaesa (2001) considered only three potential synapomorphies to support this clade: (1) sclerotization of dorsal and ventral plates,

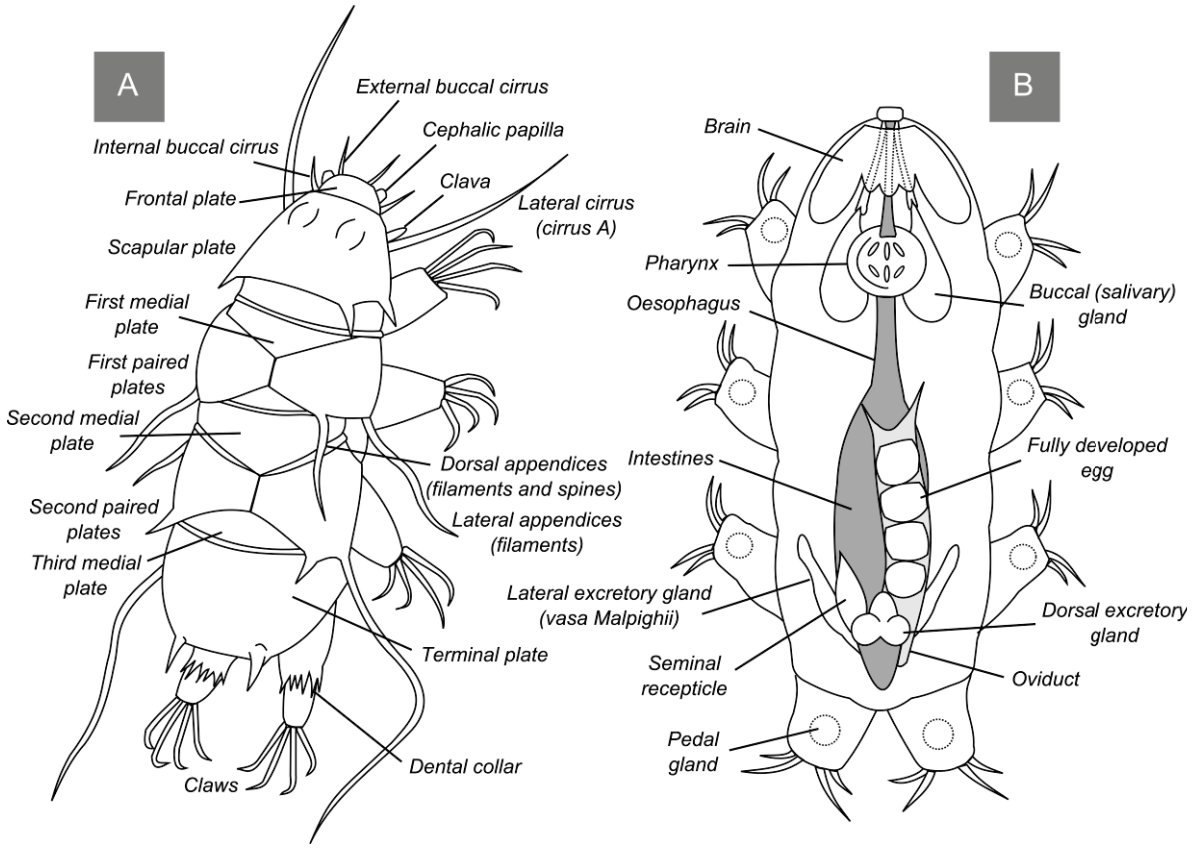


Fig. 4.1 | Tardigrade anatomy. A, the external anatomy of *Echiniscus apuanus* Bertolani 1946 (redrawn from Ramazzotti and Maucci 1983, fig. 164); and **B**, internal anatomy of *Macrobiotus* sp. (Schultze 1834) (redrawn from Ramazzotti and Maucci 1983, fig. 1).

(2) disintegration of muscular sheets below the epidermis, and (3) bismuth staining of the Golgi body (Locke and Huie 1977). Mayer *et al* (2013) also considered the possession of a stomatogastric ganglion a potential synapomorphy of this clade. Some morphological features, such as cuticular structure, may instead support close affinities with nematodes (Crowe et al. 1971, Dewel and Clark 1973, Ruppert and Barnes 1994). Unfortunately molecular evidence remains equivocal with some analyses favouring close affinities between tardigrades and nematodes (Philippe *et al*. 2005, Roeding *et al*. 2007, Lartillot and Philippe 2008, Sørensen *et al*. 2008, Bleidorn *et al*. 2009, Hejnol *et al*. 2009, Meusemann *et al*. 2010, Pick *et al*. 2010, Andrew 2011), whilst others favour panarthropod affinities (Garey *et al*. 1996, Giribet *et al*. 1996, Mallatt *et al*. 2004, Rota-Stabelli *et al*. 2010, 2011, Campbell *et al*. 2011).

Roughly 1100 species of tardigrades have been described (Guidetti and Bertolani 2011, Nielsen 2011, Zhang 2011a), and divided into three classes: Heterotardigrada Marcus 1927, Eutardigrada Marcus 1927, and Mesotardigrada Rahm 1937. The heterotardigrades are predominantly marine, but also contains terrestrial armoured forms (Nelson and Higgins 1990). The majority of tardigrades, 712 species (Guidetti and Bertolani 2011, Zhang 2011a) are represented by Eutardigrada; these unarmoured terrestrial and fresh water forms include some of

the best studied taxa, including ***Milnesium tardigradum*** and ***Hypsibius dujardini*** (Doyère 1840), both of which are extensively used in molecular studies (e.g. Mali *et al*. 2010). These taxa were used to represent tardigrades in the current data set. The third class, Mesotardigrada, was erected based on a single species, *Thermozodium esakii* Rahm 1937, from a hot sulphur-spring in Japan, however the type material has been lost (Nielsen 2011) and the type habitat was destroyed by an earthquake. Fossil tardigrades are rare, two examples being known from Cretaceous ambers in North America (Cooper 1964, Bertolani and Grimaldi 2000), and a further example from the Pleistocene of Italy (Durante and Maucci 1972). All are undoubtedly members of the crown group (Budd 2001a), with one, *Milnesium swolenskyi* Bertolani and Grimaldi 2000, referable to an extant genus. A possible stem-group representative from the middle Cambrian of Siberia (Müller *et al*. 1995) is yet to be formally described.

4.1.1.2. Onychophorans

The onychophorans are a small, wholly terrestrial phylum, restricted to leaf-litter communities (Picado 1911, Endrody-Younga and Peck 1983) of tropical and temperate forest regions (Monge-Nájera 1995, Gleeson 1996). Although 197 species of onychophoran have been described (Oliveira *et al*. 2012), only 177 of these appear to be valid (Mayer and Oliveira 2011, Oliveira *et al*. 2012); this may not be an accurate representation of species diversity, however, as molecular evidence indicate a high cryptic diversity (Reid 1996).

They possess an elongate, subcylindrical body of between 12 and 40 metameric segments (Wright 2012), each possessing a pair of lobopodous limbs tipped with broad ventral pads and a pair of thin terminal claws (Fig. 4.2A); the latter provide the basis for their taxon name, Onychophora Grube 1853, meaning „daw-bearing". Onychophorans typically range in size from 10 mm to 150 mm (Ruhberg 1985, Read 1988), whilst females can be 50 per cent larger than males (Campiglia and Lavallard 1973, Monge-Nájera and Morera 1994); female specimens of *Peripatus solorzanoi* Morena-Brenes and Monge-Nájera 2010, may reach lengths of 220 mm.

The head is poorly differentiated from the body but possesses a number of highly specialised appendages (Fig. 4.2). The anteriormost metameric segment of onychophorans possesses a pair of „primary" antennae (*sensu* Scholtz and Edgecombe 2006), and a pair of dorso-lateral eyes (Fig. 4.2B); the eyes are simple, composed of a cornea, optic cavity, and a pigmented „cup" (Dakin 1926, Eakin and Westfall 1965, Mayer 2006). Developmental evidence indicates the antennae are serially homologous to the more posterior metametric appendages (Mayer and Koch 2005). Other head appendages show adaptations for a carnivorous mode of life. Posterior of the eyes is a ventral pair of jaws, which project between the buccal papillae and possess slicing claws (Wright 2012); and a lateral pair of slime papillae (Fig. 4.2B). From these appendages onychophorans squirt a sticky protein which

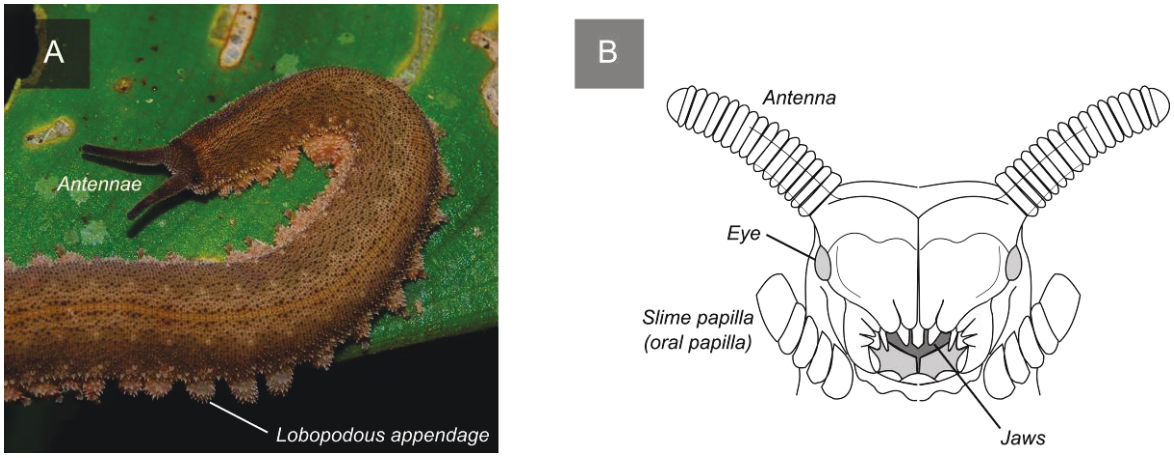


Fig. 4.2 | Onychophoran anatomy. A, the external morphology of *Peripatus* sp. (Guilding 1826); and **B**, the anterior external morphology of *Peripatopsis capensis* (Grube 1866) (redrawn from Moseley 1874, Pl. LXXV, fig. 10).

quickly hardens to immobilise prey (Haritos *et al*. 2010), typically small arthropods (Read and Hughes 1987). Onychophorans are protected from their own secretion by their hydrophobic cuticle, the texture of which is responsible for their vernacular name.

The first described onychophoran, *Peripatus juliformis* Guilding 1826, was originally considered an aberrant mollusc (Guilding 1826). Subsequent workers tended to align onychophorans with annelids (e.g. Grube 1853), or considered them a link between annelids and arthropods (Newport 1844, Siebold 1848). The supposed relationships of the onychophorans were pivotal in discussion of arthropod di- and polyphyly; in particular, similarities in the tracheal system of onychophorans and myriapods were thought indicative of close relationships under the Uniramia hypothesis (Tiegs and Manton 1958). The implication was that, if onychophorans were also closely related to annelids then typical arthropod features, e.g. arthropodization, must have arisen at least twice, once in tracheate arthropods, such as myriapods, and again in schizoramous arthropods (*see* section 1.2.5).

A close affinity between arthropods and annelids underpinned the Articulata hypothesis, as proposed by Cuvier (1816), but was usurped by molecular evidence which instead favoured the Ecdysozoa and Lophotrochozoa hypotheses (Aguinaldo *et al*. 1997, Peterson and Eernisse 2001), which unite panarthropods with cycloneuralians, and annelids with molluscs, respectively. The exact position of onychophorans with regards to euarthropods remains largely unresolved, with molecular analyses either resolving them as sister-taxon euarthropods (Dunn *et al*. 2008, Hejnol *et al*. 2009, Braband *et al*. 2010, Rota-Stabelli *et al*. 2011), sister-taxon to a euarthropod plus tardigrade clade (Edgecombe *et al*. 2000), or as part of a polytomy with other ecdysozoans (Aguinaldo *et al*. 1997, Roeding *et al*. 2007). Evidence for a sister-taxon relationship between onychophorans and euarthropods, to the exclusion of tardigrades, includes the possession of an *α*-chitin procuticle,

brain structure (Strausfeld *et al*. 2006), a dorsal, ostiate heart and haemocoelic circulation, and arthropod-type haemocyanins (Kusche *et al*. 2002).

Two families of onychophorans can be distinguished, the peripatopsids, which are found in Chile, South Africa and Australia, and the peripatids, found in the Antilles, Mexico, Central America, northern South America, West Equatorial Africa and Southeast Asia (Bouvier 1905, 1907, Ruhberg 1992, Monge-Nájera 1995). The peripatopsids were represented in the current data set by ***Euperipatoides kanangrensis*** Reid 1996; this taxon has been the focus of numerous developmental and gene expression studies (e.g. Eriksson *et al*. 2003, 2005, 2009, Eriksson and Stollewerk 2010, Eriksson and Tait 2012), and has been included in large scale molecular phylogenetic analyses (e.g. Regier *et al*. 2010). The peripatids was represented by ***Peripatus juliformis***, which likewise has been included in molecular phylogenetic analyses (Reiger *et al*. 2010). Biogeographic evidence indicates a late Triassic divergence for these families (Monge-Nájera 1995), indicating onychophorans have a long stem-lineage, however, their low preservation potential (Monge-Nájera and Hou 2002) means unequivocal fossil representatives are restricted to Tertiary ambers (***Tertiapatus dominicanus*** Poinar 2000 and ***Succinipatopsis balticus*** Poiner 2000), and Carboniferous siderite nodules (***Helenodora opinata*** Thompson and Jones 1980). All these taxa were included in the current analysis. Other putative stem-group onychophorans are discussed in the next section.

4.2. Lobopodians

The term lobopodian is widely used to refer to a paraphyletic assemblage of putative stem-group tardigrades, onychophorans and euarthropods, characterised by the possession of lobopodous appendages. The lobopodians were largely unknown as a group prior to the early 1990‟s (Ramsköld and Hou 1991), various taxa being allied to annelids (Walcott 1911a), onychophorans (Manton 1977, Whittington 1978, Thompson and Jones 1980, Robison 1985, Dzik and Krumbiegel 1989), or enigmatic forms of uncertain affinities (Conway Morris 1977, Bengtson *et al*. 1986, Briggs and Conway Morris 1986, Chen *et al*. 1989, Gould 1989,). The term lobopod was first used by Snodgrass (1938, fig. 54) to refer to a grade of evolution connecting the annelids to an onychophoran plus euarthropod clade, which was later named Lobopoda Boudreaux 1979. Others (e.g. Waggoner 1996) have used this term to refer exclusively to an onychophoran plus tardigrade clade.

Lobopodians demonstrate a wide variety of morphologies (Fig. 4.3). Perhaps the most unspecialized morphology is exhibited by *Paucipodia inermis* Chen *et al*. 1995b (Hou *et al*. 2004c) (Fig. 4.3A), which consists of a finely annulated subcylindrical body with nine pairs of undifferentiated lobopodous appendages each tipped with a small pair of claws. Although *Paucipodia* is one of the oldest lobopodians, this morphology appears to be retained by *Carbotubulus waloszeki* Haug *et al*. 2012b, the latest occurring lobopodian from the Late Carboniferous of

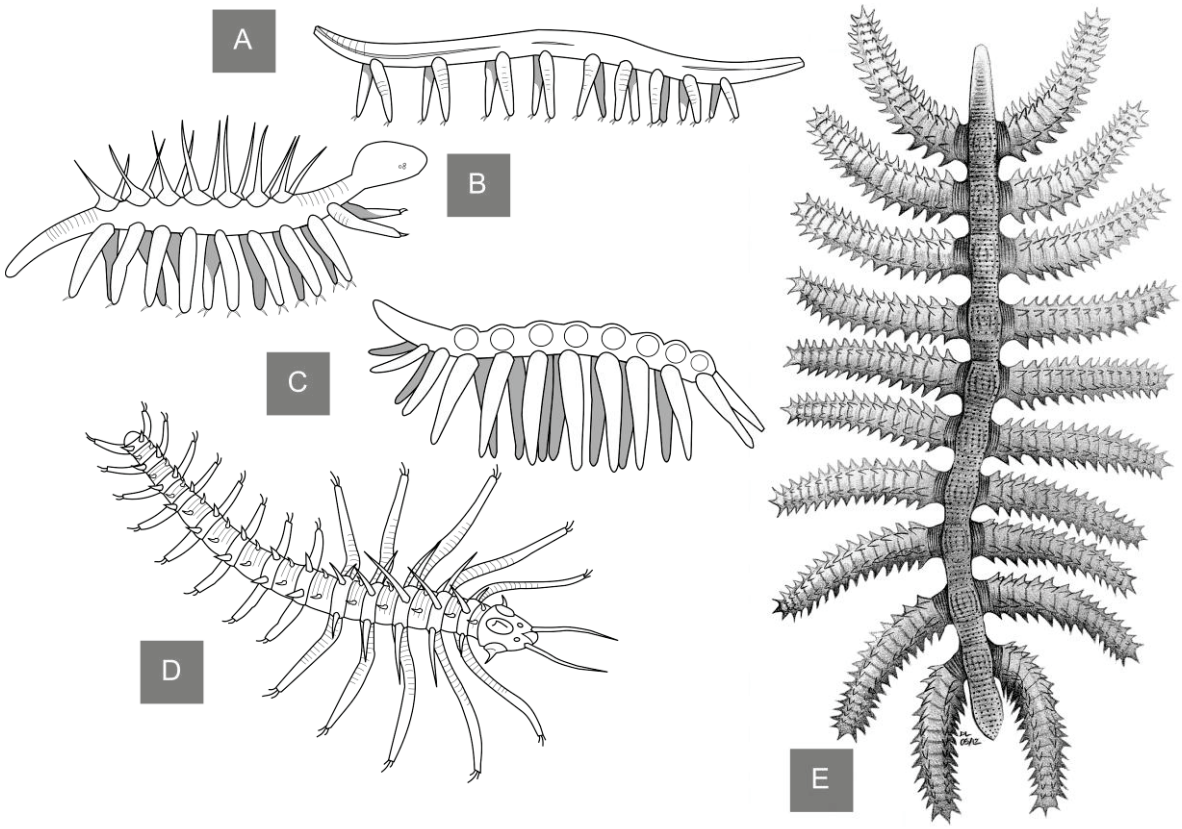


Fig. 4.3 | The diversity of lobopodians from the Cambrian Chengjiang *Konservat-Lagerstätte*. A, *Paucipodia inermis* Chen *et al*. 1995; **B**, *Hallucigenia fortis* Hou *et al*. 1995; **C**, *Microdictyon sinicum* Chen *et al*. 1989; **D**, *Luolishania longicrus* Hou and Chen 1989 (based on Ma *et al*. 2009, fig. 11; and **E**, *Diania cactiformis* Liu *et al*. 2011 (reconstruction originally published in Ma *et al*. in press, fig. 4).

Illinois. A similar morphology is exhibited by a variety of Cambrian lobopodians including *Hallucigenia* Conway Morris 1977 (Fig. 4.3B), and *Microdictyon* Bengtson, Matthews and Missarzhevsky *in* Missarzhevsky and Mambetov 1981 (Fig. 4.3C), although the latter differs in possessing elongate ventral spines and porous lateral plates. Budd (2001b) considered the evolution of dermal plates in such „armoured lobopods" to be an important step in the origin of euarthropod segmental heteronomy; however, phylogenetic analyses of lobopodians (e.g. Ma *et al*. 2009, in press, Liu *et al*. 2011, Mounce and Wills 2011, Legg *et al*. 2011) tend to resolve homonomous taxa, such as *Xenusion auerwaldae* Pompeckj 1927, closer to the arthropod stem.

Ma *et al*. (2012a) recently described multi-ocellate eyes from *Hallucigenia fortis* Hou and Bergström 1995, and *Luolishania longicruris* Hou and Chen 1989 [= *Miraluolishania haikouensis* Liu and Shu, *in* Liu *et al*. 2004] (Fig. 4.3D), from the Chengjiang biota. These eyes were considered the precursor of arthropod-type compound eyes, although most phylogenetic analyses of lobopodians (e.g. Ma *et al*. 2009, in press, Liu *et al*. 2011, Mounce and Wills 2011, Legg *et al*. 2011), do not

resolve these taxa on the euarthropod-stem, or even close to each other. Instead, *Luolishania* tends to group with the more specialized lobopodians *Onychodictyon* Hou *et al*. 1991, and the as yet undescribed „Collins Monster" (Collins 1986). Like *Hallucigenia*, all these taxa possess ventral spines, however unlike *Hallucigenia* their appendages display specialization, with the anterior-most limbs modified into antenniform appendages, and the anterior five pairs of appendages noticeably longer and more setiferous than the posterior limbs (Ma *et al*. 2009). The development of this „pseudotagmosis" may have been an important step in the origin and specialization of the arthropod bodyplan (Ma *et al*. 2009, Ou *et al*. 2012). A similar tagmosis was reported in *Diania cactiformis* Liu *et al*. 2011 (Fig. 4.3E) from the Chengjiang biota, as were arthropodized trunk limbs; both features may, however, have been misinterpreted and absent (Ma *et al*. in press). Instead *Diania* closely resembles the first lobopodian to be described, *Aysheaia pedunculata* Walcott 1911a, from the Burgess Shale.

Both *Aysheaia* and *Diania* possess a number of seemingly primitive features, such as a terminal mouth and lack of sclerotization. The anterior appendages of *Aysheaia* do however show specialization, and may be homologous to the anterior appendages of arthropods (Budd 2002). *Aysheaia* was commonly used to root earlier phylogenies of arthropods (*see* section 2.4). Increased specialization of the anterior appendages into „grasping appendages", also occurs in taxa such as *Megadictyon haikouensis* Luo and Hu *in* Luo *et al*. 1999, and the so-called „gilled lobopodians". These taxa are discussed in more detail in the next section (4.2).

A total of 15 lobopodian taxa were included in the current phylogenetic analysis: ***Antennacanthapodia gracilis*** Ou and Shu *in* Ou *et al*. 2011, ***Aysheaia*** Walcott 1911a, ***Cardiodictyon catenulum*** Hou *et al*. 1991, the **'Collins Monster'**, ***Diania cactiformis***, ***Hadranax augustus*** Budd and Peel 1998, ***Hallucigenia***, ***Jianshanopodia decora*** Liu *et al*. 2006, ***Luolishania longicruris***, ***Megadictyon haikouensis***, ***Microdicyon***, ***Onychodictyon***, ***Paucipodia inermis***, ***Siberion lenaicus*** Dzik 2011, and ***Xenusion auerwaldae***. *Microdictyon* contains at least nine species (Zhang and Aldridge 2007), most represented by isolated plates; for this reason this taxon was represented by *M. sinicum* Chen *et al*. 1989, for which remains of the entire animal are known. *Hallucigenia* contains three species (***H. fortis***, *H. sparsa* (Walcott 1911a), and *H. hongmeia* Steiner *et al*. 2012), *Aysheaia* contains two species (***A. pedunculata*** and *A. prolata* Robison 1985), and *Onychodictyon* contains two species (***O. ferox*** Hou *et al*. 1991, and *O. gracilis* Liu *et al*. 2008). Each genus was coded using a single species, *H. fortis*, *A. pedunculata*, and *O. ferox*, respectively. The other taxa assigned to these genera did not differ in coding from the selected species except in the position of missing data and, as safe taxonomic reductions, were therefore excluded prior to analyses.

4.3. 'Gilled' lobopodians and other dinocaridids

The lobopodians *Megadictyon haikouensis*, and *Jianshanopodia decora* share a number of features with „gilled lobopodians" and other dinocaridids, including enlarged frontal „grasping-appendages", a circum-oral cone and serially repeated, reniform gut glands; features indicative of a predatory mode of life (Budd 1993, 1997, Butterfield 2002, Liu *et al*. 2006). A putative frontal appendage was also reported for *Hadranax augustus* (Budd and Peel 1998) from the lower Cambrian Sirius Passet *Konservat-Lagerstätte* of northern Greenland, however, the position of the putative „frontal-appendage" makes this interpretation unlikely and it may even represent the fragmentary remains of another organism (Dzik 2011). Two other „frontal-appendage"-bearing lobopodians, *Kerygmachela kierkegaardi* Budd 1993 (Budd 1999a), and *Pambdelurion whittingtoni* Budd 1997, have also been reported from Sirius Passet.

These latter taxa differ from other „traditional" lobopodians in the possession of extensive lateral flaps, a feature they share with other dinocaridids (*sensu* Collins 1996). The function and homology of the lateral flaps has been hotly debated (Hou and Bergström 2006), with the prevailing hypotheses considering them homologous to arthropod exites (Bergström 1986, 1987, Hou *et al*. 1995, Budd 1996, Budd and Daley 2012). *Pambdelurion* possessed a mixed muscular system, consisting of both onychophoran-type peripheral musculature and euarthopod-type lever-musculature (Budd 1998). The latter was most likely used to control the movement of hydrostatic fluids in such a large animal; *Pambdelurion* may measure of 300 mm long (pers. obs.), and was an important exaptation for the origin of a hard tergal exoskeleton (Budd 1998).

Both *Pambdelurion* and *Kerygmachela* have been placed in Dinocaridida Collins 1996 [*nom. corrected* Bergström and Hou 2004] (Bergström and Hou 2004, Hou and Bergström 2006), a group that also includes *Opabinia* Walcott 1911a (Fig. 2.1) and Radiodonta Collins 1996, and has also been termed the „AOPK" group (*Anomalocaris* – *Opabinia* – *Pambdelurion* – *Kerygmachela*; *sensu* Budd 1997). The close affinities of members of this group is little disputed, however, their relationships to euarthropods have been the subject of much debate. The radiodonts, which include *Anomalocaris* Whiteaves 1892 (Fig. 4.4), *Amplectobelua* Hou *et al*. 1995, *Peytoia* Walcott 1911b (Daley and Bergström 2012), and *Hurdia* Walcott 1912 (Daley *et al*. 2009, in press), are characterised by the possession of a sclerotized circum-oral mouth apparatus, a trunk lacking appendages, and arthropodized frontal appendages (Collins 1996). The latter character is seemingly indicative of arthropod affinities. If, however, the dinocaridids represent a monophyletic group (*sensu* Hou *et al*. 1995, Bergström and Hou 2004, Hou and Bergström 2006), then arthropodization must have evolved at least twice, once amongst dinocaridids, and once on the arthropod-stem lineage. Most quantitative phylogenetic analyses resolve dinocaridids as paraphyletic with regards to euarthropods (e.g. Liu *et al*. 2007, Daley *et al*. 2009, Kühl *et al*. 2009, Ma *et al*. 2009, in press, Liu *et al*. 2011), implying that many important arthropod characters, e.g. compound eyes (Paterson *et al*. 2011)

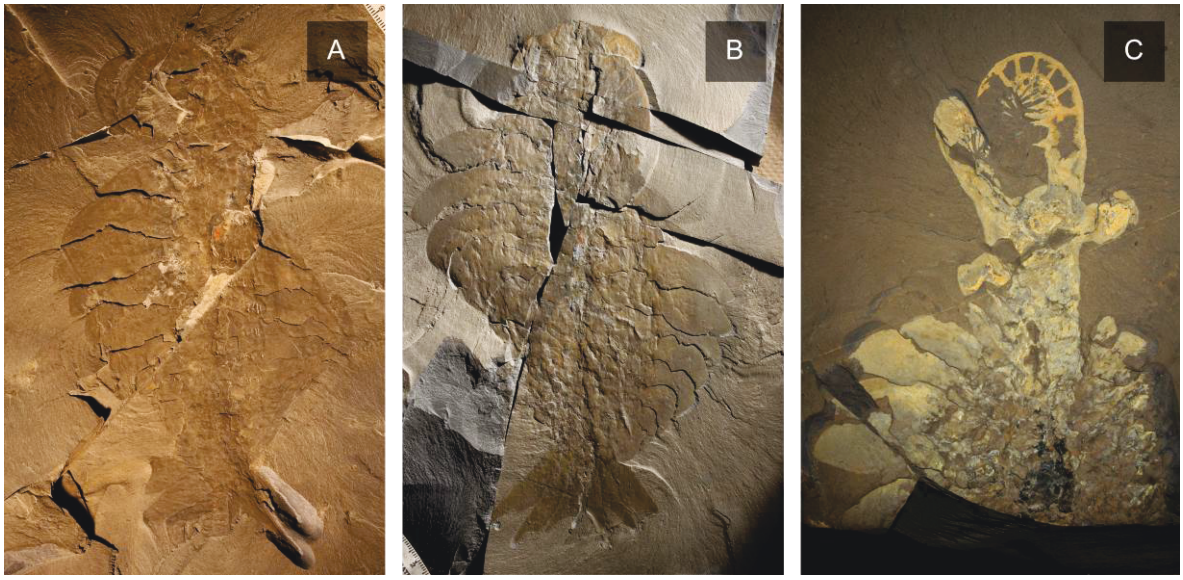


Fig. 4.4 | *Anomalocaris canadensis* Whiteaves 1892, from the middle Cambrian Burgess Shale Formation. A, ROM 51214, a dry specimen photographed using incidental lighting; **B**, ROM 51211A, a dry specimen photographed using incidental lighting; and **C**, ROM 51212, a wet specimen photographed using incidental lighting.

and arthrodization (Kühl *et al*. 2009), evolved successively in the euarthropod-stem lineage (Legg *et al*. 2012b).

A number of workers (e.g. Budd 2002, Chen *et al*. 2004, Haug *et al*. 2012c) noted similarities between the enlarged frontal appendages of anomalocaridids and „great-appendage" arthropods (*see* Fig. 6.2). A key taxon in this hypothesis is *Parapeytoia yunnanensis* Hou *et al*. 1995; this taxon was originally described as an anomalocaridid, but subsequent studies have been unable to identify putative anomalocaridid features, such as lanceolate blades and a sclerotized circum-oral cone, and have instead favoured megacheiran affinities (Daley *et al.* 2009*,* Stein 2010, Legg *et al*. 2012b). A revised view of the homology of anomalocaridid frontal appendages and megacheiran „great-appendage" is discussed elsewhere (**Chapter 7**).

Eight dinocaridids were included in the current analysis: ***Amplectobelua*** Hou *et al*. 1995, ***Anomalocaris***, ***Hurdia***, ***Kerygmachela kierkegaardi***, ***Opabinia regalis*** Walcott 1911a, ***Pambdelurion whittingtoni***, ***Peytoia nathorsti*** Walcott 1911b, and ***Schinderhannes bartelsi*** Kühl *et al*. 2009. A number of dinocaridids genera contain multiple species, including *Anomalocaris* (***A. canadensis*** Whiteaves 1892, *A. saron* Hou *et al*. 1995, *A. briggsi* Nedin 1995 [Daley *et al*. 2013]), *Amplectobelua* (***A, symbrachiata*** Hou *et al*. 1995, and *A. stephenensis* Daley and Budd 2010) and *Hurdia* (***H. victoria*** Walcott 1912, and *H. triangulata* Walcott 1912 [*see* Daley *et al*. in press]). Each genus was coded using a single species - *A. canadensis*, *A. symbrachiata*, and *H. victoria*, respectively. The other taxa assigned to these genera did not differ in coding from the selected species except in the position of missing data and were therefore excluded prior to analyses. *Cassubia infracambriensis*

Lendzion 1977 (Lendzion 1975), the oldest dinocaridid (Dzik and Lendzion 1988), may represent a composite species (pers. ob. and A. Skawina pers. comm. 05/12), and so was not included in the current analysis.

4.4. Bivalved arthropods

Bivalved arthropods are a common constituent of many Cambrian *Konservat-Lagerstätten* (Robison and Richards 1981, Briggs *et al*. 1994, Hou *et al*. 2004a), and represent an important component of some of the earliest pelagic communities (Vannier and Chen 2000). Opinion regarding the affinities of Cambrian bivalved arthropods is divided, with some authors considering them to have crustacean affinities, either within the crown-group (Walcott 1912, Resser 1929, Briggs 1976, 1977, 1978, 1992, Hou *et al*. 2004b), or as part of a more inclusive "Crustaceomorpha" Chernysheva 1960 (Schram and Koenemann 2004, Fu and Zhang 2011); "Crustaceomorpha" is a poorly defined and most likely polyphyletic grouping of crustaceans and crustacean-like taxa that excludes hexapods and myriapods. Others argue that any similarity to crustaceans is superficial with few if unequivocal features shared among these taxa; instead various Cambrian bivalved arthropods are regarded as part of the euarthropod stem-lineage, either as part of a monophyletic clade (Budd 2002), or as part of a para- or polyphyletic assemblage (Legg *et al*. 2012b, Legg 2013). Alternatively some taxa may be allied to the crustaceans, while others belong to the euarthropod stem-lineage (Briggs 1990, Hou and Bergström 1997, Wills *et al*. 1998, Hou 1999).

Cambrian bivalved arthropods display a number of different morphologies (*see* section 4.12 and 4.13.1 for more detailed discussion of mandibulate-like bivalved arthropods). A number of recent studies have highlighted similarities between Cambrian bivalved arthropods, particularly *Isoxys* Walcott 1890, and dinocaridids (Vannier *et al*. 2009, **Chapters 5-6**), emphasising the importance of these taxa in understanding the early evolution of arthropods and the origin of Euarthropoda. Recent discoveries of „great-appendage"-like limbs in Cambrian bivalved arthropods from the Burgess Shale may indicate affinities with megacheirans (Budd and Telford 2009, **Chapter 7**).

17 species of Cambrian bivalved arthropods were included in the current analysis: ***Branchiocaris pretiosa*** (Resser 1929), ***Canadaspis*** Novozhilov 1960 (***C. laevigata*** [Hou and Bergström 1991], and ***C. perfecta*** [Walcott 1912]), ***Isoxys*** (***I. acutangulus*** [Walcott 1908], ***I. auritus*** Jiang 1982, ***I. curvirostratus*** Vannier and Chen 2000, and ***I. volucris*** Williams *et al*. 1996), ***Jugatacaris agilis*** Fu and Zhang 2011, ***Loricicaris spinocaudatus*** Legg and Caron in press, ***Nereocaris*** Legg *et al*. 2012b (**Chapter 5**) (***N. exilis*** Legg *et al*. 2012b, and ***N. briggsi*** Legg and Caron in press), ***Odaraia alata*** Walcott 1912, ***Pectocaris*** Hou 1999 (***P. euryptelata*** [Hou and Sun 1988], and ***P. spatiosa*** Hou 1999), ***Perspicaris*** Briggs 1977 (***P. dictynna*** [Simonetta and Delle Cave 1975], and ***P. recondite*** Briggs 1977) and ***Protocaris***

marshi Walcott 1884. Species of *Isoxys* with soft-parts preserved were preferentially included in the current analysis; like most other genera of Cambrian bivalved arthropods, e.g. *Tuzoia* Walcott 1912, *Isoxys* is otherwise known from isolated carapaces. Isolated carapaces have been demonstrated to be of little utility in determining affinities (Siveter *et al*. 2010) and were therefore excluded from this study. The „great-appendage"-bearing Chengjiang bivalved arthropods, *Occacaris oviformis* Hou 1999, and *Forfexicaris valida* Hou 1999, are based on poorly preserved material and so were also excluded.

4.5. Fuxianhuiids

Fuxianhuiids are generally regarded as the most primitive arthropods (Chen *et al*. 1995a, Hou and Bergström 1997, Hou *et al*. 2004a, Waloszek *et al*. 2005, Bergström *et al*. 2008, Yang *et al*. 2013), and as such have figured prominently in discussion of arthropod origins. Seven unequivocal species of fuxianhuiid have been described, all from lower and middle Cambrian *Konservat-Lagerstätte* of southwest China (Hou 1987b, Hou and Bergström 1991, Chen 2005, Waloszek *et al*. 2005, Luo *et al*. 2007, Yang *et al*. 2013). Members of Fuxianhuiida Bousfield 1995, possess multi-podmerous appendages, reminiscent of lobopodian appendages, an elongate trunk, consisting of either homonomous segments or differentiated into a trunk and an abdomen, and a head capsule formed by the fusion of an anterior eye-bearing sclerite (Budd 2008) and a posteriorly expansive cephalic shield (Fig. 4.5). The appendicular composition of the fuxianhuiid head capsule has been a hotly debated issue and is discussed in detail in **Chapter 7**.

Five species of fuxianhuiid were included in the current study: ***Chengjiangocaris*** Hou and Bergström 1991 (represented by ***C. kumingensis*** Yang *et al*. 2013), ***Fuxianhuia*** Hou 1987b (represented by ***F. protensa*** Hou 1987b), ***Guangweicaris spinatus*** Luo, Fu and Hu *in* Luo *et al*. 2007 (Yang *et al*. 2008), ***Liangwangshania biloba*** Chen 2005, and ***Shankouia zhenghi*** Waloszek *et al*. 2005. *Chengjiangocaris longiformis* Hou and Bergström 1991, and *Fuxianhuia xiaoshibaensis* Yang *et al*. 2013, were not included as their coding did not significantly differ from the more completely know representatives of these genera. *Dongshanocaris foliiformis* (Hou and Bergström 1998) and *Pisinnocaris subconigera* Hou and Bergström 1998, purported fuxianhuiids (Hou *et al*. 1999) are too poorly preserved to verify their identity as a valid taxa and so were not included in the current analysis.

4.6. 'Great-appendage' arthropods

„Great-appendage" arthropods have figured prominently in recent discussion of arthropod phylogeny. Their importance was not instantly recognised, however, nor was a close relationship between various „great-appendage"-bearing taxa. Walcott

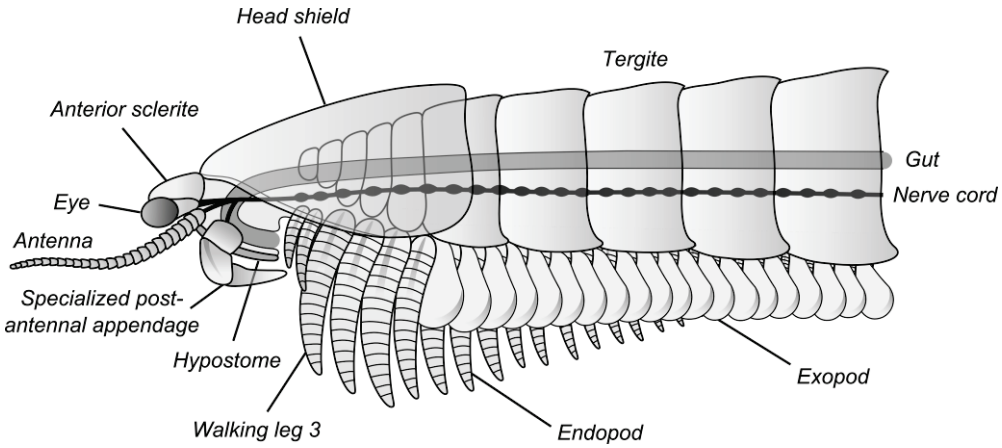


Fig. 4.5 | Reconstruction of *Chengjiangocaris kunmingensis* Yang *et al*. 2013, from early Cambrian Xiaoshilba *Konservat-Lagerstätte* in Yunnan, China. Modified after Yang *et al*. 2013, fig. 3). Image courtesy of Javier Ortega-Hernández.

(1912) allied his new Burgess Shale taxa *Leanchoilia superlata* Walcott 1912, and *Yohoia tenuis* Walcott 1912 (Fig. 6.2A-B), with separate branches of branchiopod crustaceans. Crustacean affinities were generally accepted by later workers (e.g. Fedotov 1924, Raymond 1935), with most regarding the frontal appendages as modified biramous appendages. Raymond (1935) emphasised the uniqueness of these appendage and coined the term „*great-appendage*", a term which was much later also applied to *Yohoia* (Whittington 1974). Hutchinson (1930) was perhaps the first to compare the frontal appendages of *Leanchoilia* to the chelicerae of chelicerates, suggesting they might even represent precursors of the latter, a view also advocated by Størmer (1939, 1944, 1959), although few recognised a close relationship to *Yohoia*, which was instead considered closer to crustaceans. Simonetta and Delle Cave (1975) united *Leanchoilia* and *Yohoia*, along with two other „great-appendage"-bearing arthropods from the Burgess Shale, *Actaeus armatus* Simonetta 1970 and *Alalcomenaeus cambricus* Simonetta 1970, although the reasons for doing so were not made explicit. Bergström (1980) was the first to note the shared presence of a „great-appendage" in these taxa although conceding "[It"s] impossible at present to refer the „great-appendage" arthropods to any particular group... It is not even sure that they belong together" (p. 36).

After the discovery of additional „great-appendage" arthropods from the Chengjiang biota, e.g. *Jianfengia* Hou 1987a, this opinion was seemingly altered, with Bergström (1992, Hou and Bergström 1997) later referring the „great-appendage" arthropods to a monophyletic taxon, Megacheira Hou and Bergström 1997. Since this time, megacheirans have generally been considered either representatives of the chelicerate stem-group (Bousfield 1995, Cotton and Braddy 2004, Dunlop 2005, Wills *et al*. 1998, Edgecombe *et al*. 2011, Haug *et al*. 2012c) or the euarthropod stem-group (Budd 2002, Daley *et al*. 2009). The former interpretation is based on structural similarities between the „great-appendages" of megacheirans and the chelicerae of chelicerates, both of which are chelate or

subchelate raptorial appendages with a distinct „elbow" joint (Haug *et al*. 2012a, c). The stem-group euarthropod hypothesis was originally proposed based on an absence of morphological characteristics of crown-group clades (Hou and Bergström 1997), but has since found support in some cladistic analyses (Budd 2002, Daley *et al*. 2009). In some instances (e.g. Budd 2002) the „great-appendage" has been compared to the enlarged raptorial frontal appendages of anomalocaridids, although they show little structural similarity (**Chapters 6-7**). The two hypotheses are not mutually exclusive, with some workers suggesting that megacheirans represent a transitional grade of organization between anomalocaridids and chelicerates (Bousfield 1995, Chen *et al*. 2004, Haug *et al*. 2012b). However, this hypothesis has not been demonstrated phylogenetically and is based on *a priori* assumptions of frontal limb evolution.

Fourteen species of megacheirans were included in the current analysis: ***Actaeus armatus***, ***Alalcomenaeus cambricus***, ***Fortiforceps foliosa*** Hou and Bergström 1997, ***Haikoucaris ercaiensis*** Chen *et al*. 2004, ***Jianfengia multisegmentalis*** Hou 1987a, ***Kootenichela deppi*** Legg 2013 (described in **Chapter 8**), ***Leanchoilia*** Walcott 1912 (represented by ***L. illecebrosa*** Hou 1987a, ***L. persephone*** Simonetta 1970, and ***L. superlata***) ***Oestokerkus megacholix*** Edgecombe *et al*. 2011, ***Parapeytoia yunnanensis*** (*see* section 4.3), ***Tanglangia caudatus*** Luo and Hu *in* Luo *et al*. 1999, ***Worthenella cambria*** Walcott 1911a (a putative annelid – reinterpreted in **Chapter 8**), and ***Yohoia tenuis***. *Pseudoilulia cambriensis* Hou and Bergström 1998, may be a megacheiran (*see* **Chapter 8**) but is too incompletely known to include in the current analyses.

4.7. Sanctacaris uncata

Sanctacaris uncata Briggs and Collin 1988 (Fig. 4.6), was originally considered a stem-group chelicerate (Briggs and Collins 1988, Gould 1989). Noted chelicerate features of *Sanctacaris* included: a cephalon bearing, at least six pairs of appendages, a cardiac lobe, division of the body into a putative prosoma and opisthosoma, and the presence of an anus on the last trunk segment. Subsequent phylogenetic analyses failed to resolve *Sanctacaris* close to chelicerates, instead resolving it amongst „great-appendage" arthropods, such as *Yohoia* (Wills *et al*. 1995, 1998). Chelicerate affinities were further criticized due to a lack of chelicerae (Bousfield 1995, although see Boxshall 2004 for an alternative view). Instead the cephalic appendages were reinterpreted as a „great-appendage"-like „limb basket" (Bousfield 1995), and coded as such in the phylogenetic analysis of Budd (2002), which resolve *Sanctacaris* amongst a paraphyletic assemblage of „great-appendage" arthropods.

The original material of ***Sanctacaris uncata*** (Fig. 4.6), was restudied to facilitate character coding in the current analysis. Other *Sanctacaris*-like arthropods, e.g. *Utahcaris orion* Conway Morris and Robison 1988, and *Nettapezoura basilika* Briggs *et al*. 2008, are based on poorly preserved and incomplete material and so



Fig. 4.6 | Holotype (ROM 43502) of *Sanctacaris uncata* Briggs and Collins 1988, from the Kicking Horse Member of the middle Cambrian (Series 3, Stage 5) Burgess Shale Formation. A, Part, phographed underwater using incidental lighting; **A-C**, dry specimens photographed under incidental lighting: **B**, counterpart, detailed view of the „limb-basket; **C**, part, detailed view of the right appendages; and **D**, part, detailed view of the telson.

were excluded from the current analysis. An undescribed sanctacarid (Paterson *et al*. 2008), from the lower Cambrian Emu Bay Shale, was unavailable for study.

4.8. Trilobites and trilobitomorphs

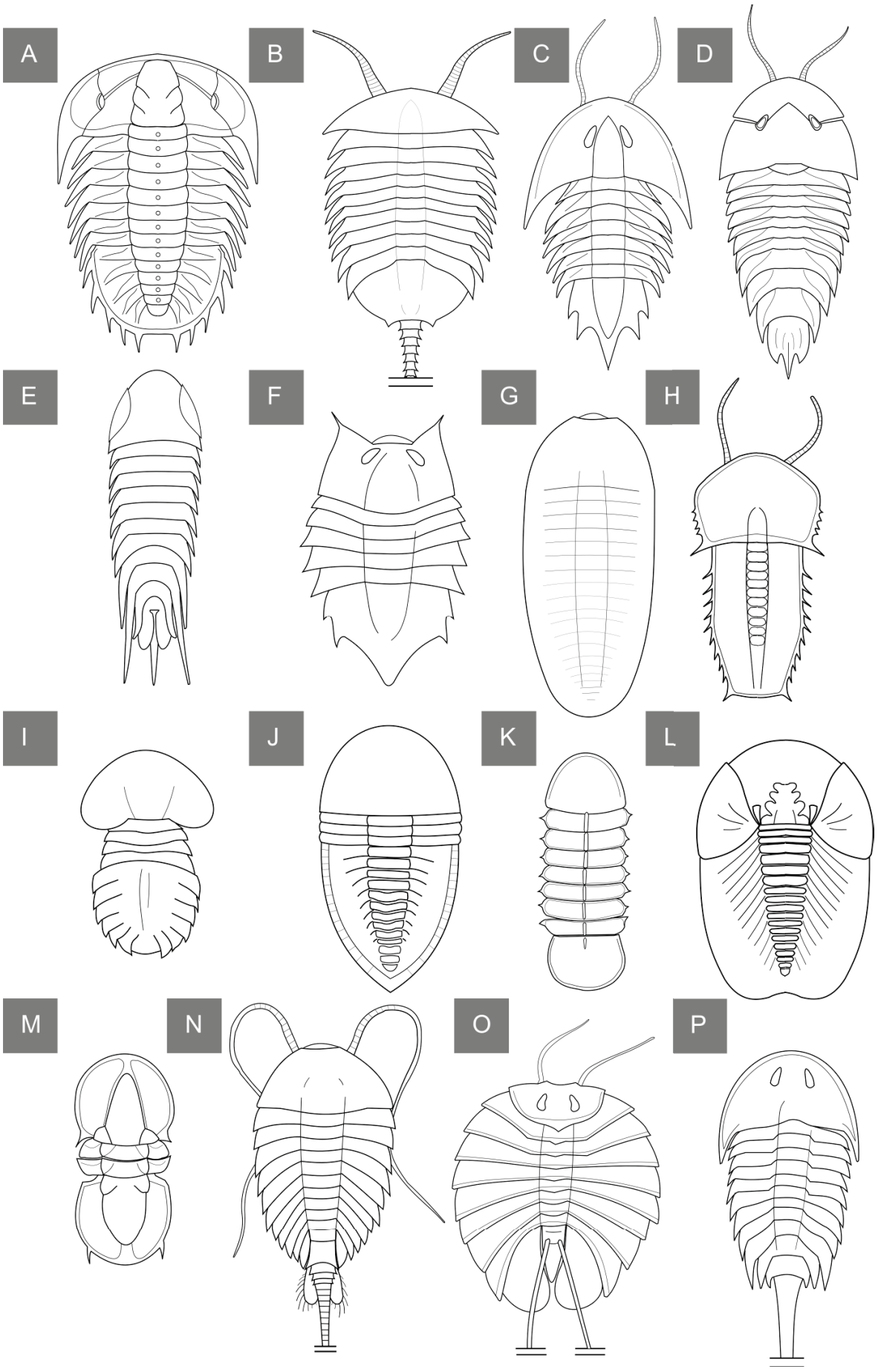
Trilobites are one of the most recognizable of fossil groups and have an extensive fossil record. Over 5000 genera have been described (Jell and Adrain 2002), encompassing some 19,606 species (Adrain 2011). They first appear in the fossil record at the base of Stage 2 (521 MYA) of the Cambrian (Geyer and Shergold 2000), defined by the roughly coeval occurrences of *Profallotaspis jakutensis* Repina *in* Khomentovskiy 1965, in Siberia (Rozanov and Sokolov 1984), *Fritzaspis* sp. in Nevada and California (Hollingsworth 2007, 2008), *Hupetina antiqua* Sdzuy 1978, in Morocco, and *Serrania gordaensis* Liñán 2008, in Spain (Hollingsworth 2008, Gradstein *et al*. 2012). Trilobite diversity reached its acme in the latest Cambrian, before declining in the Ordovician (Adrain *et al*. 1998). Their diversity continued to decline throughout the Palaeozoic (Brezinski 1999), with only five genera persisting to the end Permian and their ultimate extinction (Owens 2003).

Despite their ubiquity in the fossil record, the soft anatomy of trilobites is known from just 19 species (Hughes 2003), two of which were included in the current analysis: ***Eoredlichia intermedia*** (Lu 1940), from the Chengjiang biota, and ***Olenoides serratus*** (Rominger 1887) from the Burgess Shale (Fig. 4.7A). The commonly recovered calcite exoskeleton of trilobites is divided into three trilobed tagmata: an anterior cephalon, medial thorax, and posterior pygidium. A similar tagmosis is also widespread amongst other trilobitomorphs.

Despite numerous efforts, relationships amongst the trilobitomorphs remain partially unresolved (Edgecombe and Ramsköld 1999, Cotton and Braddy 2004, Budd 2011, Paterson *et al*. 2010, 2012, Stein and Selden 2012, Ortega-Hernández *et al*. 2013). Some clades are, however, consistently resolved in phylogenetic analyses; these clades include (1) Retifaciida Hou and Bergström 1997, (2) Petalopleura Hou and Bergström 1997 [including Xandarellida Chen, Ramsköld, Edgecombe and Zhou *in* Chen *et al*. 1996], (3) Conciliterga Hou and Bergström 1997, (4) Nektaspida Raymond 1920 [*nom. corrected* Størmer 1959, and Whittington 1985], and (5) Trilobita Walch 1771.

The retifaciids are characterized by the possession of a short, broad cephalic shield, a large oval pygidium, and an elongate multi-segmented telson (Hou and Bergström 1997, Xu 2004) (Fig. 4.7B). Just four species have been assigned to his

Fig. 4.7 (*overleaf*) | The diversity of artiopod arthropods. A, the trilobite *Olenoides serratus* Rominger 1887; **B**, the retifaciid *Retifacies abnormalis* Hou *et al*. 1989; **C**, the petalopleuran (sinoburiid) *Sinoburius lunaris* Hou *et al*. 1991; **D**, the petalopleuran (xandarellid) *Xanderella spectaculum* Hou *et al*. 1991; **E**, *Acanthomeridion serratum* Hou *et al*. 1989; **F**, the concilitergan (helmetiid) *Helmetia expansa* Walcott 1918; **G**, the concilitergan *Saperion glumaceum* Hou *et al*. 1991; **H**, the nektaspid (naraoiids) *N. spinosa* Zhang and Hou 1985; **I**, the nektaspid (liwiid) *Soomaspis splendida* Fortey and Theron 1994; **J**, the nektaspid (emucaridid) *Kangacaris zhangi* Paterson *et al*. 2010; **K**, the mollisonid *Mollisonia symmetrica* Walcott 1912; **L**, *Phytophilaspis pergamena* Ivantov 1999; **M**, the agnostid *Agnostus pisiformis* Linnaeus 1758; **N**, the vicissicaudate (xenopod) *Emeraldella brocki* Walcott 1912; **O**, the vicissicaudate (cheloniellid) *Cheloniellon calmani* Broili 1932; and **P**, the aglasipidid *Aglaspis spinifer* Raasch 1939.


A
B
C
D
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F
G
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L
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clade: ***Pygmaclypeatus daziensis*** Zhang *et al*. 2000, ***Retifacies abnormalis*** Hou *et al*. 1989, and ***Squamacula*** Hou and Bergström 1997 (including ***S. buckorum*** Peterson *et al*. 2012, and ***S. clypeata*** Hou and Bergström 1997), all of which were coded into the current analysis.

The petalopleurans are characterized by the possession of well defined pleural lobes with distinct overlap between adjoining segments (Hou and Bergström 1997) (Fig. 4.7C-D). Hou and Bergström (1997) divided Petalopleura into two orders: the monotypic Sinoburiida Hou and Bergström 1997, including the singular species ***Sinoburius lunaris*** Hou *et al*. 1991 (Fig. 4.7C); and Xandarellida, characterized by the possession of a reduced first tergite with no lateral pleura, and including ***Cindarella eucalla*** Chen, Ramsköld and Zhou *in* Chen *et al*. 1996 (Ramsköld *et al*. 1997), ***Xandarella spectaculum*** Hou *et al*. 1991 (Fig. 4.7D), and possibly also ***Luohuilinella rarus*** Zhang *et al*. 2012a. The enigmatic arthropod ***Acanthomeridion serratum*** Hou *et al*. 1989, resembles petalopleurids in overall appearance (Fig. 4.7E) and may also be referred to this group.

The concilitergans commonly resolve as the sister-taxon of trilobites in cladistic analyses (Edgecombe and Ramsköld 1999, Cotton and Braddy 2004, Ortega-Hernández *et al*. 2013), although few characters, beyond the presence of edge-to-edge pleural articulation, support this placement. Concilitergans possess a suite of characters supporting their monophyly (Ortega-Hernández *et al*. 2013), including: tear drop-shaped exopod lobes, a notched anterior cephalic margin, an anterior sclerite, and variable degrees of tergal fusion. Two distinct groups of concilitergan can be distinguished: the first, the helmetiids (Fig. 4.7F), are characterized by the possession of anteriorly reflexed tergal boundaries and broad based pygidial spines; and the second (Fig. 4.7G), a group including the skioldiids, saperiids and tegopeltids, are characterized by the possession of a fused cephalic articulation and varying degrees of trunk effacement. The latter group includes three species: ***Saperion glumaceum*** Hou *et al*. 1991, ***Skioldia aldna*** Hou and Bergström 1997, and ***Tegopelte gigas*** Simonetta and Delle Cave 1975. The helmetiids include four species: ***Helmetia expansa*** Walcott 1918, ***Kuamaia*** Hou 1987b (represented by ***K. lata*** Hou 1987b, and ***K. muricata*** Hou and Bergström 1997), and ***Rhombicalvaria acantha*** Hou 1987b. ***Australimicola spriggi*** Paterson *et al*. 2012, may also be referred to Conciliterga.

The nektaspids are the longest ranging and geographically widespread of the non-trilobite trilobitomorphs, which are otherwise restricted to the Cambrian (Hendricks and Lieberman 2007, Hendricks *et al*. 2008). The oldest nektaspid is ***Liwia plana*** (Lendzion 1975) [= ***Liwia convexa*** (Lendzion 1975), synonymised by Ramsköld *et al*. 1996], from the lower Cambrian (Series 3, Stage 2) of Poland (Dzik and Lendzion 1988), and the youngest is *Naraoia bertiensis* Caron *et al*. 2004, from the Upper Silurian (Přídolian) of Canada. Three distinct morphologies occur within nektaspids. In the first, represented by the naraoiids (Zhang *et al*. 2007), taxa possess a simple tagmosis, consisting of a single articulation and no free thoracic segments (Fig. 4.7H). The current analysis included six species of naraoiids: ***Misszhouia longicaudata*** (Zhang and Hou 1985), and five species of ***Naraoia***

Walcott 1912 (***N. bertiensis***, ***N. compacta*** Walcott 1912, ***N. spinifer*** Walcott 1931, ***N. spinosa*** Zhang and Hou 1985, and ***N. tianjiangensis*** Peng *et al*. 2012). Other purported naraoiids, namely, the late Cambrian *Martitimella rara* Repina and Okuneva 1969, and the Ordovician *Pseudonaraoia hammanni* Budil *et al.* 2003, were not included in the current analysis as they are either too poorly preserved and/or may represent pseudofossils (Robison 1984).

Other nektaspids possess free thoracic tergites, albeit a reduced number, and a represented by the liwiids (Dzik and Lendzion 1988, Budd 1999b) (Fig. 4.7.I), and the emucaridids (Paterson *et al*. 2010) (Fig. 4.7J). The emucaridids possess a bipartite hypostome and an elongate pygidium, which accounts for more than half the length of the entire trunk (Fig. 4.7J). Three species have been assigned to Emucarididae Paterson *et al*. 2010 – ***Emucaris fava*** Paterson *et al*. 2010, and two species of ***Kangacaris*** Paterson *et al*. 2010 (***K. shui*** Zhang *et al*. 2012b, and ***K. zhangi*** Paterson *et al*. 2010). Liwiids are typically isopygous, i.e. their pygidium and cephalon are roughly equal in size (Fig. 4.7I). Budd (1999b) assigned four monotypic genera to Liwiidae Dzik and Lendzion 1988; all four species were included in the current analysis: ***Buenaspis forteyi*** Budd 1999b, ***Liwia plana***, ***Soomaspis splendida*** Fortey and Theron 1994, and ***Tarricoia arrusensis*** Hammann *et al*. 1990.

As well as those clades described above, a number of other Palaeozoic arthropods may be aligned with the trilobitomorphs. *Mollisonia* Walcott 1912, from the Burgess Shale, possesses a short thorax and an isopygous pygidium (Simonetta 1964) (Fig. 4.7K), akin to the liwiids. It has, however, been excluded from major works on arthropod phylogeny (e.g. Hou and Bergström 1997), in part, because limbs are unknown from this taxon (Conway Morris and Robison 1988). Two species of *Mollisonia* were included in the current analysis ***M. sinica*** Zhang *et al*. 2002, and ***M. symmetrica*** Walcott 1912. A third species of *Mollisonia*, ***M. gracilis*** Walcott 1912, was assigned its own genus ***Houghtonites*** Raymond 1931, although this taxon is only sporadically applied (*cf*. Simonetta and Delle Cave 1975, and Briggs *et al*. 1994). Other taxa commonly allied with *Mollisonia* were also included in the current analysis; this includes ***Ecnomocaris spinosa*** Conway Morris and Robison 1988, from the middle Cambrian of Utah; ***Thelxiope palaeothalassia*** Simonetta and Delle Cave 1975, from the Burgess Shale, and ***Urokodia aequalis*** Hou *et al*. 1989, from the Chengjiang biota.

Other taxa clearly belong within Trilobitomorpha Størmer 1944, but their affinities remain uncertain. ***Phytophilaspis pergamena*** Ivantov 1999 (Fig. 4.7L), from the lower Cambrian Sinsk Biota of Siberia, was originally considered a concilitergan, based primarily on the fusion of its thoracic and pygidial segments, a feature also observed in nektaspids (Cotton and Braddy 2004). Others have highlighted other features possibly indicative of other relationships; the presence of eye slits and extensive cephalic overlap of the thoracic segments may be indicative of xandarellid affinities (Bergström and Hou 2004, Cotton and Braddy 2004), whilst the hypostome is similar to that of trilobites (Ivantov 1999, Cotton and Braddy 2004).

Other taxa whose relationships remain unresolved were also included in this analysis: ***Aaveqaspis inesoni*** Peel and Stein 2009, ***Campanamuta mantonae*** Budd 2011, ***Panlongia*** Liu *et al*. 2006 (***P. spinosa*** Liu *et al*. 2006, and ***P. tetranodosa*** Liu *et al*. 2006), and ***Siriocaris trollae*** Lagebro *et al*. 2009. Although ***Kiisortoqia soperi*** Stein 2010, was originally described as a „great-appendage" arthropod, the „frontal-appendages" in no way resemble „great-appendages" (*see* **Chapter 7**), and instead this taxon may represent a trilobitomorph.

4.8.1. Agnostus pisiformis

The agnostids have long been considered an aberrant clade of trilobites (Fortey 1997), however, the discovery of phosphatised specimens of ***Agnostus pisiformis*** Linnaeus 1758 (Fig. 4.7M), from the late Cambrian „Orsten" fauna (Müller and Walossek 1987), led to a reevaluation of agnostid affinities (Walossek and Müller 1990). They are now commonly regarded as stem-group crustaceans (Bergström and Hou 2005; Haug *et al*. 2010a, c), based on the morphology of their appendages, and have thus been excluded from cladistic analyses of trilobitomorphs (*see* Edgecombe and Ramsköld 1999). Cotton and Fortey (2004) challenged this opinion, instead regarding agnostids as derived eodiscid trilobites. Their analysis did not have an appropriate outgroup however, and was additionally weakend by the coding of a large number of autapomorphies for agnostids , and a lack of consideration of limb morphology.

4.9. Vicissicaudates

Ortega-Hernández *et al*. (2013) recently recognized a grouping of Palaeozoic arthropods united by the shared presence of a differentiated post-abdominal area lacking appendages. This clade, Vicissicaudata Ortega-Hernández *et al*. 2013, encompasses the xenopods, cheloniellids, and agalspidids, the close affinities of which have been recovered in other phylogenetic analyses (Edgecombe and Ramsköld 1999, Cotton and Braddy 2004, Paterson *et al*. 2010, 2012, Edgecombe *et al*. 2011). This clade in turn may represent the sister-taxon of Trilobitomorpha (Cotton and Braddy 2004, Ortega-Hernández *et al*. 2013), which together form the clade Artiopoda (Hou and Bergström 1997), a group characterized by the possession of lamella-bearing bilobate exopod shafts on post-antennal limbs (Stein and Selden 2012).

Xenopoda Raymond 1920 (*sensu* Hou and Bergström 1997), includes three species, all of which were included in the current analysis: ***Emeraldella*** Walcott 1912 (***E. brocki*** Walcott 1912 [Fig. 4.7N], and ***E. brutoni*** Stein *et al*. 2011), and ***Sidneyia inexpectans*** Walcott 1911c. These taxa all possess latero-ventral „flaps" projecting from a cylindrical pre-telson somite (Hou and Bergström 1997, Stein *et al*. 2011, Ortega-Hernández *et al*. 2013). Stein *et al*. (2011) also presented evidence for

the close affinities of *Emeraldella* and ***Molaria spinifera*** Walcott 1912, including the shared possession of a flagelliform telson, elongate caudal tergites lacking extensive pleura, and an anterior articulating ridge on the tergite; however, none of these characters are restricted to these taxa. Few studies have supported the monophyly of xenopods instead tending to resolve *Sidneyia* and *Emeraldella* as successive plesions of Cheloniellida Broili 1933 (Cotton and Braddy 2004, Edgecombe *et al*. 2011, Ortega-Hernández *et al*. 2013).

Like xenopods, the cheloniellids possess a pair of modified appendages on their pre-telson somite; these structures are arguably homologous (Ortega-Hernández *et al*. 2013), however, unlike the xenopod „flaps", the furcae of cheloniellids are dorsally located (Fig. 4.7O). The cheloniellids are characterized by their possession of an unfused or reduced cephalic shield and anterio-laterally flexed trunk tergites (Dunlop and Selden 1997, Ortega-Hernández *et al*. 2013). Six described species of cheloniellids were included in this study: ***Cheloniellon calmani*** Broili 1932, ***Duslia insignis*** Jahn 1893, ***Neostrabops martini*** Caster and Macke 1952, ***Paraduslia tailmaae*** Dunlop 2002, ***Pseudoarthron whittingtoni*** Selden and White 1984, ***Triopus draboviensis*** Barrande 1872; and undescribed taxon from the Fezouata Formation of Morocco (Van Roy 2006b, Van Roy *et al*. 2010), was also included.

For a long time the agalspidids were treated as a „bucket taxon" for problematic taxa (Van Roy 2006b, Ortega-Hernández *et al*. 2013). Systematic study of various aglaspidid taxa (Van Roy 2006b, Ortega-Hernández *et al*. 2010a, b, 2013, Lerosey-Aubril *et al*. 2013) has helped to „clear out the wastebasket" and now a stable diagnosis of aglaspidids is starting to emerge. Ortega-Hernández *et al*. (2013) made the distinction between Aglaspidida *sensu lato* Walcott 1911c [*nom. corrected* Briggs *et al*. 1979] and Aglaspidida *sensu stricto*; under this scheme aglaspidids are broadly characterized by the presence of an elevated marginal rim and differentiated glabellar lobes, whereas true aglaspidids (Aglaspidida *sensu stricto*) are those taxa with a mineralized cuticle, anterior tergal processes and postventral plates (Fig. 4.7P). Taxon sampling follows Ortega-Hernández *et al*. (2013) and includes 14 described species: ***Aglaspella granulifera*** Raasch 1939, ***Aglaspis spinifer*** Raasch 1939, ***Australaglaspis stonyensis*** Ortega-Hernández *et al*. 2010a, ***Beckwithia typa*** Resser 1931, ***Chlupacaris dubia*** Van Roy 2006a, ***Chraspedops modesta*** Raasch 1939, ***Cyclopites vulgaris*** Raasch 1939, ***Flobertia kochi*** Hesselbo 1992, ***Glypharthrus thomasi*** (Walter 1924), ***Kodymirus vagans*** Chlupáč and Havlíček 1965, ***Kwanyinaspis maotianshanensis*** Zhang and Shu 2005, ***Quasimodaspis brentsae*** Waggoner 2003, ***Tremaglaspis unite*** Fortey and Rushton 2003 (Fortey and Rushton 2009), ***Uarthrus instabilis*** Raasch 1939; and an undescribed taxon from the Ordovician of China (Fortey and Theron 1994, Ortega-Hernández *et al*. 2013).

Raasch (1939) considered aglaspidids to be merostomates, closely allied to xiphosurans. This view was adopted by most subsequent workers (e.g. Størmer 1944), however, Briggs *et al*. (1979) rejected chelicerate affinities after additional

preparation of *Aglaspis spinifer* specimens was unable to reveal chelicerae, and Hesselbo (1992) considered the frontal appendages of this taxon to be antenniform. Despite this, subsequent phylogenetic analyses continued to recover close affinities between aglaspidids and chelicerates (e.g. Wills *et al*. 1995, 1998, Dunlop and Selden 1997), although these studies did not consider the antennae of aglaspidids and trilobites to be homologous to the chelicerae of chelicerates (*see* **Chapter 7**). These same studies have also recovered cheloniellids as the sister-taxon of euchelicerates.

4.10. Marrellomorphs

The marrelomorphs are a small group of Palaeozoic arthropods, renowned for their bizarre morphology (Van Roy 2001). Although generally regarded as a clade (Kühl *et al*. 2008, Rak *et al*. in press), some workers have cast doubt on its monophyly (Hou and Bergström 1997, Lin *et al*. 2006). The marrellomorphs can be broadly divided into two groups, the Marrellida Raymond 1935 [*nom. corrected* Størmer 1944], and the Acercostraca Lehmann 1955 (Fig. 4.8). The marrellids are characterized by the possession of extensive mediolateral extensions of the cephalic shield, and a lack of tergal pleura (Kühl *et al*. 2008) (Fig. 4.8). The acercostracans are characterized by the possession of a large dorsal shield that covers the entire body and appendages (Kühl *et al*. 2008) (Fig. 4.8). There are few characters shared by these two groups, although the possession of numerous (more than 25) trunk appendages, which reduce in size towards the posterior of the animal, has been considered diagnostic of this clade (Wills *et al*. 1995, 1998).

Like many other Palaeozoic arthropods, the affinities of marrellomorphs have remained enigmatic, with various hypotheses proposed. Briggs and Fortey (1989) and Wills *et al*. (1995, 1998) considered them the most primitive biramous arthropods, based on their pattern of head segmentation. Siveter *et al*. (2007a), reanalysed the data set of Wills *et al*. (1998), but modified it by including their newly described taxon, *Xylokorys chledophilia* Siveter *et al*. 2007a, and instead resolved marrellomorphs as stem-lineage crustaceans; a position also recovered by Ortega-Hernández *et al*. (2013).

Generally just five species are unequivocally assigned to Marrellomorpha Beurlen 1930 (Fig. 4.8); note that although the name Marrellomorpha is often attributed to Beurlen (1934), it name was actually proposed four years earlier (Beurlen 1930, p. 503-504). Three previously described species of marrellid were included in the current analysis: ***Furca bohemica*** Fritsch 1908, from the Ordovician Letna Formation in the Czech Republic (Rak *et al*. in press), ***Marrella splendens*** Walcott 1912, from the Burgess Shale in Canada (García-Bellido and Collins 2006), and ***Mimetaster hexagonalis*** (Gürich 1931), from the Devonian Hünsruck Slate in Germany (Kühl and Rust 2010); an undescribed marrellomorph from the Ordovician Fezouta Formation of Morocoo (Van Roy 2006b, Van Roy *et al*. 2010), was also included. Just two species of acercostracan have been described: ***Vachonisia***

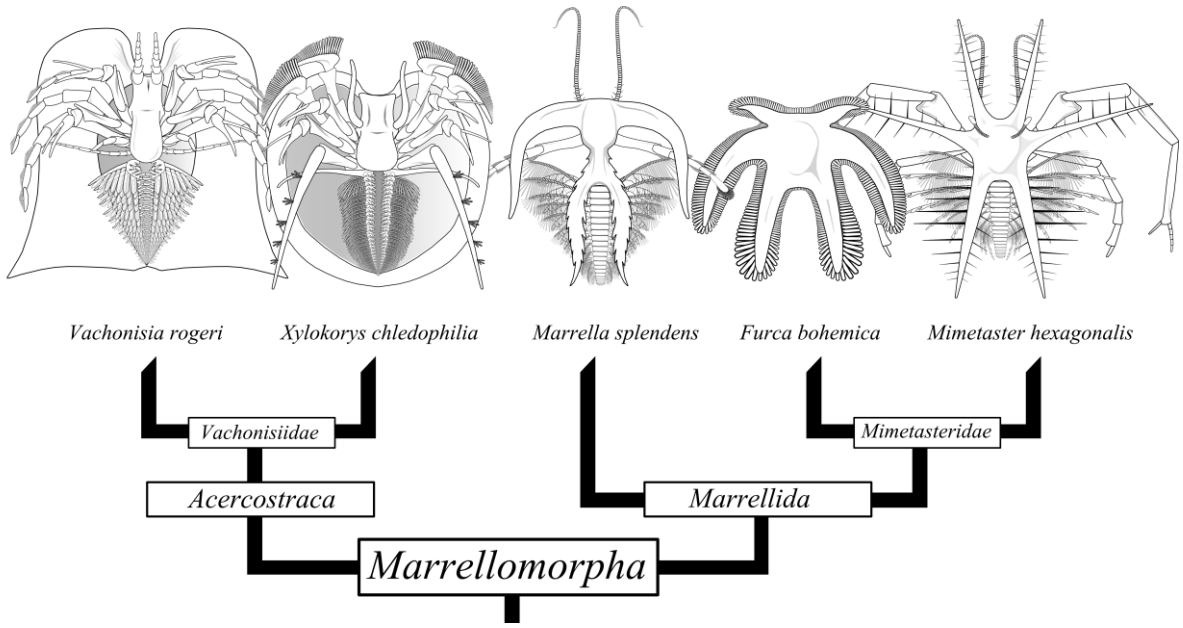


Fig. 4.8 | The phylogeny of marrellomorph arthropods. Modified after Rak *et al*. (in press, fig. 8).

rogeri (Lehmann 1955), and ***Xylokorys chledophilia***. Other potential marrellomorphs, namely *Marria walcotti* Ruedemann 1931, and *Paramarria galenensis* Wells 1944, might not even be arthropods (Simonetta 1962) and so were not included in the current analysis.

4.11. Parvancorinomorphs and other putative 'Precambrian arthropods'

Lin *et al*. (2006) questioned the monophyly of Marrellomorpha, instead considering *Vachonisia* a possible post-Cambrian representative of Parvancorinomorpha Lin *in* Lin *et al*. 2006, based on the shared possession of a single dorso-ventrally flattened shield with a heart shaped body cavity. Lin *et al*. (2006) also argued that a similar dorsal shield was present in the purported Precambrian „arthropods", *Mialsemia semichatovi* Fedonkin 1985, *Parvancorina minchami* Glaessner 1958, *Praecambridium sigillum* Glaessner and Wade 1966, and *Vendia sokolovi* Keller 1969. The arthropod affinities of these taxa are highly questionable (Naimark and Ivantov 2009). All have the glide reflection symmetry characteristic of many Ediacaran organisms (Waggoner 1996), as opposed to bilateral symmetry in arthropods, and they are not included in this analysis.

The „skaniids" were also assigned by Lin *et al*. (2006) to Parvancorinomorpha. Three described species of skaniids were included in the current analysis: ***Primicaris larvaformis*** Zhang *et al*. 2003, and ***Skania*** Walcott 1931 (***S. fragilis*** Walcott 1931 [Fig. 4.9], and ***S. sundbergi*** Lin *in* Lin *et al*. 2006); and an undescribed

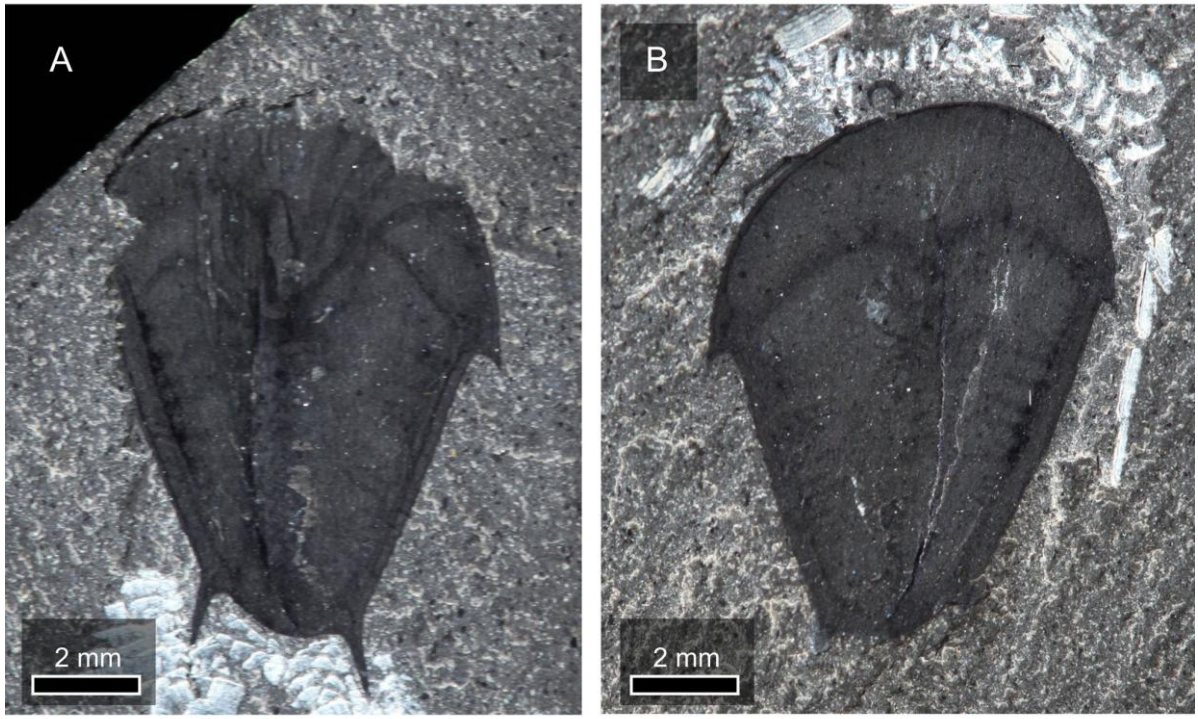


Fig. 4.9 | The holotype (NMNH 83950) of *Skania fragilis* Walcott 1931 from the Walcott Quarry Member of the middle Cambrian (Series 3, Stage 5) Burgess Shale Formation. **A**, part; and **B**, counterpart.

skaniid from the Ordovician of Morocco (Van Roy *et al*. 2010). Unlike other parvancorinomorphs, skaniids possess unequivocal arthropod features, including arthropodized appendages, setiferous exites, and a hypostome.

4.12.Bradoriids

The bradoriids are a poorly defined group, and possible „waste-basket" taxon (Jones and McKenzie 1980), of early Palaeozoic pelagic and epibenthic bivalved arthropods. The first bradoriids occur in the lower Cambrian, just prior to the first appearance of trilobites in the overlying *Parabadiella* Biozone (Hou *et al*. 2002, Topper *et al*. 2011), and the group went extinct in the middle Ordovician (Williams *et al*. 2007), between which they established a cosmopolitan distribution (Williams *et al*. 2007). Bradoriids are known from a number of Cambrian *Konservat-Lagerstätten*, including the Burgess Shale (Siveter and Williams 1997), Sirius Passet (Siveter *et al*. 1996), and the Chengjiang biota (Hou *et al*. 2002, Hou *et al*. 2010, Duan *et al*. in press). The latter is significant in preserving the only evidence of bradoriid soft-part anatomy in the fossil record (Hou *et al*. 1996, 2010, Shu *et al*. 1999, Duan *et al*. in press). The soft-anatomy is known from just two species: ***Kunmingella douvillei***

(Mansuy 1912), and ***Kunyangella cheni*** Huo 1965; however, its discovery finally allowed hypotheses regarding their affinities to be tested (Hou *et al*. 2010).

Bradoriida Raymond 1935, were traditionally allied to ostracods (e.g. Sylvester-Bradley 1961), a view still upheld by some (e.g. Hinz 1993, Gonzalo and Hinz-Schallreuter 2002). Arguments in favour of this assignment typically centre on the shared presence of a bivalved carapace, a feature that has convergently evolved in numerous arthropod groups (Walossek 1993, Legg *et al*. 2012b) and is therefore unlikely to be a reliable diagnostic character. The soft-anatomy of bradoriids precludes their alignment with ostracods, or even to crown-group crustaceans (Hou *et al*. 1996). Hou *et al*. (2010) coded both bradoriids and phosphatocopids (*see* section 4.13.1) into the phylogenetic matrix of Wills *et al*. (1998), and resolved both as part of the crustacean stem-lineage, consistent with previous hypotheses of relationship based on soft-part anatomy (Hou *et al*. 1996, Shu *et al*. 1999, Williams *et al*. 2007, 2008).

4.13.'Orsten' crustaceomorphs

The term „Orsten" is used to refer to preservation of small fossils, typically less than 2 mm (Maas *et al*. 2006), by calcium phosphate replacement (Edgecombe and Legg 2013). Originally named for the „Orsten" stinkstone of Sweden (Müller 1964, 1979a), this style of preservation is geographically widespread (Maas *et al*. 2006), occurring in Australia (Walossek *et al*. 1993), Canada (Roy and Fåhræus 1989, Walossek *et al*. 1994), Russia (Müller *et al*. 1995), China (Dong *et al*. 2005a, b), Poland (Walossek and Szaniawski 1991), and the UK (Siveter *et al*. 2001, 2003b), and occurs from the lower Cambrian (Siveter *et al*. 2001, 2003b) to the lower Ordovician (Andres 1989, Roy and Fåhræus 1989).

The most common components of „Orsten" faunas are „crustacean" meiofauna (Walossek and Müller 1998). Some of these taxa may be referred to crown-group Crustacea. *Skara* Müller 1983, resembles extant copepods and mystacocarids (Haug *et al*. 2011b); *Rehbachiella kinnekullensis* Müller 1983, represents a stem-lineage branchiopod (Walossek 1993, Olesen 2004, 2007, 2009), and *Yicaris dianensis* Zhang *et al*. 2007, is comparable to extant cephalocarids and branchiopods.

Most „Orsten" „crustaceans" lack definite features of the crustacean crown-group, and instead have been considered stem-group eucrustaceans (Haug *et al*. 2010a, b). Such forms include: *Agnostus pisiformis* (*see* section 4.8.1), ***Cambropachycope clacksoni*** (Walossek and Müller 1990) , ***Goticaris longispinosa*** (Walossek and Müller 1990), ***Henningsmoenicaris scutula*** (Walossek and Müller 1990), ***Martinssonia elongata*** Müller and Walossek 1986, ***Musacaris gerdgeyeri*** Haug *et al*. 2010b, ***Oelandocaris oelandica*** Müller 1983, and ***Sandtorpia vestrogothiensis*** Haug *et al*. 2010a, all of which were included in the current analysis.

4.13.1. Phosphatocopids

The phosphatocopids are a cosmopolitan clade of bivalved arthropods, typically just represented in the fossil record by isolated carapace valves (Waloszek 1999). Their soft-anatomy is known exclusively from those found in „Orsten" deposits (Walossek *et al*. 1993, Siveter *et al*. 2001, 2003b, Dong *et al*. 2005a, b). Like the bradoriids (*see* section 4.12), phosphatocopids were originally thought to share affinities with the ostracods (Müller 1964), however, they lack eucrustacean synapomorphies, and instead have been placed on the eucrustacean stem-lineage (Siveter *et al*. 2003b, Maas and Waloszek 2005). Siveter *et al*. (2003b) placed Phosphatocopida Müller 1964 as sister-taxon to Eucrustacea Kingsley 1894, within Labrophora Siveter *et al*. 2003b, so-named because of the shared presence of an enlarge, overhanging „lip".

Roughly 60 species of phosphatocopid have been described (Waloszek 1999, Siveter *et al*. 2003b). Three species were included in the current study: ***Hesslandona*** Müller 1964 (represented by ***H. angustata*** Maas *et al*. 2003, ***Klausmuelleria salopensis*** Siveter *et al*. 2003b, and ***Vestrogothia*** Müller 1964 (represented by ***V. spinata*** Müller 1964).

4.14. Tanazios dokeron

Tanazios dokeron Siveter *et al*. (2007c) (Fig. 4.10), from the Silurian Herefordshire *Konservat-Lagerstätte*, has a simple tagmosis, consisting of a cephalon and a long, homonomous trunk comprising 64 segments, each bearing a pair of biramous appendages. Siveter *et al*. (2007c) likened the trunk to that of remipedes or myriapods, and using the data matrix of Wills *et al*. (1998), resolved *Tanazios* as part of the eucrustacean stem-lineage but noted it lacks features of Labrophora, such as a lack of well-defined coxa on the antennae; Labrophora are the least inclusive group containing phosphatocopids and eucrustaceans, united by the presence of a fully formed mandible on the first post-antennal segment (Siveter *et al*. 2003b).

Boxshall (2007) questioned the conclusions of Siveter *et al*. (2007c), noting that many adult crustaceans lack antennal coxae, although they may be present earlier in their ontogeny. Boxshall (2007) also reinterpreted the head configuration of *Tanazios*, as proposed by Siveter *et al*. (2007c), instead regarding the short antennulae (*sensu* Siveter *et al*. 2007c), as frontal filaments, sensory organs originating from the protocerebral neuromeres of the brain (Frase and Richter 2013). Coding using this reinterpretation, recent computational cladistic analyses have resolved *Tanazios* as part of the mandibulate stem-lineage (Rota-Stabelli *et al*. 2011). ***Tanazios dokeron*** was included in the current analysis and coded using Siveter *et al*. (2007c), with the subsequent reinterpretations of Boxshall (2007).

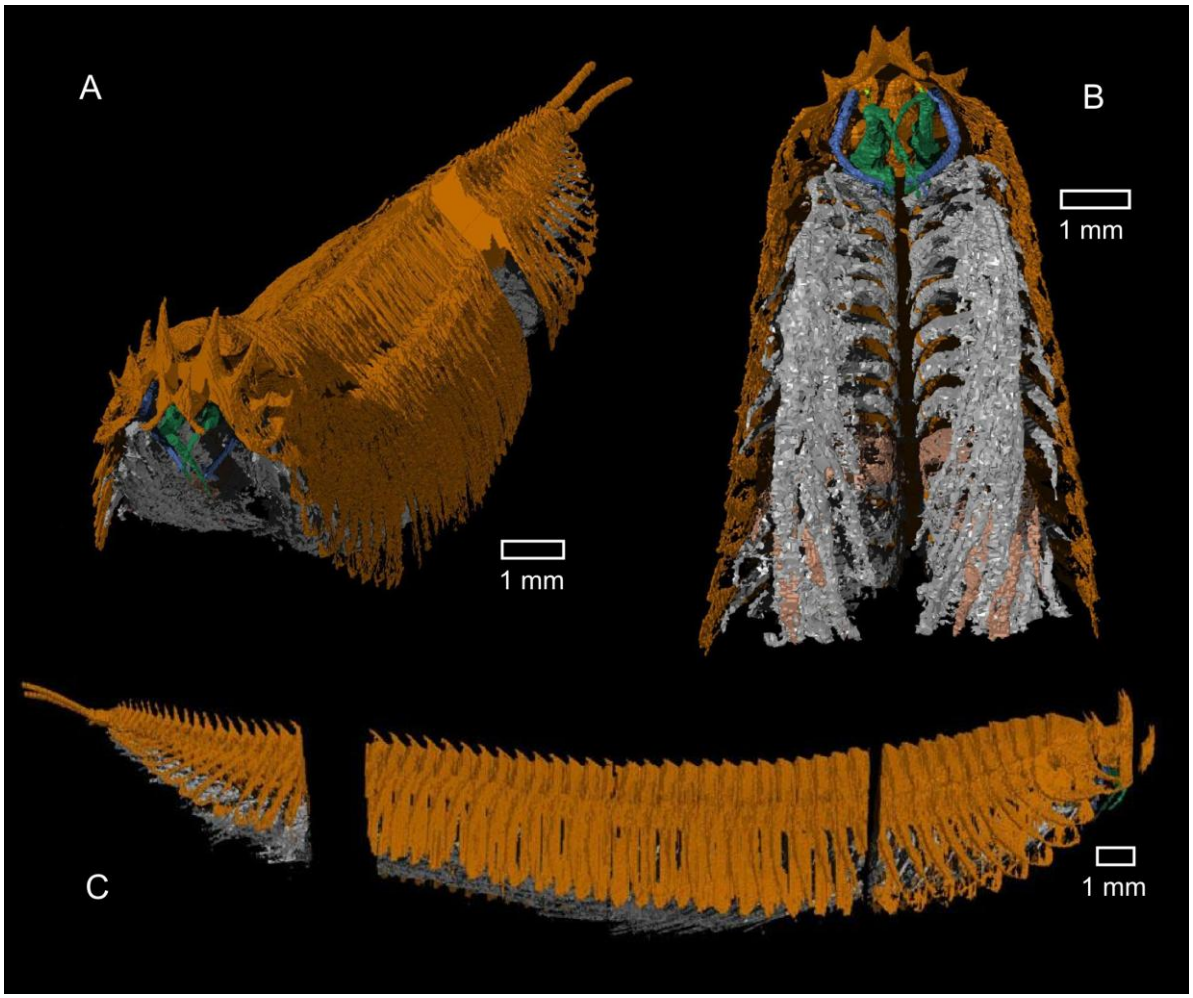


Fig. 4.10 | A virtual reconstruction of the holotype (OUMNH C. 29601) of *Tanazios dokeron* Siveter *et al*. 2007b, from the Wenlock (Silurian) Herefordshire *Konservat-Lagerstätte*. A, anterolateral view; **B**, anteroventral view of the head region; and **C**, lateral view.

4.15. Euthycarcinoids

Euthycarcinoids are characterized by the possession of multi-podomerous uniramous appendages, a bipartite cephalon, and a trunk divided into a distinct pre- and post-abdominal region (Ortega-Hernández *et al*. 2010c). Perhaps no other groups has undergone as many, or as disparate, phylogenetic reassignments as the euthycarcinoids (Edgecombe and Morgan 1999); they have variously been regarded as trilobitomorphs (Reik 1964, Schram 1971), as sister-taxon to aglaspidids (Starobogatov 1988), as sister-taxon to Euarthropoda (Schram and Emerson 1991) as an independent branch of arthropod evolution (Delle Cave and Simonetta 1991), or with affinities to chelicerates and hexapods (Simonetta and Delle Cave 1980). Most studies favour mandibulate relations for euthcarcinoids, however, and they have variously been regarded as copepods (Handlirsch 1914), branchiopods (Riek 1968), a separate class of crustaceans (Gall and Grauvogel 1964), or an aquatic

ancestor of extant uniramous arthropods (Bergström 1979, 1980, Schram and Rolfe 1982, Schultka 1991, McNamara and Trewin 1993, Wills *et al*. 1995, 1998). The most recent cladistic analyses to include euthycarcinoids resolved them as stem-mandibulates (Vaccari *et al*. 2004).

Nine unequivocal euthycarcinoids were included in the current analysis: ***Apankura machu*** Vaccari *et al*. 2004, ***Euthycarcinus*** Handlirsch 1914, ***Heterocrania ryniensis*** (Hirst and Maulik 1926), ***Kalbarria brimmellae*** McNamara and Trewin 1993, ***Kottixerxes*** Schram 1971, ***Schramixerxes gerem*** (Schram and Rolfe 1982), ***Smithixerxes*** Schram and Rolfe 1982, ***Sottyxerxes*** Schram and Rolfe 1982, and ***Synaustrus brookvalensis*** Riek 1964. Non-monospecific taxa were coded according to their most completely known representatives: *Euthycarcinus* (*E. ibbenburensis* Schultka 1991, ***E. kessleri*** Handlirsch 1914, and *E. martensi* Schneider 1983), *Kottixerxes* (*K. anglicus* Wilson and Almond 2001, and ***K. gloriosus*** Schram 1971), *Smithixerxes* (***S. juliarum*** Schram and Rolfe 1982, and *S. pustulosus* Wilson and Almond 2001), and *Sottyxerxes* (***S. multiplex*** Schram and Rolfe 1982, and *S. pieckoae* [Schram and Rolfe 1982]). The euthycarcinoid-like ***Arthrogyrinus platyurus*** Wilson and Almond 2001, was also included.

5. New bivalved arthropods from the Burgess Shale

5.1. Introduction

The Burgess Shale Formation and neighbouring Stephen Formation, located in the Canadian Rocky Mountains, are renowned for containing an exceptionally well-preserved fossil fauna including some of the earliest representatives of extant phyla, and their putative stem-group representatives (Gould 1989, Briggs and Fortey 2005, Brysse 2008). A large number of stem-group euarthropods have been recovered from these sites (**Chapter 4**), including members thought to be close to the base of the crown-group („upper stem-group euarthropods" *sensu* Budd 2008), such as bivalved arthropods (section 4.4), megacheirans (section 4.6) and *Sanctacaris uncata* Briggs and Collins 1988 (section 4.7) (Budd 2002, 2008). The purported basal placement of these taxa with regards to the euarthropod crown-group makes them of particular importance for understanding the plesiomorphic condition of Euarthropoda, and polarizing relationships amongst its constituent clades (Budd 2008, Budd and Telford 2009). The following **chapters** (**5-8**) contain detailed descriptions of putative „upper stem-group euarthropods from the Burgess Shale Formation and Stephen Formation, including descriptions of new material (herein, **Chapter 8**) and re-examinations of previously described material (**Chapters 6-7**). The observations made within these chapters were coded into the phylogenetic analysis (**Chapter 3, Appendix 2**), the results of which are discussed in **Chapter 10**.

A diverse assemblage of bivalved arthropods is known from the Middle Cambrian (Series 3, Stage 5) Burgess Shale Formation in British Columbia, Canada (Walcott 1912, Whittington 1974, Briggs 1976, 1977, 1978, 1981, Briggs *et al*. 1994, García-Bellido *et al*. 2009b). The majority of these taxa were originally discovered and described by Charles Doolittle Walcott (1912), with later additions by Charles Resser (1929), based on Walcott"s original material. At the time, few Burgess Shale-type

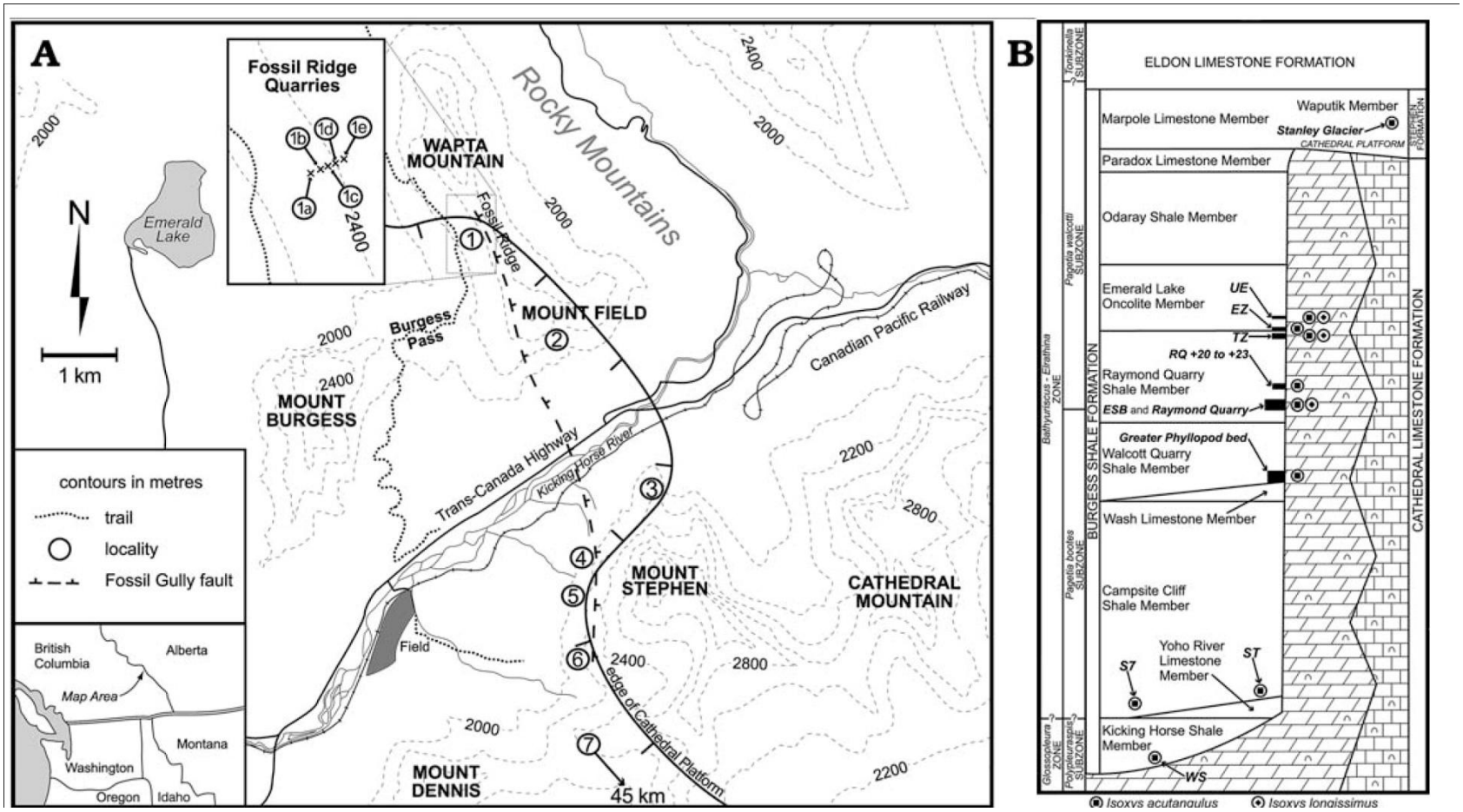


Fig. 5.1 | The distribution of Burgess Shale-type (BST) localities in the vicinity of Field, British Columbia. Reproduced from García-Bellido *et al*. (2009b). **A**, Topographical map. Numbers indicate localities yielding Burgess Shale-type fossils: 1, West slope of Fossil Ridge: 1a, Greater Phyllopod bed, Walcott Quarry; 1b, Raymond Quarry; 1c, "*persephone* layer" (RQ +20 to +23); 1d, "*Tuzoia* layer"; 1e, Collins Quarry – "*Ehmaniella* Zone" (EZ) and "Upper "*Ehmaniella*" (UE); 2, South face of Mt. Field; 3, North shoulder of Mt. Stephen (ESA, ESB); 4, S7 locality (= Tulip beds); 5, Mt. Stephen Collins Quarry (WS) (formerly locality 9); 6, Mt. Stephen Trilobite Beds (ST); 7, Stanley Glacier. **B**, Stratigraphic section of the Burgess Shale and Stephen Formation. Circles indicate layers where *Isoxys* Walcott 1890, were recovered.

localities (BSTs) were known, with the majority of material collected from the „Phyllopod Bed" (Fig. 5.1), formerly United States National Museum (USNM) locality 35k, situated between Mount Field and Wapta Mountain in Yoho National Park (British Columbia, Canada). Most of the original Walcott bivalved arthropod material from the „Phyllopod Bed", together with new fossil collections made on Fossil Ridge by the Geological Survey of Canada in 1966 and 1967, and the Royal Ontario Museum in 1975, was later studied by Derek Briggs (1976, 1977, 1978, 1981), then a postgraduate student at the University of Cambridge working under Harry Whittington. Renewed interest and exploration by the Royal Ontario Museum (ROM) led to the discovery of other BSTs in the vicinity of Yoho National Park (Collins *et al*. 1983); this included locality S7 (now Tulip Beds *sensu* O'Brien and Caron 2012) and locality 9 (Collins Quarry *sensu* Fletcher and Collin 1998). Bivalved arthropods are rare in the Tulip Beds. Three specimens deposited in the ROM were curated as *Branchiocaris* and represent a new genus and species (described herein). In contrast, bivalved arthropods are extremely common at the Collins Quarry locality. Collins *et al*. (1983) noted that *Branchiocaris*, a taxon otherwise known from just five specimens (Briggs 1976), accounted for 8 per cent of the total fauna recovered from this locality. There has only been occasional mention of this material, mainly within preliminary faunal lists (Collins *et al*. 1983, Briggs and Robison 1984, Briggs and Collins 1988, Fletcher and Collins 1998, 2003), including reference to possible juvenile specimens (Briggs and Robison 1984). Herein bivalved arthropod material previously referred to *Brachiocaris*, from both the Tulip Beds and Collins Quarry locality, is systematically described and referred to new taxa – *Nereocaris exilis* Legg *et al*. 2012b, *N. briggsi* Legg and Caron in press, and *Loricicaris spinocaudatus* Legg and Caron in press.

The contents of this chapter have been published, in part, in the *Proceedings of the Royal Society B* (Legg *et al*. 2012b), and the journal *Palaeontology* (Legg and Caron in press).

5.2. Locality, material and methods

5.2.1. Geological settings and associated fauna

Material described in this chapter was recovered from two main localities: the Tulip Beds locality (formerly S7 *sensu* Fletcher and Collins 1998, 2003), so named for the abundance of the so-called "tulip-like" *Siphusauctum gregarium* O'Brien and Caron 2012; and Collins Quarry locality (formerly locality 9 *sensu* Collins *et al*. 1983); both discovered in the early 1980s on the western slopes of Mount Stephen (Fig. 5.1; Collins *et al*. 1983).

Nereocaris briggsi and *Loricicaris spinocaudatus* were both recovered from Collins Quarry, The Collins Quarry locality is an exposure of the Kicking Horse Shale

Member of the Burgess Shale Formation (Fig. 5.1). This is the oldest Member of the Burgess Shale Formation; the resident trilobites, particularly *Glossopleura* sp., *Polypleuraspis insignis* and *Pagetia bootes*, indicate it belongs to the *Polypleuraspis insignis* Subzone of the *Glossopleura* Biozone (Fletcher and Collins 1998, 2003) of the Middle Cambrian (Series 3, Stage 5).

Fletcher and Collins (1998) recognized four units within the Kicking Horse Shale Member consisting of ferruginous-weathering thin limestones, limy siltstone and nodular limestones, at the bottom (Unit 1), covered by lenticular calcareous silty mudstones (Unit 2), homogenous platy calcareous siltstones (Unit 3), and interbedded limestones and slaty siltstones at the top (Unit 4). The Collins Quarry is located within Unit 3 and possesses a distinctive soft-bodied fauna characterized by the arthropod *Alalcomenaeus cambricus* Simonetta 1970, which accounts for the majority (58 per cent) of fossils recovered at this site (Collins *et al*. 1983, Briggs and Collins 1999). Minor faunal elements include the arthropods *Naraoia*, *Canadaspis*, *Plenocaris*, and *Sanctacaris*; an undescribed lobopodian; several sponges; the lophotrochozoan *Wiwaxia*; and the ctenophore *Xanioascus* (Collins *et al*. 1983, Collins 1986, Briggs and Collins 1988, Conway Morris and Collins 1996, Fletcher and Collins 1998, 2003, Rigby and Collins 2004).

Specimens of *N. exilis* were recovered from talus on the slopes of the “Tulip Beds” locality. Their lithology indicates they are derived from the Campsite Cliff Shale Member of the Burgess Shale Formation. This Member occurs stratigraphically above the Kicking Horse Shale Member, between Yoho River Limestone Member Wash Limestone Member (Fig. 5.1), and is referred to the lowermost *Bathyuriscus-Elrathia* Biozone (Fletcher and Collins 1998) of the Middle Cambrian (Series 3, Stage 5).

The Campsite Cliff Member consists primarily of blocky and silty mudstones, with fossiliferous horizons restricted to calcareous claystones characterized by millimetre scale event deposit muds (O‟Brien and Caron 2012). The “Tulip Beds” fauna is dominated by the enigmatic *Siphusauctum gregarium* and anomalocaridids (Daley and Budd 2010). The remaining fauna is relatively abundance but not very diverse and includes sponges, lobopodian, priapulids and arthropods (O‟Brien and Caron 2012), including various bivalved arthropod species (pers. obs.).

5.2.2. Specimen examination and photography

All specimens are deposited in the Royal Ontario Museum (ROM), Toronto, Canada. For comparative purposes additional material attributed to *Branchiocaris* deposited in the ROM and Smithsonian National Museum of Natural History (NMNH), Washington D.C., USA, was also studied.

ROM specimens were examined using a Nikon SMZ1500 binocular microscope with a drawing tube attached. All specimens were photographed using a Nikon D700 with a Nikon AF-S Micro Nikkor lens with a polarising filter. A variety of lighting conditions were utilised during specimen examination, however the best

photographic results were obtained when using low angle crossed polarized light (Schaarschmidt 1973) and immersing specimens in water, as recommended by Bengtson (2000); unless stated otherwise photos of specimens presented herein were taken under these conditions.

5.2.3. Anatomical terminology

Anatomical terms do not necessarily imply homology with features described elsewhere using similar terminology, but, rather they are used for the sake of convenience and to avoid *ad hoc* discussions of primary and secondary homology. For instance, the term *carapace* is used in the broad sense to refer to an anterior and posterior expansion of the cephalic shield, often enclosing the cephalic region and, at least, the anterior trunk limbs (*cf*. Hou and Bergström 1997). Among extant crustacean groups, however, the carapace can arise from different somites, making „carapaces" in different taxa potentially analogous rather than homologous. We would require either additional developmental (embryonic) data or phylogenetic information in order to determine whether many of these anatomical terms used refer to analogous or homologous structures. Embryos and early developmental stages are, however, unlikely to be present in Burgess Shale-type deposits, whereas additional phylogenetic information would require *a priori* knowledge of relatedness, something that could be inferred but not proven, and could result in circular reasoning.

Additional terminology generally follows Hou and Bergström (1997) with the following exceptions and emendations: the term *anterior sclerite* is used to refer to the most anterior, often pre-appendicular and eye bearing, head segment of many basal arthropods (*sensu* Budd 2008). The term *head* refers to the anterior part of the body that bears limbs differentiated for sensory functions or food gathering (*sensu* Bergström *et al*. 2008). This term is preferred to *cephalon*, which is delimited by the posterior boundary of a dorsal cephalic shield (*sensu* Bergström *et al*. 2008), a feature that may have been modified into a *carapace* (*sensu* Hou and Bergström 1997) in bivalved arthropods. The remainder of the body (the *trunk*) is divided into an anterior limb-bearing section, the *thorax*, and a posterior segment, the *abdomen*, which is distinguished either by being limbless or by the differentiation of segments. The term *process* is used to refer to any spine-like projection, regardless of position, for instance, *telson process* refers to entire or articulated lateral and medial spine-like processes on the telson (*sensu* Briggs 1976). Hou and Bergström (1997) used the terms *endopod* and *exopod* to refer to the respective inner and outer branches of a biramous appendage, arising from the basis. A basis cannot be distinguished in the filiform appendages of many bivalved arthropods and may be a later development in arthropod phylogeny (Legg *et al*. 2012b), rendering this definition invalid, however the terms *endopod* and *exopod* are retained for the sake of convenience, and refer to the inner and outer limb branches respectively, irrespective of basal attachment.

5.3. Systematic Palaeontology

Phylum ARTHROPODA Siebold 1848 *sensu* Legg and Vannier in press

Discussion. A number of suprageneric taxa have been erected to encompass various bivalved arthropods. There is little consensus regarding the composition of these groups however and recent cladistic analyses indicates that many of their groups may be para- or even polyphyletic (Legg *et al*. 2012b, Legg and Vannier in press, Legg and Caron in press). For this reason the newly described taxa are not assigned to suprageneric taxa.

Nomenclatural note. The name Arthropoda is often attributed to Siebold and Stannius, 1845, however, the volume this refers to was actually published in 1848. In addition, Siebold was the sole author of Arthropoda, although Siebold and Stannius were the joint editors of the volume in which it appeared.

Genus ***NEREOCARIS*** Legg, Sutton, Edgecombe and Caron, 2012b

1983	*Branchiocaris*; Collins, Briggs and Conway Morris, p. 165 (*in partim*).
1984	*Branchiocaris*; Briggs and Robison, p. 7, 12 (*in partim*).
1988	*Branchiocaris*; Briggs and Collins, p. 780 (*in partim*).
1998	*Branchiocaris*; Fletcher and Collins, p. 422 (*in partim*).
2003	*Branchiocaris*; Fletcher and Collins, p. 1833, 1835 (*in partim*).
2012b	*Nereocaris* Legg, Sutton, Edgecombe and Caron, p. 4699.
In press	*Nereocaris* Legg, Sutton, Edgecombe and Caron; Legg and Caron.

Type species. *Nereocaris exilis* Legg *et al*. 2012b, from the Middle Cambrian (Series 3, Stage 5) Tulip Beds exposure of the Campsite Cliff Shale Member (Burgess Shale Formation) on Mount Stephen (Yoho National Park, British Columbia, Canada), by original designation.

Included species. Nereocaris briggsi Legg and Caron in press.

Etymology. After *Nereus*, the Greek titan often depicted in ancient artwork with a fish-like tail, reminiscent of this taxon, and *caris*, Latin for crab and a common suffix of bivalved Cambrian arthropods.

Diagnosis. Arthropod with stalked lateral eyes and a single median-eye; a laterally compressed bivalved carapace with antero-ventral hook-like processes; telson bearing a subtriangular medial process and elongate lateral processes composed of three segments (diagnosis emended by Legg and Caron in press).

Nereocaris exilis Legg, Sutton, Edgecombe and Caron, 2012b
Figures 5.2-5.4

v*2012b	*Nereocaris exilis* Legg, Sutton, Edgecombe and Caron, p. 4699-4704, figs. 1, S1-S2.
In press	*Nereocaris exilis* Legg, Sutton, Edgecombe and Caron; Legg and Caron.

Etymology. From the Latin *exilis* meaning “slender”, in reference to its elongate caudal abdomen.

Specimens. Holotype ROM 61831, part (Figs. 5.2A, E, 5.3A, 5.4A-B) and counterpart of an almost complete specimen with the anterior preserved in lateral aspect, the abdomen demonstrating notable torsion and the posterior preserved in dorso-ventral aspect; plus Paratypes ROM 61832, part (Figs. 5.2B. 5.3B) and counterpart of a partial abdomen and postero-ventral section of a carapace; and ROM 61833 (Figs. 5.2C-D, F, 5.3C), an almost complete specimen preserved in an oblique-lateral aspect.

Occurrence. All material referred to this taxon was collected from the talus of the slopes of the Tulip Beds locality (O‟Brien and Caron 2012), formerly S7 (*sensu* Fletcher and Collins 1998), Mount Stephen, Yoho National Park, British Columbia, Canada. The lithology indicates specimens originate from the Campsite Cliff Shale Member of the Burgess Shale Formation; *Bathyuriscus-Elrathia* biozone, Cambrian, Series 3, Stage 5 (O‟Brien and Caron 2012).

Diagnosis. Arthropod with stalked lateral eyes and a single rod-shaped median eye; a bivalved carapace with a postero-dorsal keel and hook-like antero-ventral spines;

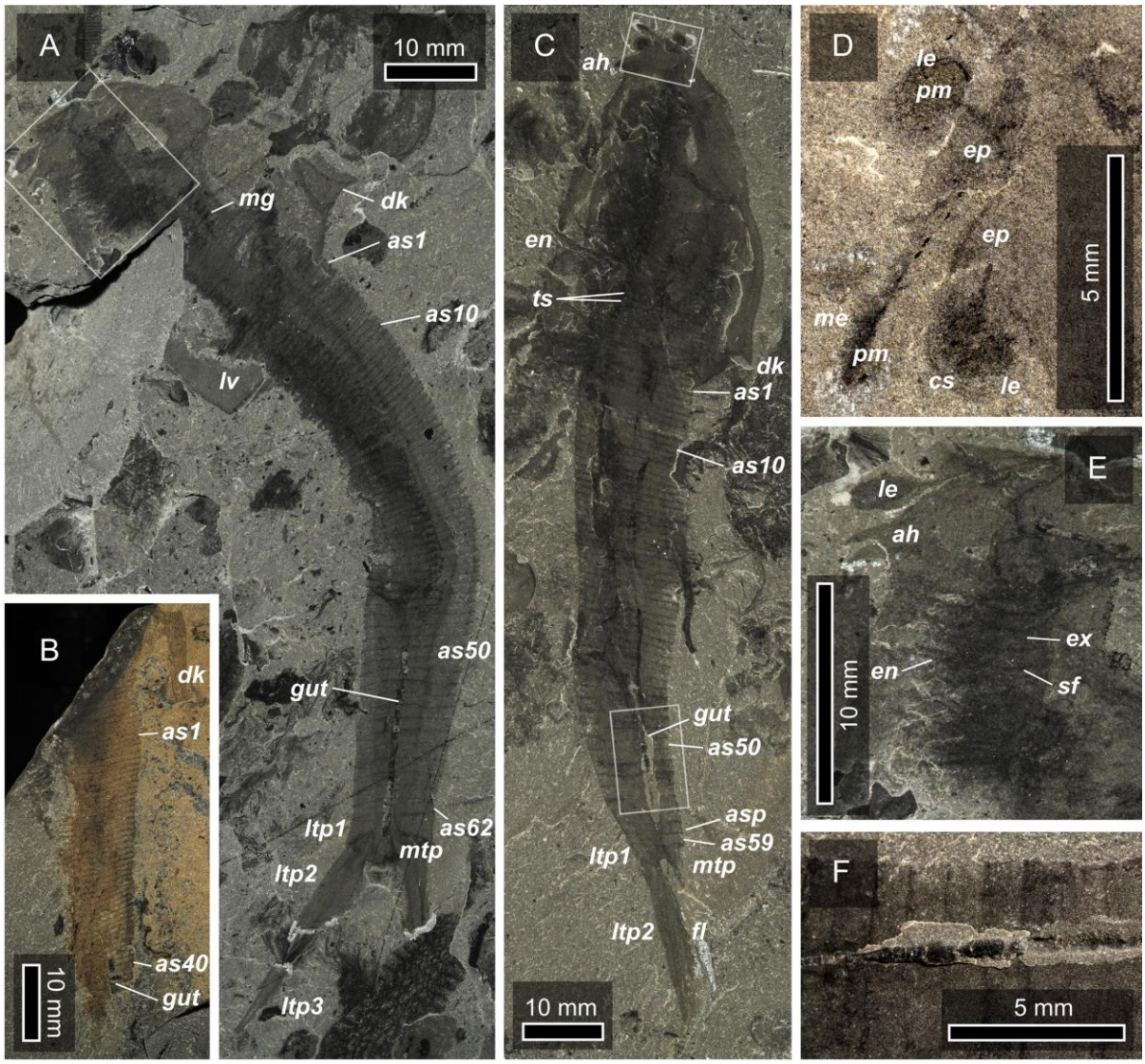


Fig. 5.2 | *Nereocaris exilis* Legg *et al*. 2012b, from the Cambrian (Stage 3) of British Columbia. A, Holotype, ROM 61831; **B**, Paratype, ROM 61832; and **C**, Paratype ROM 61833; **D**, details of the ocular region located in the top box of **C**, immersed in water; **E**, details of the appendicular region located in the box of **A**; and **F**, details of the posterior part of the gut located in the lower box of **C**, showing three-dimensional preservation. All specimens were photographed using low-angle cross-polarized light. Accompanying camera lucida drawings in Fig. 5.3. Abbreviations: ah, anterior hook-like processes; as1-62, abdominal somites 1-62; cs, corneal surface; dk, dorsal keel; en, endopod; ep, eye peduncle; ex, exopod; fl, fluke; gut, gut; le, lateral eyes; ltp 1-3, lateral telson process elements 1-3; lv, left (carapace) valve; mg, midgut glands; mtp, medial telson process; pm, photoreceptive material; sf, setal fringe; and ts, thoracic segments.

trunk composed of a thorax of 30-40 somites bearing a homonomous series of biramous limbs and an elongate abdomen of approximately 60 ring-like somites; telson composed of a small triangular medial process and elongate lateral processes comprising three segments.

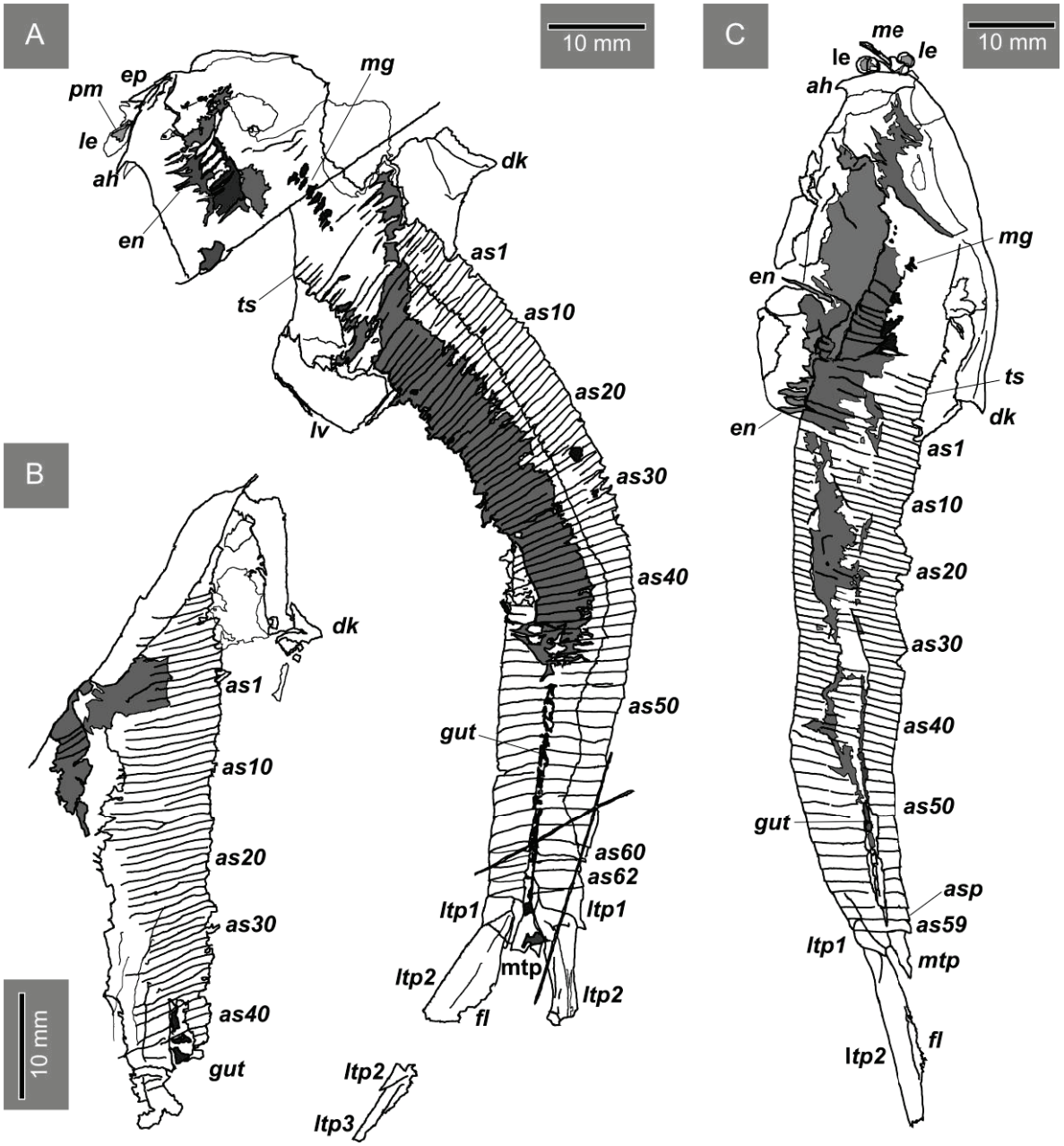


Fig. 5.3 | Interpretive camera lucida drawings of *Nereocaris exilis* specimens in Fig. 5.2. A, Part of ROM 61831; **B**, Part of ROM 61832; and **C**, ROM 61833. Abbreviations: ah, anterior hook-like processes; as1-62, abdominal somites 1-62; dk, dorsal keel; en, endopod; ep, eye peduncle; ex, exopod; fl, fluke; gut, gut; le, lateral eyes; ltp 1-3, lateral telson process elements 1-3; lv, left (carapace) valve; mg, midgut glands; mtp, medial telson process; and ts, thoracic segments.

Comparative description.

Size. The longest specimen, ROM 61831 (Fig. 5.2A), is 142 mm long, measured from the anterior-most tip of the carapace to the distal tip of the telson processes. ROM 61833 has a preserved length of 127 mm (Fig. 5.2C), although the distal tips of the telson processes are not preserved.

Carapace. The anterior region of all specimens is preserved in lateral aspect (Fig. 5.2A-C). In ROM 61831 the telson is preserved in dorso-ventral aspect and the abdomen has a distinct torsion (Fig. 5.2A). This indicates that the stable orientation of the carapace upon death was lateral, and hence that it was laterally compressed in life; this contrasts with other coeval bivalved arthropods with a laterally expanded carapace, e.g. *Odaraia* (Briggs 1981), which typically preserve in dorso-ventral aspect. The carapace is subovoid with a restricted anterior gape and expands strongly towards the posterior, reaching its highest point near the postero-dorsal margin where it expands into a subtriangular fin-like keel (Fig. 5.2A-C). The posterior margin is only slightly curved, meeting the ventral margin at an approximate right angle at the posterior-most point of the carapace. Short recurved hook-like processes occur in the antero-ventral margin of the carapace.

Head structure and eyes. The head region is poorly delimited and no evidence for limb specialization is preserved. The lateral eyes protrude from the anterior margin of the carapace (Figs. 5.2A, C-D, 5.3A, C) and consist of two parts: a proximal peduncle and a distal corneal surface. The attachment site of the peduncle is unclear, but appears to converge on a single point, presumably an anterior sclerite. The lateral eyes of RM 61833 are 2.3 mm in diameter (Fig. 5.2D). The central region of each lateral eye is preserved as a highly reflective material, and is surrounded by a narrow margin of unreflective material (Fig. 5.2D). A small rod of reflective material extends from the reflective area of the eye into the peduncle. In other coeval bivalved arthropods, e.g. *Odaraia*, this reflective material has been interpreted as fossilized photoreceptive material (Briggs 1981). A single elongate medial process, 3.9 mm long, originates between the lateral eyes (Fig. 5.2C-D). This projection appears unsegmented, bears reflective material in the form of a medial filament extending from the base to the tip, and a distally bulbous, it is hence tentatively interpreted not as an appendage but as a medial eye, as proposed for a similar structure in *Jugatacaris* (Fu and Zhang 2011).

Appendages. The limbs are best preserved in ROM 61831 (Figs. 5.2A, E, 5.3A, 5.4A-B). They represent a homonymous series of biramous arthropodized appendages, comprising a long (8.6 mm), thin endopod of more than 10 podomeres, and a small subovoid exopod fringed with fine setae (Figs. 5.2E, 5.4A-B). Appendages are restricted to the carapace region and decrease in size towards the posterior carapace margin.

Trunk somites. The thorax is poorly sclerotized, but annulated, and consists of 30-40 segments; a one-to-one correspondence between appendages and these segments is likely, but cannot be demonstrated. In contrast to the thorax, the abdomen is well sclerotized and extremely long, accounting for other half of the total body length (69

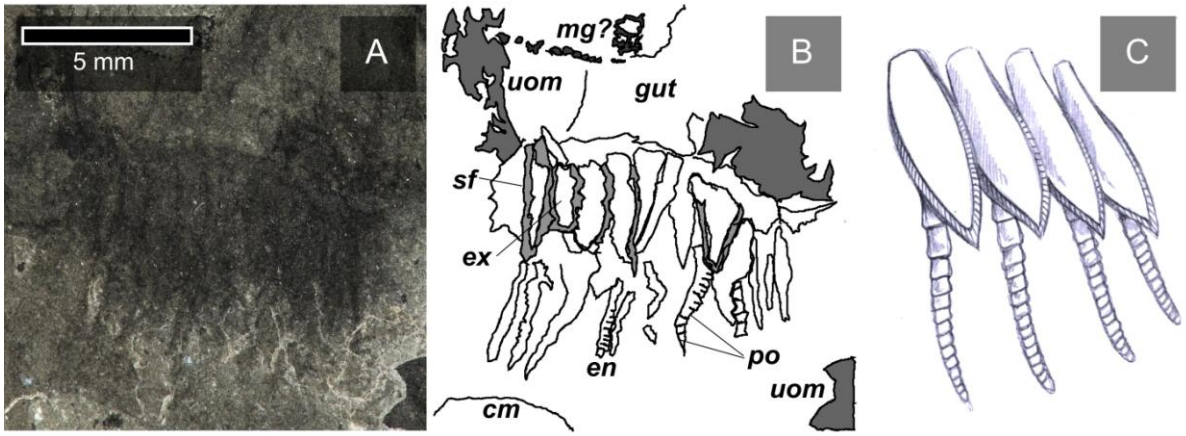


Fig. 5.4 | Details of the thoracic appendages of *Nereocaris exilis*. A, close up view of the appendages of ROM 61831; **B**, accompanying camera lucida drawing of **A**, and **C**, reconstruction of the appendages of *Nereocaris exilis*. Abbreviations: cm, carapace margin; en, endopod; ex, exopod; mg, midgut glands; pd, podomeres; sf, setal fringe; and uom, unidentified organic matter.

per cent of total body length in ROM 61831 and 67 per cent in ROM 61833). The abdomen consists of approximately 60 somites (62 in ROM 61831, Figs. 5.2A, 5.3A; 59 in ROM 61833, Figs. 5.2C, 5.3C). Separate tergites and sternites are not evident; each somite instead consists of a complete ring. The anterior somites are more closely spaced (12 per 10 mm) than the posterior ones (6.5 per 10 mm).

Gut. An elongate and dark medial structure within the abdomen is interpreted as a gut trace and is present in all specimens (Figs. 5.2A-C, F, 5.3). It is preserved in a range of styles, varying between and within specimens from faint staining to highly reflective areas with noticeable relief, the latter preferentially occurring posteriorly (Fig. 5.2C, F). The gut terminates within the telson (Figs. 5.2A, C, 5.3A, C). Darkly stained villi preserved adjacent to the gut in the thorax may represent midgut glands (Figs. 5.2A, 5.3A).

Telson. The telson bears three sets of spinose processes: one medial and two sets of lateral processes. The medial process is short (6 mm in ROM 61833) and subtriangular (Fig. 5.2C, 5.3C). Each lateral process set consists of three elements. The most proximal processes are subrectangular and possess short spines on their postero-lateral margins (Figs. 5.2A, C, 5.3A, C). The remaining processes are long (33 mm in ROM 61831 and 23 mm in ROM 61833), and appear fused and spinose. A fluke-like expansion of the telson processes is present in ROM 61833 (Figs. 5.2C, 5.3C).

Remarks.

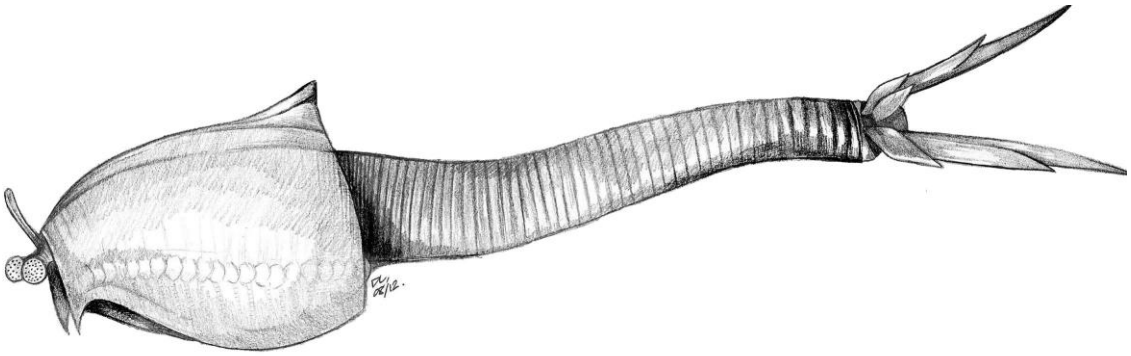


Fig. 5.5 | A reconstruction of *Nereocaris exilis*.

Although material referred to this taxon was originally curated as *Branchiocaris* sp., *Nereocaris exilis* shows a number of distinct characteristics warranting its assignment to both a new species and genus, including a lack of specialized head appendages, hook-like processes on the antero-ventral margin of the carapace, a high dorsal keel on the posterior margin of the carapace, an elongate limb-less abdomen and an elongate telson with tripartite lateral processes (Fig. 5.5). Many of these features are present in the congeneric *N. briggsi*, however *N. exilis* differs from the latter in general proportions and number of abdominal somites. The largest specimen of *N. exilis* is 142 mm long, whereas the largest specimens of *N. briggsi* are roughly 60 mm long. It is possible that this represents a sampling bias and actually *N. briggsi* represents younger individuals of *N. exilis*, however, when plotted on a line regression *N. exilis* clustered outside of the extrapolated growth curve for *N. briggsi*. Each species also show little variation in the number of abdominal somites suggesting they are not added throughout ontogeny.

Although the medial eye is reported from a single specimen, the presence of a similar structure in *N. briggsi* indicates that it is most-likely a medial eye and not an appendage, algal fragment or abiogenic structure. This is also backed up by similar structures in other Cambrian bivalved arthropods, e.g. *Jugatacaris* Fu and Zhang, 2011.

Nereocaris briggsi Legg and Caron, in press
Figures 5.6-5.10

v*in press *Nereocaris briggsi* Legg and Caron, p. 1-25, figs. 4-8.

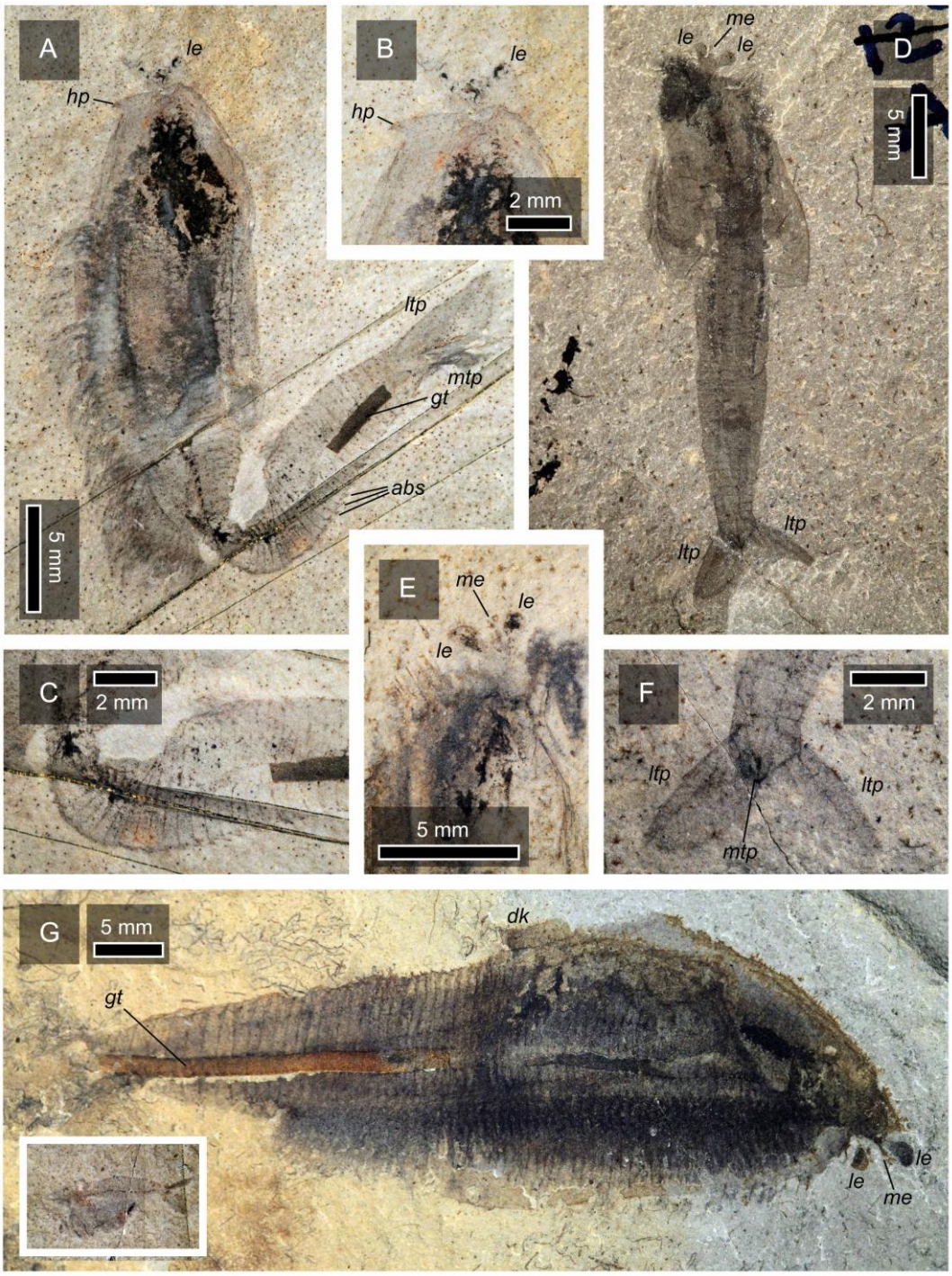


Fig. 5.6 | *Nereocaris briggsi* Legg and Caron in press, from the Kicking Horse Member of the Burgess Shale Formation, British Columbia. A, the holotype, ROM 62153; **B**, detailed view of the anterior of ROM 62153; **C**, detailed view of the trunk of ROM 62153; **D-F**, paratype ROM 62163; **E**, detailed view of the anterior of ROM 62163 (counterpart); **F**, detailed view of the telson of ROM 62163; and **G**, size variation in *Nereocaris briggsi*, the largest (ROM 62161) and smallest (ROM 62155; inset) preserved specimens. Abbreviations: abs; abdominal spines; dk, dorsal keel; gt, gut; hp, hook-like processes; le, lateral eyes; ltp, lateral telson processes; me, medial eye; mtp, medial telson process.

Etymology. To honour Professor Derek E. G. Briggs (Yale University, Connecticut,

USA) for his work on Cambrian arthropods, particularly the bivalved arthropods of the Burgess Shale.

Specimens. Holotype ROM 62153 (Fig. 5.6A-C), a complete specimen preserved in an oblique-lateral orientation and with notable torsion of the abdomen. Paratype ROM 62163 (Fig. 5.6D-F), a complete specimen preserved in an oblique-dorsal orientation. An additional 188 specimens are also referred to this taxon.

Occurrence. All material referred to this taxon was collected from the Collins Quarry exposure (locality 9 *sensu* Collins *et al*. 1983) of the Kicking Horse Shale Member (Burgess Shale Formation) situated on the western slope of Mount Stephen in Yoho National Park (British Columbia, Canada); *Polypleuraspis insignis* Subzone of the *Glossopleura* Zone (Fletcher and Collins 1998, 2003) of the Middle Cambrian (Series 3, Stage 5).

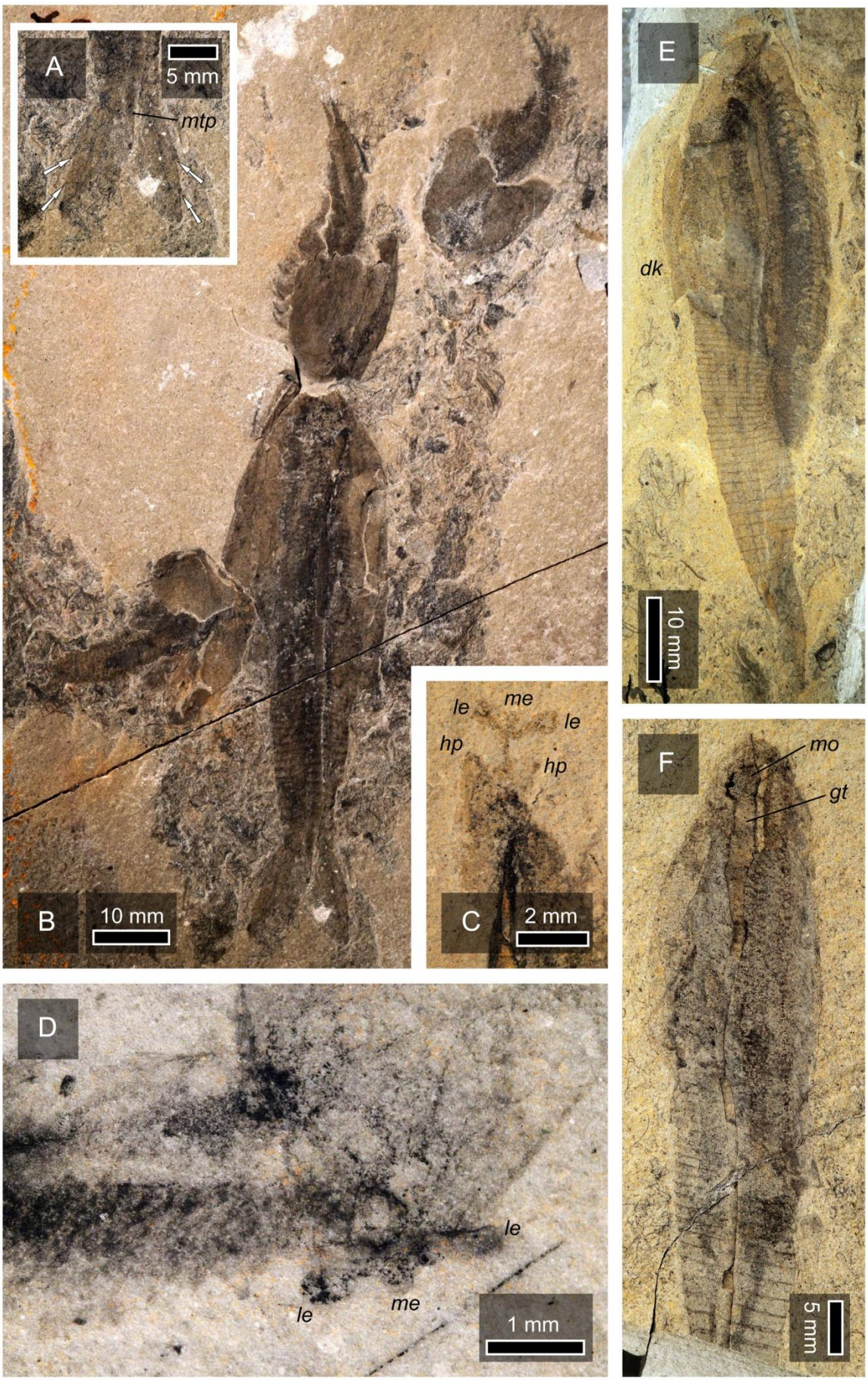
Diagnosis. Hook-shaped processes followed by serration on the antero-ventral margin of the carapace; rod-shaped medial eye which does not project beyond the anterior margin of the lateral eyes; trunk endopods elongate, composed of c. 30 podomeres; thorax consists of c. 50 segments, 20 of which extend beyond the posterior margin of the carapace and bear short spines; abdomen composed of c. 10 ring-like somites; lateral telson processes composed of three overlapping segments.

Comparative description.

Size. Specimens assigned to this taxon show a great variety in length from c. 8 mm (ROM 62155; Fig. 5.6G *inset*) to c. 60 mm (Figs. 5.6G, 5.7A-B, E-F), with the largest specimen measuring 66 mm (ROM 62161; Fig. 5.6G); length was measured from the distal-most edge of the head to the posterior tip of the telson, excluding telson processes. Average body length is 26.5 mm (*n* = 101).

Carapace. The anterior region of most specimens (*n* = 112) is preserved in lateral or a slight lateral-oblique orientation, indicating that in life, the bivalved carapace was

Fig. 5.7 (*overleaf*) | *Loricicaris spinocaudatus* Legg and Caron in press, and *Nereocaris briggsi* Legg and Caron in press, from the Kicking Horse Member of the Burgess Shale Formation, British Columbia. A, detailed view of the telson of *Nereocaris briggsi*, specimen ROM 62169, arrows indicate boundaries between lateral telson process elements; **B**, ROM 62169, displaying two specimens of *Loricicaris spinocaudatus* (top right) and two specimens of *Nereocaris briggsi* (middle and left); **C**, detailed eye structure of ROM 62162; **D**, detailed view of the anterior of ROM 62157; **E**, ROM 62164; and **F**, ROM 62158). Abb; reviations: dk, dorsal keel; gt, gut; hp, hook-like processes; le, lateral eye; me, medial eye; and, mo, mouth opening.


A
5 mm
mtp
B
10 mm
C
le
me
le
hp
hp
2 mm
D
le
le
me
1 mm
E
dk
10 mm
F
mo
gt
5 mm

most likely laterally compressed. A large number of specimens are preserved with the carapace slightly disassociated but with the anterior still attached to the head (see for example Figs. 5.7D, 5.8A, D, 5.10F). Specimens in „butterfly" position (i.e. with both right and left carapace valves preserved as mirror images) are rare (e.g. Figs. 5.7D, 5.8A) and indicate that the carapace is not fused along the ventral margin. The anterior margin of the carapace is straight (Figs. 5.6A, D, 5.9, 5.10E), and a hook-shaped process is present on the antero-ventral margin of each valve (Figs. 5.6A-B, 5.7C, 5.8C, 5.10E) followed by small spines along the margin (Fig. 5.8D-E). The antero-lateral margins of the carapace expand posteriorly with the carapace eventually becoming more tubular (Figs. 5.6A, G, 5.7B, E-F); the posterior margin is straight. The carapace is weakly sclerotized in some specimens, e.g. ROM 62157 (Fig. 5.7D), making the detail of the underlying trunk visible. A small subtriangular process is present on the postero-ventral margin of the carapace (Figs. 5.6G, 5.7E).

Eyes. The eyes are located on an elongate stalk which expands anteriorly into an isosceles trapezoid (Figs. 5.6A-B, D-E, 5.8C, 5.10B); this stalk appears to preferentially protrude from the antero-ventral margin of the carapace (Figs. 5.6A-B, D-E, 5.7C). Movement of the eyes appears to be limited to the individual eye peduncles which show a degree of flexibility (Figs. 5.7C, 5.9, 5.10B) and may have been capable of independent movement. The distal portion of the eye, the corneal surface, can be distinguished by the presence of reflective material (Figs. 5.6A-B, G, 5.7D, 5.8A, D-E, 5.9, 5.10A-C, E); similar material has been interpreted as photoreceptive tissues in other taxa, e.g. *Odaraia* (Briggs 1981). Individual ommatidia could not be distinguished but possible nervous tissues are present in the eyes (Figs. 5.7D, 5.10B). A medial structure is present between the two eye stalks (Figs. 5.6E, G, 5.7C-D, 5.9, 5.10B, E).The medial eye does not extend beyond the anterior limits of the lateral eyes although it may be extended into a rod-like process (Figs. 5.6G, 5.7C).

Head structure. Too few specimens are adequately preserved to provide unequivocal details of the anterior cephalic region. Strictly speaking *Nereocaris briggsi* does not have a discernible head because specialized frontal appendages, e.g. antennae or Specialized Frontal Appendages (SPAs) are absent. This is considered a genuine absence because reduced appendages, indistinguishable from the trunk appendages, are present in the anterior region of the carapace, originating just posterior to the eye stalk (Figs. 5.7, 5.10B). It is not possible to tell whether these anterior appendages are homologous to the specialized frontal-appendages of other arthropods as their relationship to the mouth cannot be determined based on available material. A few specimens show the oral region (e.g. Fig. 5.7F); the mouth is preserved as an ovoid depression at the end of a straight gut. This is significant bending of the gut and the mouth opens ventrally. There is no associated



Fig. 5.8 | *Nereocaris briggsi* Legg and Caron in press, from the Kicking Horse Shale Member of the Middle Cambrian, Burgess Shale Formation. A-B, ROM 62168; **B**, detailed view of the appendages of ROM 62168; **C**, ROM 62163; **D-E**, ROM 62167; and **E**, detailed view of he anterior carapace region of ROM 62167, showing marginal serration.

hypostomal plate or oral circlets. A possible anterior sclerite is discernable in some specimens (e.g. Fig. 5.9).

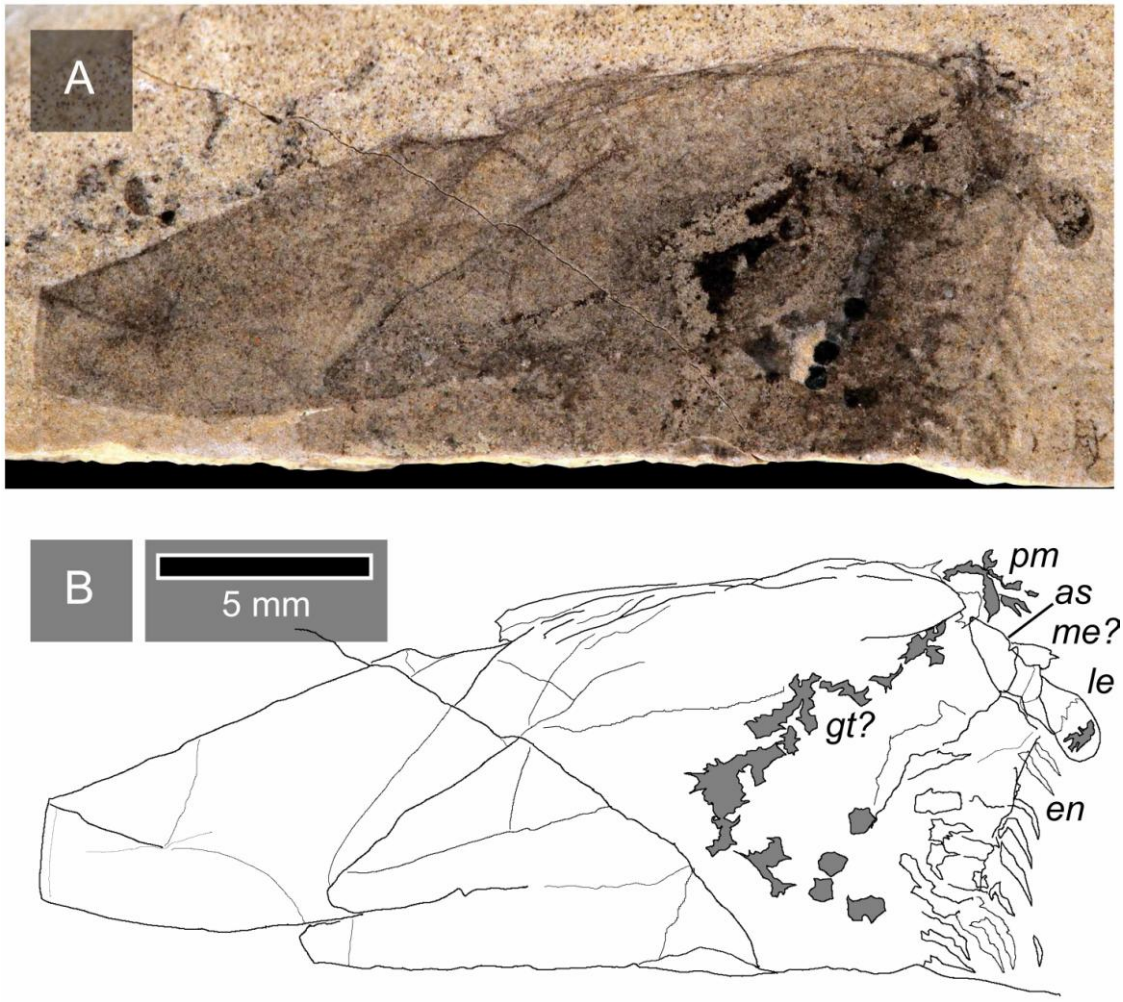


Fig. 5.9 | Detailed view of the anterior of ROM 62154 (counterpart) with interpretive camera lucida drawing (B). Demonstrating a lack of specialized appendages in the anterior of the carapace. Abbreviations: as, anterior sclerite; en, endopod; gt, gut; le, lateral eye; me, medial eye; and, pm, photoreceptive material.

Gut. The gut is preserved, at least in part, in all specimens of *Nereocaris briggsi*, even in specimens that are otherwise poorly preserved, and can be used as a tool for identification; it consists of a simple tube with a very gradual posterior tapering and it is often three-dimensionally preserved (Figs. 5.6A, G, 5.7F). Associated glands are absent.

Appendages. Although numerous specimens preserve traces of trunk appendages their delicate nature makes it difficult to decipher much detail. The overlap of the right and left series of appendages in laterally compressed specimens makes the exact number of appendages difficult to determine; the fortuitous preservation of the posterior appendages in ROM 62161 demonstrates that there is a single pair of appendages per somite (Fig. 5.6G). ROM 62161 also demonstrates that the anterior appendages were enclosed within the carapace during life and it is only due to post-mortem dissociation of the carapace that they occur outside. There are at least 30

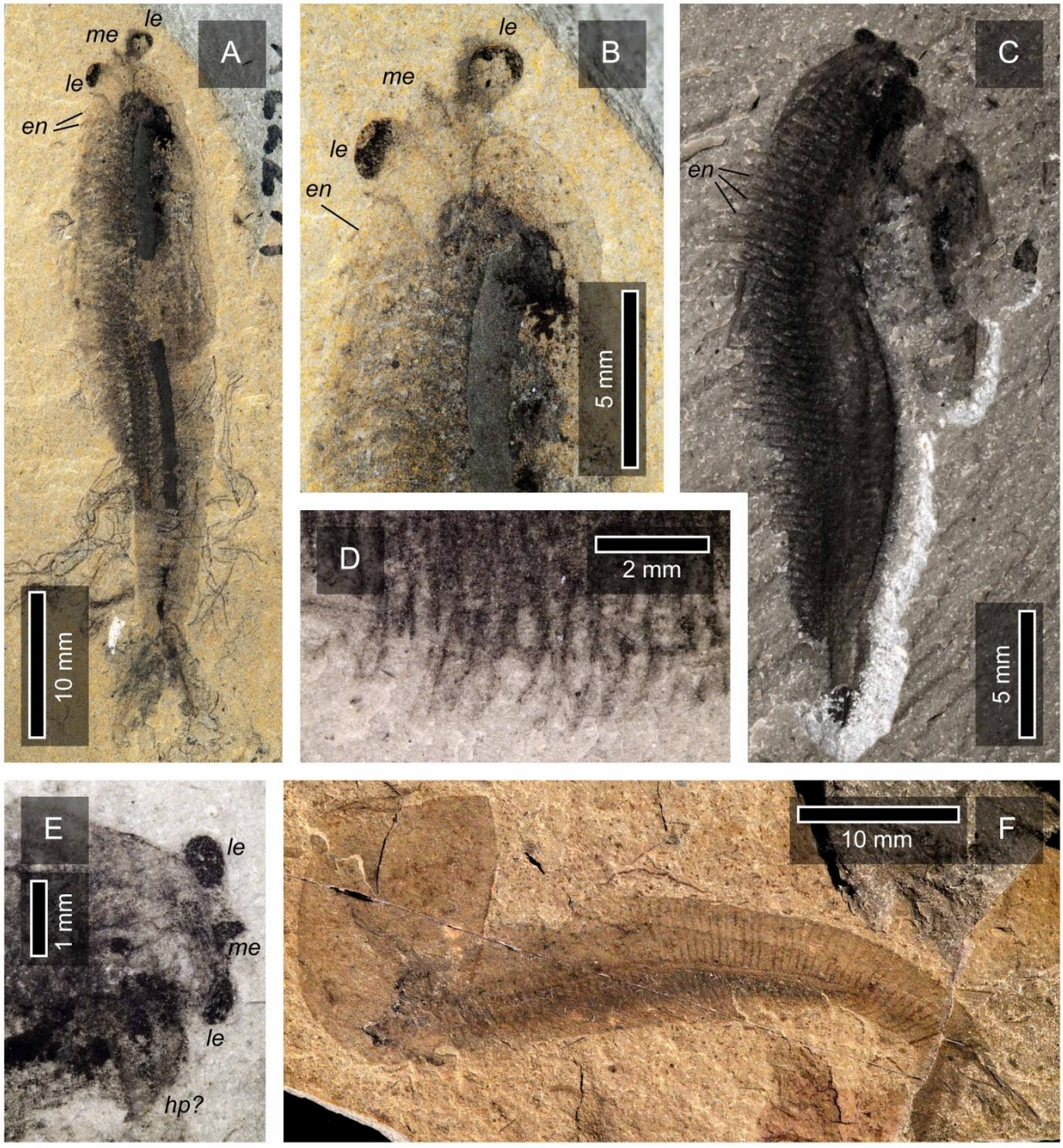


Fig. 5.10 | *Nereocaris briggsi* Legg and Caron in press, from the Kicking Horse Shale Member of the middle Cambrian Burgess Shale Formation, British Columbia. A-B, ROM 62159; **B**, a detailed view of the anterior carapace region of ROM 62159; **C-E**, ROM 62156; **D**, detailed view of the appendages of ROM 62156; **E**, detailed view of the ocular region of ROM 62156; and **F**, ROM 62166. Abbreviations: en, endopods; le, lateral eye; and me, medial eye.

pairs of appendages within the carapace and about 20 beyond the posterior of the carapace. The endopods get noticeably longer towards the posterior of the carapace, reaching their maximum length at its highest point (Fig. 5.6G), and then taper gradually towards the end of the series. Individual podomeres could be distinguished in a few specimens (Figs. 5.8B, 5.10D), where they are discernable in

the distal parts of the posterior endopods; at least 10 podomeres can be distinguished in these portions indicating that the entire appendage many have had as many as 30 podomeres. The morphology of the exopods could not be determined adequately. In a closely related species, namely *Nereocaris exilis*, the exopods are small, less than half the length of the endopod, and nearly indistinguishable from the proximal portion of the appendages. They do, however, form a dark band of organic matter (Legg *et al*. 2012b); the proximal portions of the appendages of *Nereocaris briggsi* are also punctuated by such dark bands (Figs. 5.7E, 5.10A, C).

Trunk somites. The somites beneath the carapace are more lightly sclerotized than those of the posterior thorax and abdomen, making the exact number of somites difficult to discern; this is best seen in ROM 62166 (Fig. 5.10F). Assuming there is a single pair of appendages per somite, as there is in the posterior of the taxon then there was at least 30 anterior thoracic somites, 20 posterior thoracic somites and 16-25 abdominal somites; only the posterior somites appear to exhibit variation in number, however does not appear to be a link to size, meaning that there was either considerable intraspecific variation or sexual dimorphism. The abdominal somites possess minor spines, taper and gradually increase in length towards the telson (Figs. 5.6F, 5.7A, 5.8D).

Telson. The outline of the telson is preserved in a large number of specimens, however, the detailed morphology can only be distinguished in a few. The actual telson is small and ovoid (Fig. 5.6F), and flanked by three elongate processes: one medial and two lateral. The medial process is often relatively poorly preserved compared to the lateral processes but is small and lanceolate in dorsal view. The medial processes of ROM 62153 (Fig. 5.6A) projects dorsally and appears to be slightly recurved, like that of *Odaraia* (Briggs 1981). The lateral processes appear either acicular or acuminate, and even slightly ovate, depending on the orientation to bedding; they are more acicular in lateral view and subovate in dorsal view (Fig. 5.6F). The lateral telson processes are composed of three segments, the most distal of which is subtriangular (Figs. 5.6F, 5.7A, 5.8D); the outer margins of the lateral processes are spinose and show considerable overlap resulting in a serrated appearance (Figs. 5.6F, 5.7A, 5.8D).

Remarks.

This taxon possesses a number of features previously thought to be unique to *Nereocaris exilis*, indicating that it belongs in the same genus; this includes a rod-shaped medial eye, an anterior pair of hook-shaped processes on the antero-ventral margin of the carapace and tripartite lateral telson processes. Other characters supporting a close relationship, although not necessarily features unique to these taxa, include a laterally compressed carapace and multipodomerous, almost

filamentous endopods, also present in *Pectocaris* Hou 1999, and *Jugatacaris* Fu and Zhang 2011, (Hou 1999, Hou *et al*. 2004b, Fu and Zhang 2011), and a medial telson process, present in the aforementioned taxa and *Odaraia* (Briggs 1981). Few, if any, features are reminiscent of *Branchiocaris*, making the original assignment of this taxon questionable. *Nereocaris exilis* differs in overall body proportions. In addition, the medial eye of *Nereocaris briggsi* is not as elongate as that of *N. exilis*, and never extends beyond the anterior margin of the lateral eyes. Although the lateral processes are tripartite, they show considerable overlap, almost resembling the lateral processes of *Waptia* (Walcott 1912), whereas those of *N. exilis* are apparently unfused and capable of independent movement (Legg *et al*. 2012b). Specimens of *Waptia* cf. *fieldiensis* from the Spence Shale Member of Utah (Briggs *et al*. 2008, fig. 12) show a striking similarity to this new taxon, especially in the morphology of the lateral telson processes, however unequivocal features of *N. briggsi* are not preserved, and these specimens should possibly be referred to using open nomenclature.

Genus ***LORICICARIS*** Legg and Caron in press.

1983	*Branchiocaris*; Collins, Briggs and Conway Morris, p. 165 (*in partim*).
1984	*Branchiocaris*; Briggs and Robison, p. 7, 12 (*in partim*).
1988	*Branchiocaris*; Briggs and Collins, p. 780 (*in partim*).
1998	*Branchiocaris*; Fletcher and Collins, p. 422 (*in partim*).
2003	*Branchiocaris*; Fletcher and Collins, p. 1835 (*in partim*).
in press	*Loricicaris* Legg and Caron, p. 7.

Type species. *Loricicaris spinocaudatus* Legg and Caron in press, from the Middle Cambrian (Series 3, Stage 5) Collins Quarry exposure of the Kicking Horse Shale Member (Burgess Shale Formation) on Mount Stephen (Yoho National Park, British Columbia, Canada), by monotypy.

Etymology. From the Latin *lorica*, meaning armoured or armour plating, referring to the spinose appearance of the abdomen.

Diagnosis. Arthropod with highly convex and reticulate bivalved carapace with a subtriangular process on the postero-dorsal margin; uniramous appendages consisting of a single ramus, the exopod, the anterior-most of which are flap-like which grade and reduce into more rod-like filaments posteriorly, present on all trunk somites; posterior trunk somites spinose, with at least 15 spines per segment; telson

rounded and spinose, terminating with two ventrally positioned lateral processes each bearing small spines.

Loricicaris spinocaudatus Legg and Caron in press
Figures 5.7, 5.11-5.13

v.1983 *Branchiocaris*; Collins, Briggs and Conway Morris, p. 163, fig. 3C.
*in press *Loricicaris spinocaudatus* Legg and Caron, p. 1-25, figs. 1-3.

Etymology. From the Latin *spinosus* and *cauda*, meaning spiny and tail, respectively, in reference to the spinose abdomen and telson of this species.

Specimens. Holotype ROM 62143 (Fig. 5.11A-C), a nearly complete specimen with frontal appendages and possible eyes present, preserved in lateral orientation. Paratype ROM 43188 (Fig. 5.11D-F), a nearly complete specimen preserved in ventral view. This specimen has previously been figured by Collins *et al*. (1983, fig. 3C). An additional 26 specimens are also referred to this taxon.

Occurrence. All material referred to this taxon was collected from the Collins Quarry exposure (locality 9 *sensu* Collins *et al*. 1983) of the Kicking Horse Shale Member (Burgess Shale Formation) situated on the western slope of Mount Stephen in Yoho National Park (British Columbia, Canada); *Polypleuraspis insignis* Subzone of the *Glossopleura* Zone (Fletcher and Collins 1998, 2003) of the Middle Cambrian (Series 3, Stage 5).

Diagnosis. As for genus.

Comparative description.

Size and general appearance. The longest specimen, ROM 62151 (Fig. 5.12A), measuring 41 mm from the distal tip of the carapace to the posterior-most tip of the telson (allowing for curvature), not including the telson processes. The shortest preserved specimen, ROM 62149 (Fig. 5.12B), measures 12 mm, but the body is twisted and the trunk is partially folded underneath the carapace, suggesting that the measured length is a minimal estimate of the size of the specimen. The average length of individuals, based on specimens that have both the anterior edge of the

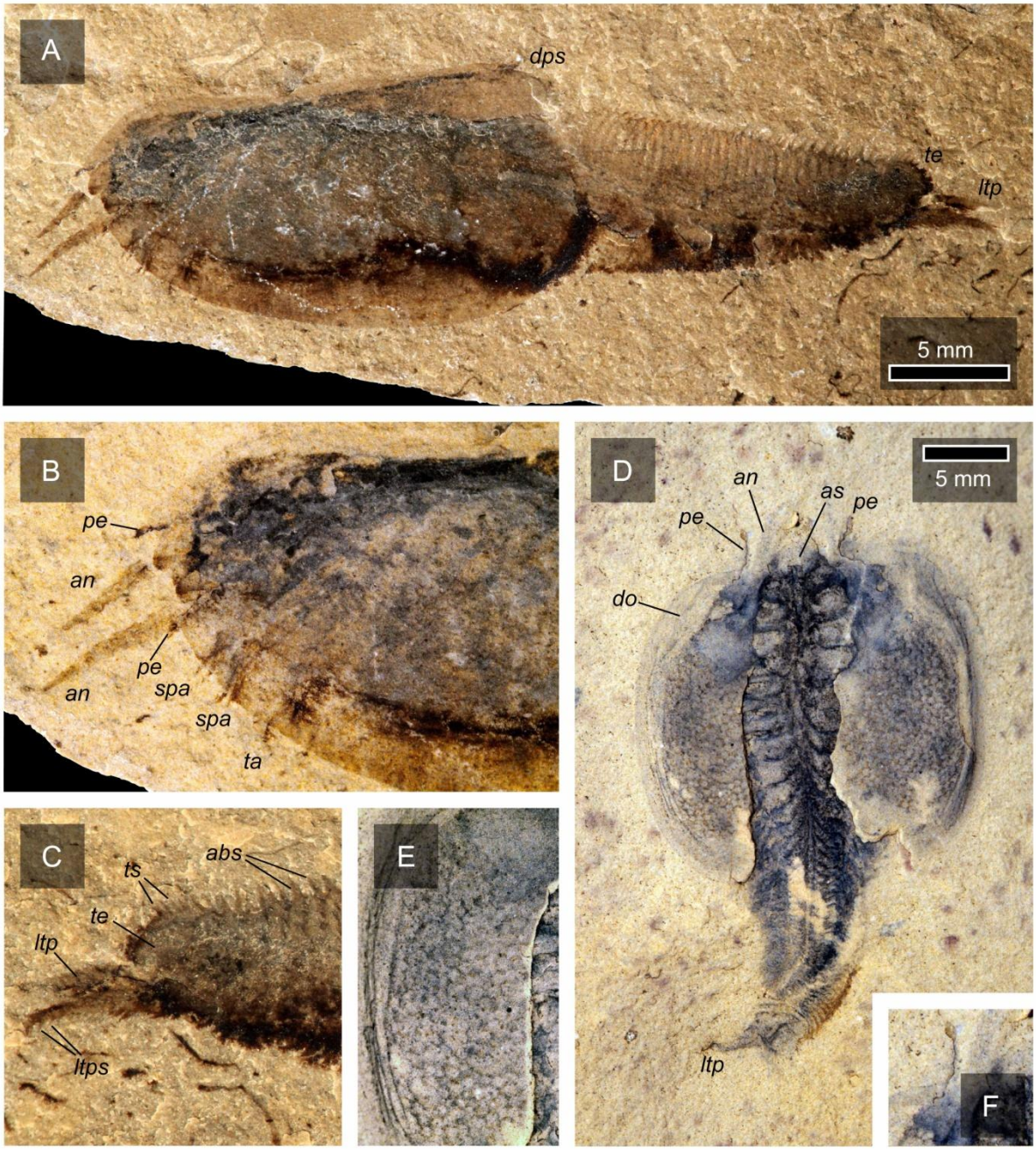


Fig. 5.11 | *Loricicaris spinocaudatus* Legg and Caron in press, from the Kicking Horse Shale Member of the middle Cambrian Burgess Shale Formation. A-C, the holotype ROM 62143; **B**, detailed anatomy of the head of ROM 62143; **C**, details of the telson and posterior trunk of ROM 62143 (counterpart); **D-F**, paratype, ROM 43188; **E**, detailed view of the carapace of ROM 43188 showing the polygonal structure of the trunk reticulation; and **F**, detailed view of the putative right eye of ROM 43188. Abbreviations: abs, abdominal spines; an, antenna; as, anterior sclerite; do, doublure; dps, dorso-posterior spine; ltp, lateral telson process; ltps, secondary spines on lateral telson process; pe, putative eye; spa, specialized post-antennal appendage; ta, trunk appendage; te, telson; and, ts, telson spine.

carapace and the distal-posterior most tip of the abdomen preserved (*n* – 24), is 27 mm. Smaller individuals are generally poorly sclerotized, with the underlying

sediment visible below their carapace (e.g. Fig. 5.12B). Size and poor sclerotization of these specimens indicate that they are juveniles.

Carapace. The carapace covers roughly 65 per cent of the total body length (calculated based on 24 specimens). ROM 43188 (Fig. 5.11D) is the only specimen that preserves the ventral morphology in sufficient detail to determine that the carapace is equivalent in length to c. 14-16 somites, including the head region. The carapace is subtrapezoidal, almost reniform in general outline with a height to length ratio of 5:11, and a slight posterior expansion (Fig. 5.11A). The anterior margin of the carapace lacks any projections, e.g. rostra. The dorsal fold is straight (Figs. 5.11A, 5.12A, C). A small spinose process occurs at the posterior end of the hinge line (Figs. 5.11A, 5.12A, C); this is also the highest point of the carapace. Striations on the margin of the carapace represent compression artefacts and indicate that the carapace was slightly convex. This tends to occur near the margins of the carapace, often in association with a doublure-like structure (Figs. 5.11D, 5.12B-D), although it is unclear if this feature is the result of compaction or a natural structure. The concavity of the carapace is also demonstrated by ventrally preserved specimens, e.g. ROM 43188 (Fig. 5.11D), in which the carapace almost completely encloses the appendages. A faint reticulation of the carapace can be seen in several specimens and consists of numerous subhexagonal polygons (Fig. 5.11E). Attachment of the carapace could not be determined but the position of the abdomen in specimens with a splayed carapace, e.g. ROM 62148 (Fig. 5.12C), may indicate that it was not attached along the entire length of the thorax. There is no evidence of muscle scars.

Eyes. Some specimens possess structures that might be tentatively interpreted as eyes (Figs. 5.11A-B, D-F). They are unreflective and seem to originate from the external margin of the carapace rather than the lateral region of the head. The structures consist of a thin filamentous stalk with a bulbous tip (Fig. 5.11F). The bilaterally symmetrical nature of these structures makes it unlikely they are abiogenic, but as far as I am aware there are no analogous structures amongst extant arthropods.

Head structure. The exact extent of the head is unclear due to the absence of adequately preserved specimens but may be composed of at least three segments based on ROM 62143 (Fig. 5.11A-B, D): an anterior sclerite and two limb bearing segments. A subcircular anterior sclerite projects beyond the anterior of the carapace (Figs. 5.11D, 5.12C-D, 5.13B-C). No hypostome or mouth opening could be identified posterior to the anterior sclerite in the available material.

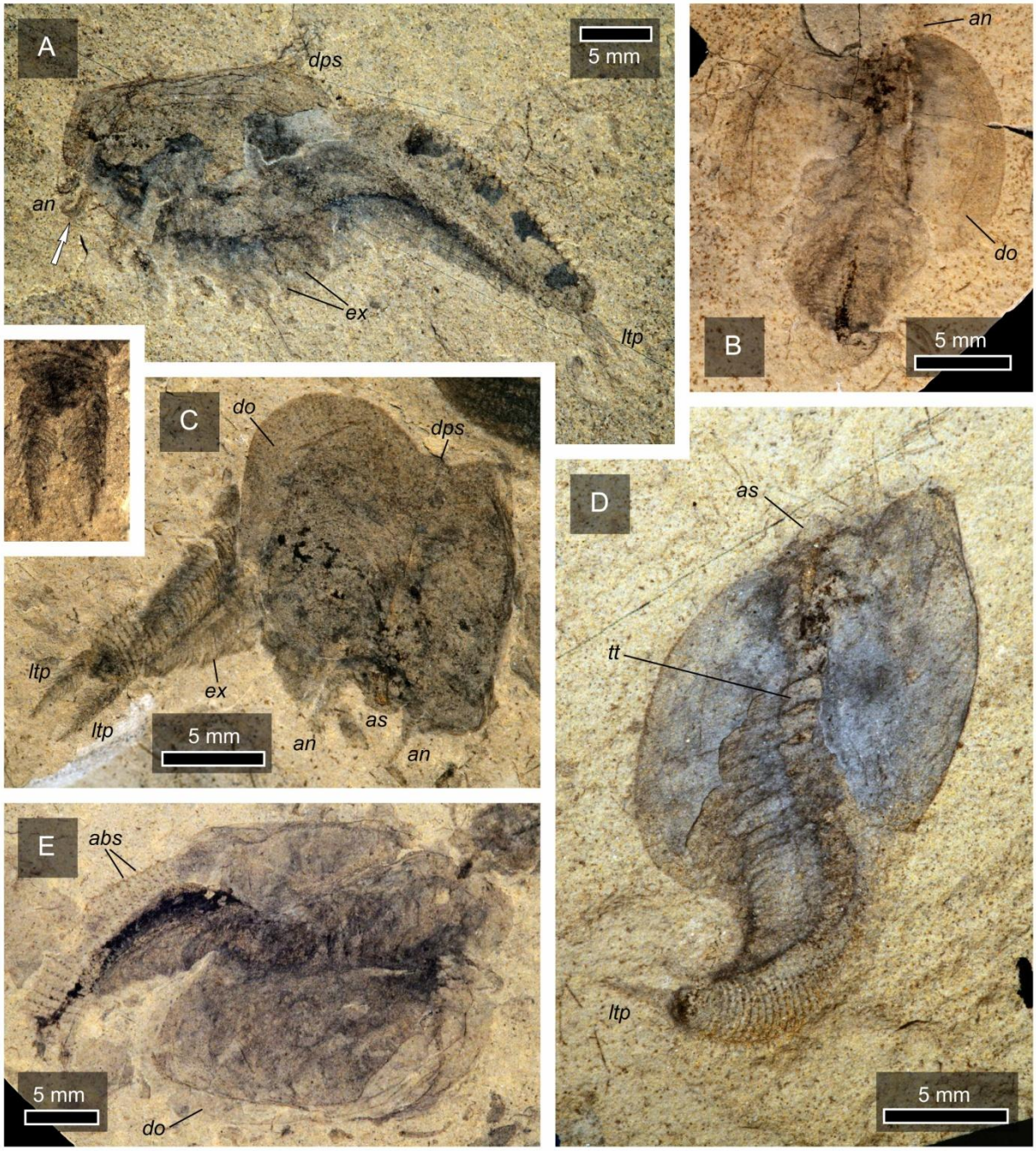


Fig. 5.12 | *Loricicaris spinocaudatus* Legg and Caron in press, from the Kicking Horse Shale Member of the middle Cambrian Burgess Shale Formation, British Columbia. A, ROM 62151, the largest known specimen of *Loricicaris spinocaudatus*, arrows indicate possible taphonmic bending of the antennae; **B**, ROM 62149, the smallest known specimen of *Loricicaris spinocaudatus*; **C**, ROM 62148, *inset*, showing a detailed view of the telson with setiferous spines; **D**, ROM 62150; and, **E**, ROM 62147. Abbreviations: abs, abdominal spines; an, antenna; as, anterior sclerite; do, doublure; dps, dorso-posterior spine; ex, exopods; ltp, lateral telson process; and tt, trunk tergites.



Fig. 5.13 | *Loricicaris spinocaudatus* Legg and Caron in press, from the Kicking Horse Shale Member of the middle Cambrian Burgess Shale Formation. A, ROM 62146; **B-C**, ROM 62145; and **C**, detailed view of the head region of ROM 62145. Abbreviations: abs, abdominal spines; ans, antennal setae; as, anterior sclerite; gt, gut; and, spa, specialized post-antennal appendage.

A pair of antenna-like frontal appendages, are preserved in 12 specimens. In some specimens, antennae are bent about half way along their length (Figs. 5.12A, 5.13C); these appendages appear to preferentially bend dorsally, which may be the result of muscular decay. This contrasts with better-preserved specimens, whose antennae are straighter with a slight ventral curvature (Fig. 5.11A-B, D). The antennae are robust, i.e. non-filamentous, with c. 10 individual podomeres and delicate setae along their margins (e.g. Figs. 5.11A-B, 5.13C). The nature of the attachment between the antennae and the head is unclear.

A second pair of specialized appendages is present behind the antennae. These appendages are more rarely preserved than the antennae and only in a few specimens are they preserved in any detail (Figs. 5.11A-B, 5.13C); these

appendages resemble the “principal appendages” (*sensu* Briggs 1976) of *Branchiocaris*, elsewhere known as specialized post-antennal appendages (SPAs; Yang *et al*. 2013, Legg *et al*. in review). Due to the slight oblique orientation of some specimens both the left and right appendages can be seen (Fig. 5.11A-B). The distal tips of these appendages are bifurcate, although not chelate, i.e. they appear to originate from the same loci rather than from separate podomeres. The faint outline of a bulbous distal podomere attached to a slender shaft can be distinguished, although individual podomeres cannot.

Gut. The gut consists of a simple tube with little relief, which terminates within the telson (e.g. Fig. 5.13A). Midgut glands are not present.

Appendages. Trunk appendages are present in at least 12 specimens. They can best be observed in specimens that have undergone post-mortem dissociation of the carapace from the rest of the body, thereby allowing the appendages to protrude beyond the carapace margin (see for example Figs. 5.12A, 5.13A). Appendages are uniramous, with only the exopods present. The exopods decrease in length towards the posterior of the animal, gradually changing from elongate subtriangular flaps to filamentous rods (Fig. 5.11D). The appendages are present on all by the pre-telson somite (Fig. 5.11D). The exopods are fringed with a dark band of organic material which may represent respiratory setae. The proximal region of the exopod is lobate.

Trunk somites. The anterior trunk somites are usually obscured by the bivalved carapace, however, in a few specimens (Figs. 5.11D, 5.12D) part of the carapace has been removed, revealing the underlying somites. About 14-16 somites are preserved. A change in somite size is associated with a change in exopod morphology from subtriangular flaps to filamentous rods. The number of somites not covered by the carapace appears to vary amongst specimens, even among those of similar size, and may represent a post-mortem artefact. 32 post-carapace somites are present in ROM 62143 (Fig. 5.11A), however a larger specimen (ROM 62147) has closer to 22 (Fig. 5.12E). The post-carapace somites are distinguished by their dorsal processes and short size; like the anterior somites they decrease in size posteriorly. Small triangular processes are present on the postero-dorsal and postero-lateral margins of the somites; there were c. 15 spines per somite (Figs. 5.11A, C, 5.12A, E, 5.13A).

Telson. A comparison of telsons preserved in lateral and parallel orientation indicates that the telson is wedge-shaped and very convex. A dorsal row of spines is present on the telson of ROM 62143 (Fig. 5.11A, C). This taxon has no medial telson process, but lateral telson processes are located ventrally and widely separated by the telson; they are straight, acuminate and tend to be preserved parallel to each

other, indicating that they were rigid and incapable of lateral movement. In ROM 62148 the telson is fringed with numerous setiferous spines (Fig. 5.12C, *inset*).

Remarks.

Loricicaris spinocaudatus shares a suite of characters with *Branchiocaris*, hence its original assignment. These characters include a convex bivalved carapace with a straight hinge and a posterior carapace process, an elongate trunk with posteriorly decreasing somites ending in a rounded telson with ventrally placed lateral processes, a head composed of an anterior sclerite and two limb-bearing segments, an anterior pair of antennae and a pair of SPAs, uniramous trunk appendages with elongate subtriangular exopods and no endopods, and putative eyes on the antero-lateral margin of the carapace. None of these features are restricted to *Branchiocaris* however, and *Loricicaris* exhibits a number of similarities to other bivalved arthropods, particularly *Perspicaris* (Briggs 1977) and *Canadaspis* (Briggs 1978); all of these taxa possess a spinose trunk and acuminate-shaped lateral telson processes. Briggs and Robison (1984) described specimens of *Branchiocaris pretiosa* (Resser 1929) from the Middle Cambrian Wheeler Formation of Utah with a spinose trunk. Such a feature is lacking in the type material from the Burgess Shale, however, indicating these specimens may be referred to *Loricicaris* rather than *Branchiocaris*, pending further study. The trunk of *Loricicaris* is unlike that of *Canadaspis* and *Perspicaris* which feature limbless abdomens. All together though *Loricicaris* resembles *Branchiocaris*, *Perspicaris* and *Canadaspis*, the unique combination of characters observed in *Loricicaris* supports its status as a new genus.

5.4. Modes of life

Nereocaris exilis, *N. briggsi* and *Loricicaris spinocaudatus* show adaptations to a nektonic lifestyle. All have weakly sclerotized appendages that do not extend beyond the ventral margin of the carapace, indicating they were ill-equipped for benthic ambulation. *Nereocaris* shows a number of possible adaptations to a nektonic habit, such as a tall and laterally compressed carapace. The latter could serve as an effective keel that could enable high speed manoevering. The exopods of *N. briggsi* are absent, or, at least, could not be distinguished in the available material, but are relatively small in the closely related *N. exilis*, indicating they were probably not the main source of propulsion; in contrast, their telsons show both considerable flexion (see for example Fig. 5.6F and 5.7A) and a broad fluke-like structure. These structures would not only serve to produce a propulsive force but may also have acted as a rudder (Plotnick and Baumiller 1988), further indicating the agile nature of these animals.

The gut of *N. briggsi* consists of a simple, relatively wide tube (see for example Fig. 5.6G), often preserved in three dimensions; this, and the absence of

accessory glands or diverticulae is indicative of a constant and nutrient-rich food source, and is common amongst extant deposit feeders (Lopez and Levington 1987, LA Wilson 2006). This mode of feeding is further supported for *N. briggsi*, which shows no evidence of limb specialization – which is usually required for scavenging or predation – and no specialized mouth apparatus, which would be required for grazing. The lack of limb and mouthpart specialization, combined with the proposed locomotory style and possible mud-filled gut, is consistent with it belonging to a low trophic level.

Although nektonic, *Loricicaris* does not appear to have been as agile as *N. briggsi*. The lateral processes in *Loricicaris* are consistently recovered in the same orientation, indicating that they were not capable of independent movement. In addition the telson of *Loricicaris* is bulbous and would not have acted as either an effective rudder or fluke, although its enlarged anterior exopods may have acted as paddles. The exact feeding habit of *Loricicaris* is unclear; the gut is rarely preserved and, in instances when it is, reveals few discernible details. The specialization of the anterior limbs may indicate considerable manipulation of food items, i.e. predation or scavenging, however, the apparent absence of well developed eyes may preclude the former.

6. A reinvestigation of the enigmatic arthropod Isoxys

6.1. Introduction

The characteristic bivalved carapace of *Isoxys* (Fig. 6.1), with prominent antero- and postero-dorsal spines, is a common constituent of many Cambrian *Konservat-Lagerstätten* (Vannier and Chen 2000, García-Bellido *et al*. 2009a, b, Stein *et al*. 2010, Fu *et al*. 2011). It is known from 16+ species distributed over 14 such localities (Wang *et al*. 2010) and was one of the first Burgess Shale-type arthropods described (Walcott 1890). Despite its ubiquity and long history of study its affinities have remained obscure; this is attributed to the lack of information regarding soft-part anatomy of this taxon which is mostly preserved as isolated *dorsal shields* (*sensu* Stein *et al*. 2010), often referred to as a *carapace*. Recently new collections in China, Australia and Canada have recovered specimens of *Isoxys* with soft-anatomy preserved, specifically visual organs, the gut, and limb morphology (Vannier and Chen 2000, Vannier *et al*. 2009, García-Bellido *et al*. 2009a, b, Stein *et al*. 2010, Fu *et al*. 2011, Schoenemann and Clarkson 2011). These new discoveries have prompted a reconsideration of the affinities of *Isoxys*. In particular, the recent recovery of raptorial frontal appendages in specimens from the Chegjiang biota (Vannier and Chen 2000, Fu and Zhang 2011), Burgess Shale (García-Bellido *et al*. 2009a) and Sirius Passet Lagerstätten (Stein *et al*. 2010) has led some (e.g. Vannier *et al*. 2009) to consider *Isoxys* related to the „great-appendage" arthropods. This hypothesis has been challenged based on a lack of consensus regarding the segmental affinities of the „great-appendage" of other taxa (Fu *et al*. 2011). The difference in limb morphology between different species of *Isoxys* has also led some to propose that these taxa may not be congeneric (Stein *et al*. 2010, Fu and Zhang 2011). Few have tested the monophyly of this genus or tried to determine its affinities using cladistic analyses, a notable exception being Vannier *et al*. (2009) who resolved *Isoxys* as sister-taxon to the anomalocaridids. Before testing either the

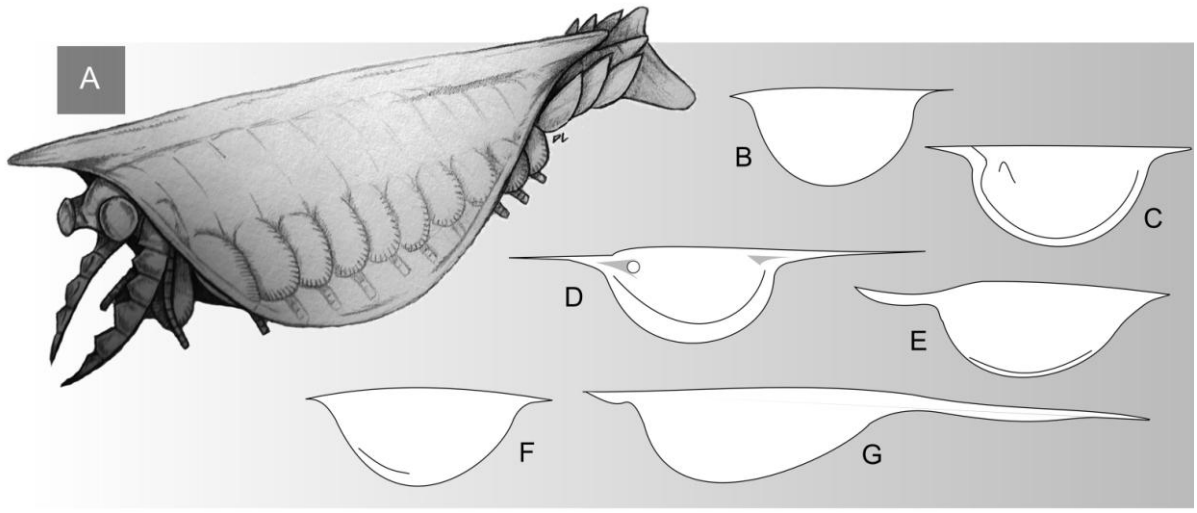


Fig. 6.1 | The cosmopolitan arthropod *Isoxys* Walcott 1890. A, reconstruction of *Isoxys acutangulus* Walcott 1908, from the middle Cambrian Burgess Shale, based on the description of García-Bellido *et al*. (2009b) and additional morphological interpretations presented herein; **B-G**, variation in dorsal shield morphology (redrawn from Vannier and Chen 2000, fig. 1), represented by **B**, *I. acutangulus*; **C**, *I. auritus* Jiang 1982; **D**, *I. volucris* Williams *et al*. 1996; **E**, *I. curvirostratus* Vannier and Chen 2000; **F**, *I. chihoweanus* Walcott 1890; and **G**, *I. longissimus* Simonetta and Delle Cave 1975.

affinities or interrelationships of *Isoxys* a morphological reinterpretation of this taxon must be undertaken and homology statements constructed.

The contents of this chapter have been published, in part, in *Lethaia* (Legg and Vannier in press).

6.2. Previous work

The paucity of soft-part remains known from *Isoxys* has precluded determination of its affinities (Delle Cave and Simonetta 1991, Williams *et al*. 1996). The earliest descriptions of *Isoxys* were generally vague and contained little discussion of affinities (Walcott 1890, 1908). There was a trend among many early arthropod workers to align Cambrian bivalved arthropods with either branchiopod or phyllocarid crustaceans (e.g. Walcott 1912), and the latter was also true of *Isoxys* (Richter and Richter 1927, Brooks and Caster 1956), although little justification was given for this assignment. Rolfe (1969) noted similarities in carapace morphology between *Isoxys* and archaeostracan phyllocarids, including a weakly mineralized carapace and an entire dorsal hinge line, however none of the proposed characters is exclusive to these taxa and a similar morphology may have evolved many times within Arthropoda (Hou and Bergström 1997).

The first detailed description of the soft-anatomy of *Isoxys* was by Shu *et al.* (1995), although possible body segments had previously been noted for *I. communis*

from the Emu Bay Shale (Glaessner 1979). Shu *et al*. (1995) considered *Isoxys* to be a crustacean, however, their interpretations were later challenged as "speculative" (Vannier and Chen 2000:296), and the putative crustacean features, such as two pairs of antennae, could not be verified. Later, Vannier *et al*. (2006) tentatively assigned *Isoxys* to the enigmatic Thylacocephala Pinna *et al*. 1982, a clade of malacostracan crustacean-like arthropods with enlarged raptorial frontal appendages, although later rejected this opinion (Vannier *et al*. 2009).

The discovery of elongate prehensile raptorial appendages in *Isoxys* prompted comparison with „great-appendage" arthropods (García-Bellido *et al*. 2009a) and also prompted a reassessment of its monophyly (Stein *et al*. 2010, Fu *et al*. 2011). The only cladistic analysis to date to include *Isoxys* (Vannier *et al*. 2009) resolved it among "great-appendage" arthropods, as sister-taxon to a clade composed of *Occacaris* Hou 1999, and *Forfexicaris* Hou 1999, both bivalved arthropods with „great-appendages" from the Chengjiang biota; this more inclusive clade resolved as sister-taxon to the anomalocaridids *Anomalocaris* Whiteaves 1892, and *Parapeytoia* Hou *et al*. 1995 [although see Daley *et al*. 2009, Stein 2010, Legg *et al*. 2012b; and Legg 2013, for an alternative interpretation of *Parapeytoia*]. Close relationships between *Isoxys* and other „great-appendage"-bearing bivalved arthropods was challenged by Fu *et al*. (2011) who questioned the segmental affinities of many putative „great-appendages" and argued that it carried little phylogenetic significance.

6.3. Morphological interpretation

This section is not intended as a complete reinterpretation of the morphology of *Isoxys* but rather a discussion of key characteristics – specifically the dorsal shield, frontal appendages, trunk appendages, posterior tail fan and digestive glands – which may help to determine the affinities and interrelationships of is contained species.

6.3.1. Dorsal shield

The dorsal shield of *Isoxys* shows considerable intraspecific variation, although species assigned to this taxon always possess extensive antero- and posterolateral spines (Fig. 6.1). The dorsal shields of some species possess an extensive dorsal fold, e.g. *I. auritus* (Shu *et al*. 1995), reminiscent of other bivalved arthropods; whereas others lack such a fold, e.g. *I. curvirostratus* (Vannier and Chen 2000). The dorsal shield may also differ in micro-ornament, which may be reticulate, e.g. *I. auritus* (Shu *et al*. 1995) or striate, e.g. *I. curvirostratus* (Vannier and Chen 2000). This has led some (e.g. Fu *et al*. 2011) to infer that all species referred to *Isoxys* may not be congeneric.

Although a diagnostic characteristic of *Isoxys* (Vannier and Chen 2000, García-Bellido *et al*. 2009a, b, Stein *et al*. 2010, Fu *et al*. 2011), the phylogenetic significance of the antero- and posterolateral spines is unclear. Similar spines occur in larval malacostracans (García-Bellido *et al*. 2009b, Vannier *et al*. 2009) and halocypridid ostracods (Vannier and Chen 2000) and may represent a convergent adaptation to a pelagic lifestyle (Vannier and Chen 2000, García-Bellido *et al*. 2009b, Vannier *et al*. 2009); the slender nature of the spines reduces drag during swimming (Vannier and Chen 2000).

6.3.2. Frontal appendages

Much of the debate regarding the affinities and monophyly of *Isoxys* has concerned the morphology of its frontal appendages. The frontal appendages of *Isoxys* were originally compared to the raptorial appendages of „short-great-appendage" arthropods, such as *Leanchoilia* Walcott 1912, *Alalcomenaeus* Simonetta 1970, *Yohoia* Walcott 1912, *Jianfengia* Hou 1987a, *Haikoucaris* Chen *et al*. 2004, and *Fortiforceps* Hou and Bergström 1997; the „great-appendages" of which are composed of a proximal unit consisting of a two-segmented peduncle separated from the distal group of two-to-four chelate-to-subchelate podomeres by a distinct „elbow" joint (Figs. 6.2A-B; Haug *et al*. 2012c). Supposed similarities between the appendages of „short-great-appendage" arthropods and *Isoxys* appear to be overstated. Although a two-segmented peduncle was reported in specimens of *I. acutangulus* (García-Bellido *et al*. 2009a, Vannier *et al*. 2009), a re-examination of the figured material could not identify such structures (see Fig. 6.2C-D) and elements identified as peduncular elements by García-Bellido *et al*. (2009a, fig. 3A) are indistinguishable from the more distal spinose elements.

Frontal appendages are preserved in five species: *I. acutangulus* Walcott 1908, *I. auritus* Jiang 1982, *I. communis* Glaessner 1979, *I. curvirostratus* Vannier and Chen 2000, and *I. volucris* Williams *et al*. 1996; and although they differ in podomere count and overall length they have a conserved morphology. They are generally elongate with podomeres reduce in size towards the distal end lacking chelate or subchelate spines (Fig. 6.2C-F). Instead the perpendicular spines project from the centre of each podomere like those of anomalocaridids, particularly *Anomalocaris* (Fig. 6.2G-H). In *I. volucris* the spines appear bifurcate, like those of the putative anomalocaridid *Tasmiocaris* Daley and Peel 2010 (*cf*. Stein *et al*. 2010, fig. 2; and Daley and Peel 2010, fig. 1). Podomere boundaries are poorly delineated in many specimens of *Isoxys* although podomere number can be inferred from the position of the spines. There are at least five spinose podomeres in *I. acutangulus* (Fig. 6.2C-D) and *I. curvirostratus*, seven in *I. volucris* and as many as 13 in juvenile specimens of *I. auritus* (Fig. 6.2E-F) – a number comparable to *Anomalocaris* (*n* = 14; Fig. 6.2G-H). The spines of *Isoxys* are located on the concave inner margin of an anteriorly curved appendage (Fig. 6.2C-F), comparable to those of „short-great-

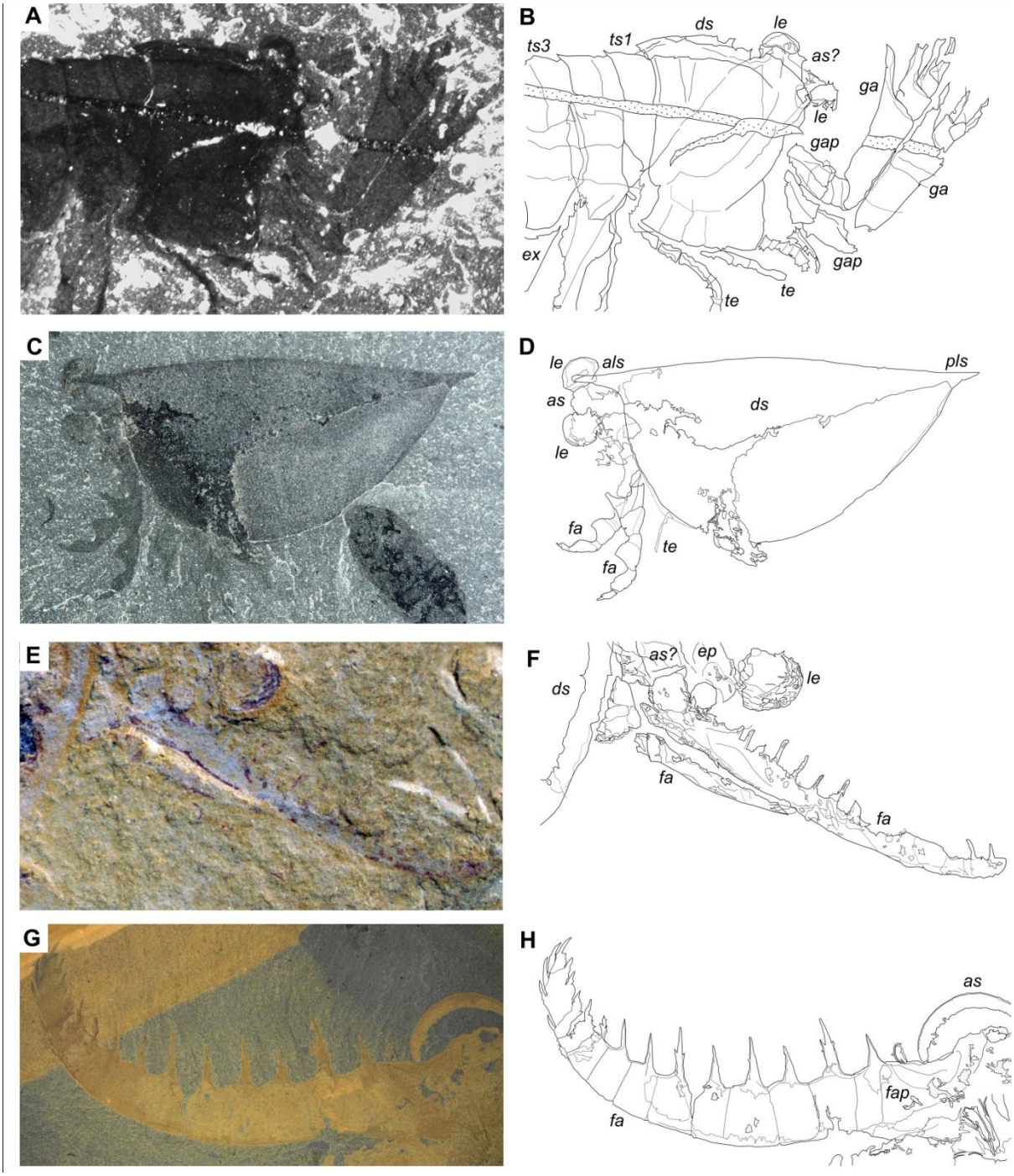


Fig. 6.2 | Frontal appendages of basal arthropods. A, the „short-great-appendages" of *Yohoia tenuis* Walcott 1912 (NMNH 155621) with **B**, interpretive sketch; **C**, *Isoxys acutangulus* (ROM 51211) with **D**, interpretive sketch; **E**, detailed view of the „great-appendages of *I. auritus* (YDKS 43) with **F**, interpretive sketch; and **G**, the „great-appendage of *Anomalocaris canadensis* Whiteaves 1892, with **H**, interpretive sketch. Abbreviations: als, anterolateral spine; as, anterior sclerite; ds, dorsal shield; ex, exopod; fa, frontal appendage; fap, frontal appendage peduncle; ga, „great-appendage"; gap, „great-appendage" peduncle; le, lateral eye; pls, posterolateral spine; te, trunk endopod; and, ts, trunk somite. Image **A** courtesy of Joachim Haug, image **B** courtesy of Diego García-Bellido, and image **C** courtesy of Allison Daley.

appendage" arthropods, whereas those of anomalocaridids are typically located on the concave inner margin of a posteriorly curved appendage (Fig. 6.2G-H). This is arguably not a big difference and could come about through torsion of the limb. The variation in limb morphology may imply different feeding strategies achieved via differences in the prehensile motion of the limbs.

Fu *et al*. (2011) considered the frontal appendages of *Isoxys* to originate from the deutocerebral somite, and rejected homology with frontal appendages of other bivalved „great-appendage" arthropods, namely *Occacaris* and *Forfexicaris*. The hypothesis of Fu *et al.* (2011) was based on a misinterpretation of head organization in *Occacaris* and *Forfexicaris*, which were thought to possess a pair of appendages anterior of the „great-appendage", which they considered to originate from the deutocerebral somite and tritocerebral somite respectively. This was based on comparisons with extant mandibulate arthropods which typically possess an antenniform deutocerebral appendage (Fig. 6.3). Antenniform appendages are completely unknown from *Forfexicaris* and the supposed antennae of *Occacaris* are indistinguishable from the trunk endopods and have most likely been misidentified. The exact morphology of the „great-appendage" of *Occacaris* is hard to determine from the one poorly preserved specimen but that of *Forfexicaris* resembles the „great-appendage" of other „short-great-appendage" arthropods.

„Short-great-appendages" were generally considered homologous to the chelicerae of chelicerates and would therefore belong to the deutocerebrum (Fig. 6.3; Damen *et al*. 1998, Telford and Thomas 1998, Dunlop 2005, Haug *et al*. 2012c), however recent descriptions of neural tissues in fuxianhuiids suggests the „great-appendages" innovate from the tritocerebral neuromeres of the brain (Ma *et al*. 2012b, Yang *et al*. 2013, **Chapter 7**).

The pedunculate eye stalks and the „great-appendages" of *Isoxys* are situated beneath an anterior sclerite (*sensu* Budd 2008), a weakly sclerotized anterior plate (Fig. 6.2C-D). The eyes of extant arthropods, and their nearest extant outgroup, onychophorans, originate from the protocerebrum, the anteriormost ganglion of the arthropod brain (Fig. 6.3; Strausfeld 2012). The close association of the ocular sclerite and „great-appendages" of *Isoxys* may indicate they originate from the same somite, i.e. they are both protocerebral, or the appendages may be deuterocerebral. In either case, the „great-appendage" of *Isoxys*, and by extension anomalocaridids, would not be segmentally homologous to the „great-appendages" of „short-great-appendage" arthropods (Fig. 6.3). See **Chapter 7** for further discussion.

6.3.3. Trunk appendages

Although the anterior appendages are clearly arthropodized, i.e. they consist of discrete segments, the detailed morphology of the trunk limbs is unclear. The limbs are biramous, however endopods are sometimes absent which may indicate they were more weakly sclerotized than the exopods. In cases where the endopods are

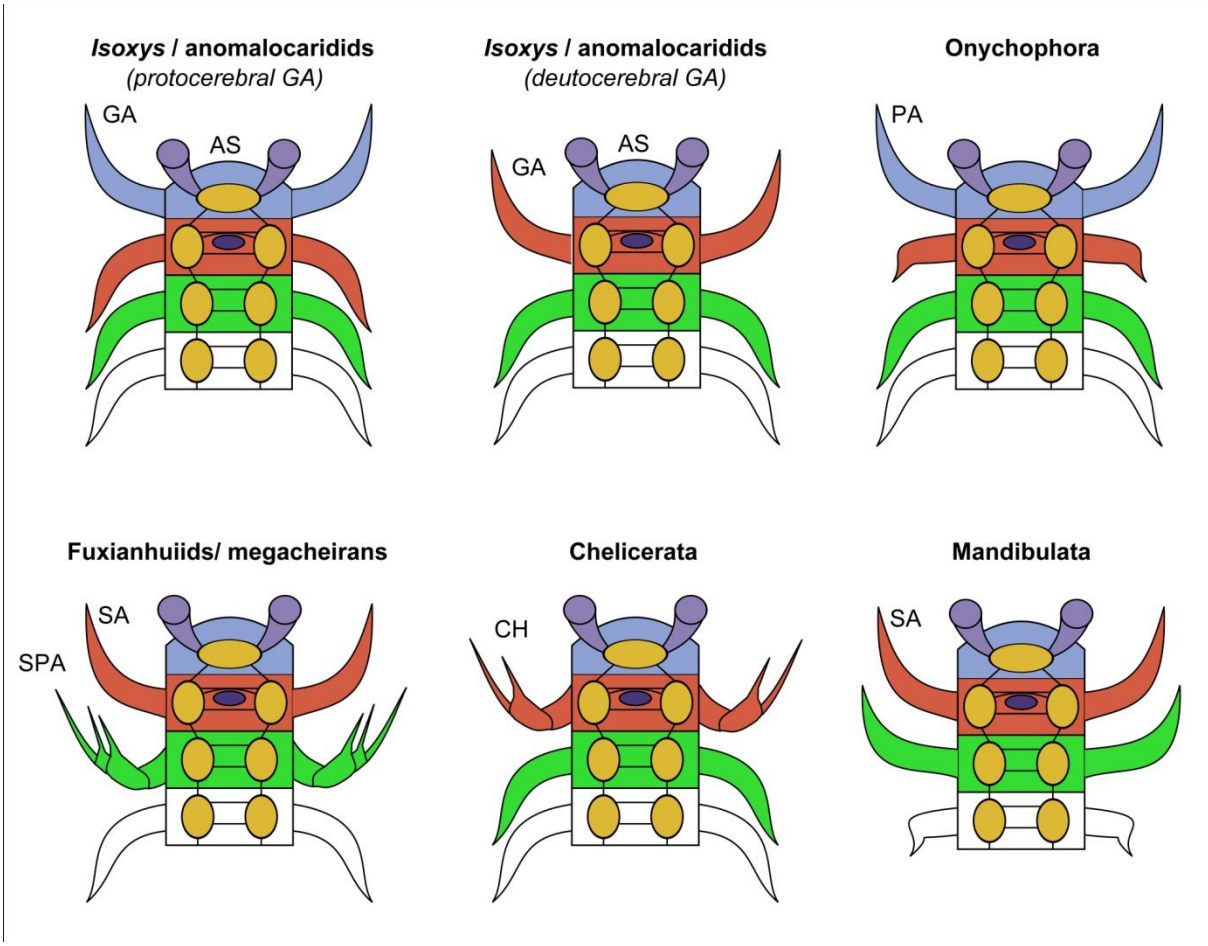


Fig. 6.3 | Head organization in panarthropods (based on Scholtz and Edgecombe 2006, fig. 3). Neural tissues in yellow; structures associated with the protocerebrum are in blue, including the mouth which is embryologically associated with the protocerebrum but later may move posteriorly to the deutocerebral somite; deutocerebral somites and associated structures in red; and tritocerebrum and associated structures in green. Black lines in the central mass indicate nerve connections. Abbreviations: as, anterior sclerite; ch, chelicerae; ga, „great-appendages"; pa, primary antennae; sa, secondary antennae; and, spa, specialized post-antennal appendages.

preserved, individual podomeres could not be distinguished – this may also be due to their poor sclerotization. Notable exceptions are *I. curvirostratus* in which the endopods display more than 10 well-delineated podomeres (Fu *et al*. 2011, fig. 4A), and *I. volucris*, which has really weakly sclerotized appandages, at least when compared to the frontal appendages, although approximately 10 podomeres can be discerned (Stein *et al*. 2010, fig. 2). A high number of endopod podomeres is regarded as a primitive characteristic of arthropods, with seven representing the crown-group condition (Boxshall 2004). Such weakly sclerotized endopods are also present in other Cambrian bivalved arthropods, particularly *Nereocaris* Legg *et al*. 2012b, *Jugatacaris* Fu and Zhang 2011, and *Pectocaris* Hou 1999 (see also Hou *et al*. 2004b).

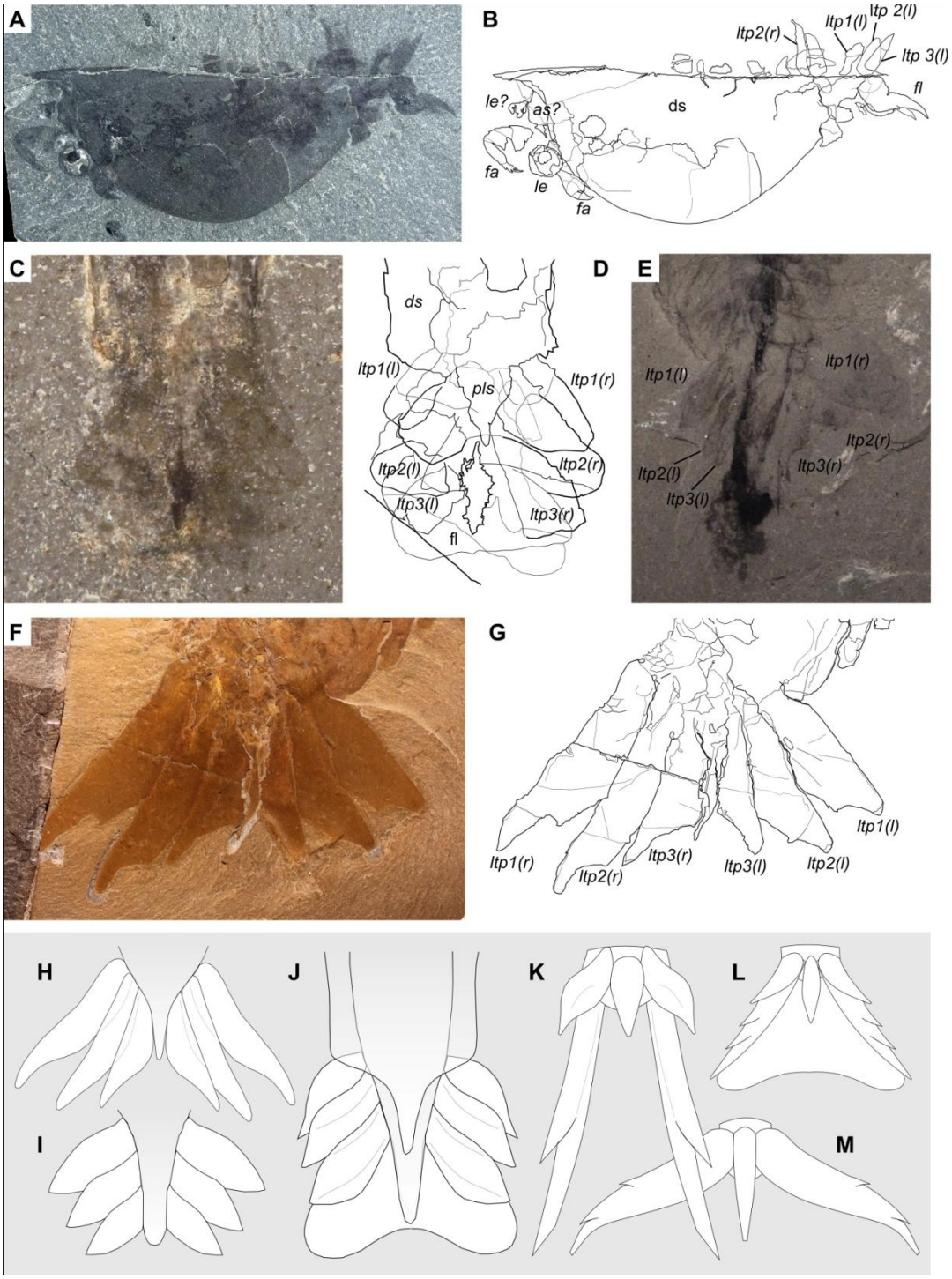


Fig. 6.4 | Posterior trunk and telson of dinocaridids and basal arthropods. A, *Isoxys acutangulus* (ROM 57899), preserved in lateral aspect with **B**, interpretive sketch; **B**, close-up view of the telson and lateral telson processes of *I. acutangulus* (ROM 57907), with **D**, interpretive sketch; **E**, the posteriot tail fan of *Opabinia* Walcott 1912 (NMNH 131217), preserved in lateral view; **F**, close-up of the tail fan of *Anomalocaris* (ROM 51211), with **G**, interpretive sketch; **H-M**, reconstructions of the posterior tail fan and telsons of dinocaridids and basal arthropods; **H**, *Anomalocaris*; **I**, *Opabinia*; **J**, *Isoxys*; **K**, *Nereocaris*; **L**, *Jugatacaris*; and **M**, *Odaraia*. Abbreviations: as, anterior sclerite; ds, dorsal shield; fa, frontal appendage; fl; fluke; le, lateral eye; ltp, lateral telson process; and pls, posterolateral spine.

The exopods are best preserved in *I. volucris*, in which they are subovoid and have a fringe of fine setae. Similar exopods are common among basal arthropods and have been reported from other bivalved arthropods, e.g. *Nereocaris*, *Pectocaris*, and *Perspicaris* Briggs 1977, and fuxianhuiids, e.g. *Fuxianhuia* Hou 1987b, and *Shankouia* Waloszek *et al*. 2005, but are distinct from „short-great-appendage" arthropods, some of which, e.g. *Fortiforceps*, have fine setae but lack ovoid exopods, and others of which, e.g. *Alalcomenaeus* and *Leanchoilia*, possess subovoid exopods but have spinose setae.

6.3.4. Posterior trunk and telson

The posterior trunk and telson are known exclusively from *I. acutangulus* (Fig. 6.4A-D, J), from the Burgess Shale Formation (*see* Fig. 5.1B). The posterior was originally described as consisting of a single segment, a fluke-like telson, with posteriorly deflecting exopods abutting it in some specimens (García-Bellido *et al*. 2009a); a re-examination of this material indicates that the putative exopods are actually distinct from the other exopods of the body and are better interpreted as lateral telson processes (*sensu* Legg *et al*. 2012b). Unlike the exopods, the lateral telson processes are subtriangular and lack a setal fringe (Fig. 6.4C-D). A similar arrangement is seen in both the dinocaridids *Opabinia* Walcott 1912 (Fig. 6.4E, I) and *Anomalocaris* (Fig. 6.4F-H), and basal bivalved arthropods, particularly *Nereocaris* (Fig 6.4K), *Jugatacaris* (Fig. 6.4L), *Pectocaris*, and to a lesser degree *Odaraia* Walcott 1912 (Fig. 6.4M). In the dinocaridids the lateral flaps project dorsally (Fig. 6.4E), as observed in laterally compressed specimens. The majority of specimens of *I. acutangulus* with lateral telson processes are dorso-ventrally compressed however, a single laterally preserved specimen indicates that the telson processes also project dorsally (Fig. 6.4A-B).

6.3.5. Digestive glands

Both *I. acutangulus* (Fig. 6.5A, C) and *I. communis* preserve an extensive series of reniform midgut glands. Similar glands have also been reported from a diversity of extant and Cambrian panarthropods, including *Opabinia* (Fig. 6.5B, D), *Anomalocaris*, a variety of bivalved arthropods, „great-appendage" arthropods (Butterfield 2002), fuxianhuiids (Zhu *et al*. 2004) and trilobitomorphs (Vannier and Chen 2002). There glands are thought to function as storage organs in organisms with infrequent but rich diets (Butterfield 2002, Vannier and Chen 2002), i.e. carnivores and scavengers. Their presence therefore has major implications for the ecology of the earliest arthropods. Legg *et al*. (2012b) recently argued that the most basal arthropods were filter or deposit feeders based on gut morphology and frontal limb structure, and were not carnivourous as had been advocated elsewhere (Maas *et al*. 2004). The presence of midgut glands in *Isoxys*, as well as the large

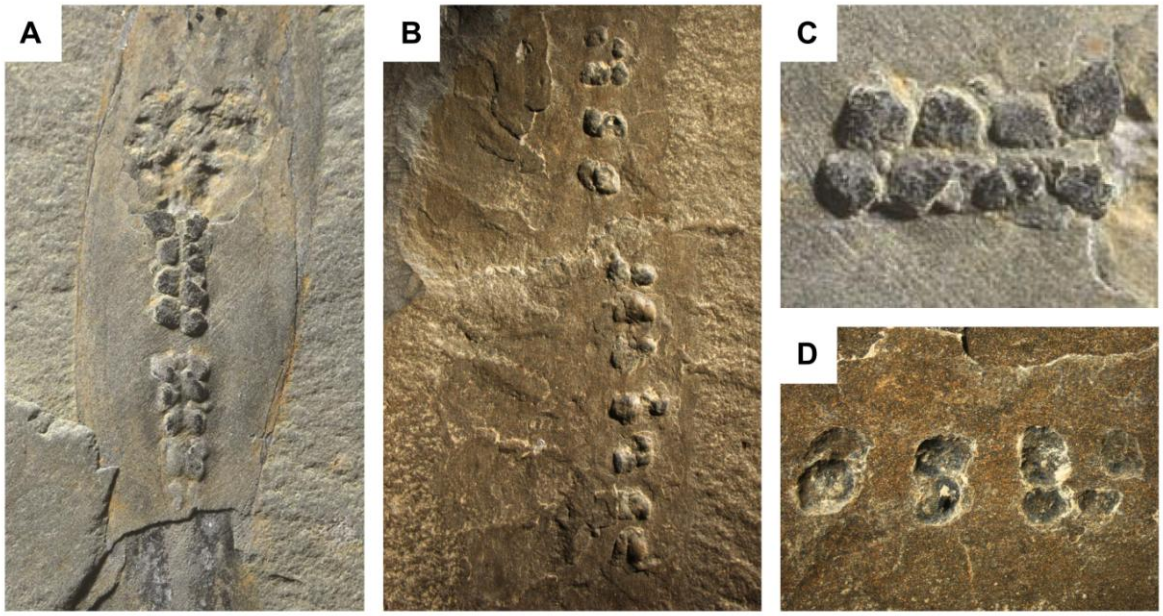


Fig. 6.5 | Digestive glands of *Isoxys* and *Opabinia*. A, *Isoxys acutangulus* (ROM 57904); **B**, *Opabinia* (ROM 59874); **C**, close-up view of the gut glands of *I. acutangulus* (ROM 57904); and **D**, close-up view of the gut glands of *Opabinia* (ROM 59874). Images **B** and **D** courtesy of Allison Daley.

pedunculate eyes and prehensile frontal appendages, indicate it was a predator with an infrequent source of nutrition.

6.4. Implementation

The morphological similarities between *Isoxys* and other Cambrian panarthropods, particularly anomalocaridids, were taken as evidence of „primary homology" (Pinna 1991), and coded as such in the phylogenetic analysis (**Chapter 3**). Given the uncertainty regarding the segmental affinities of the frontal appendages of *Isoxys* and anomalocaridids, this feature was given its own character (ch. **205**), and variations in it morphology were accommodated by character **206** (*see* **Appendix 2**).

7. Head structure *in* Cambrian bivalved arthropods

7.1. Introduction

Understanding the segmental organization of the head has been one of the most challenging endeavours in arthropod biology; studied by comparative anatomists, developmental biologists and palaeontologists alike, this issue is a fundamental aspect of arthropod phylogeny and has thus been hotly debated (*see* Scholtz and Edgecombe 2006, Richter et al. 2013, and references therein). Two significant advances in this area have drastically altered our views on the segmental organization of the arthropod head region: i) the demonstration that the chelicerae/chelifores, the raptorial frontal appendages of euchelicerates and pycnogonids, are homologous to the first antennae (= antennules) of mandibulates (Damen *et al*. 1998, Telford and Thomas 1998); and that ii) onychophorans (velvet worms), the likely sister group of living arthropods, bear an antenna-like appendage that is innervated from the protocerebral region of the brain (Eriksson *et al*. 2003, 2010). How these disparate appendages originated, and in the case of the onychophoran antenna, what their subsequent fate was, remains a point of contention. Although fossil material has been advocated as providing a potential solution to the problem (Budd 2002), a full consensus on its significance has yet to be reached (Scholtz and Edgecombe 2006).

The megacheirans (*sensu* Hou and Bergström 1997), or „short-great-appendage" arthropods, have played a central role in discussions of fossil arthropod head segmentation. All representatives possess an enlarged frontal appendage with chelate or subchelate spines on the distal podomeres, and a two-segmented peduncle separated from the distal podomeres by a distinct „elbow" joint (Haug *et al*. 2012c) and should thus correspond to the deutocerebral somite (Damen *et al*. 2008, Telford and Thomas 1998). Others have argued the „great-appendages" originate from either the protocerebral (Budd 2002) or tritocerebral somite (Cotton and Braddy 2004) citing as evidence the presence of putative antenniform, purportedly

deutocerebral, appendages anterior to the „great-appendages" in *Fortiforceps foliosa* Hou and Bergström 1997. The hypothesis of Cotton and Braddy (2004) relied on the older view that the chelicerae were associated with the tritocerebrum (Weygoldt 1985, Bitsch and Bitsch 2007); the morphological interpretation for the antennae of *F. foliosa*, however, has been questioned (e.g. Bergström and Hou 2005), although a similar configuration has been proposed for other stem-group euarthropods, including several fuxianhuiid species (i.e. *Fuxianhuia protensa* Hou 1987b, *F. xiaoshibaensis* Yang *et al*. 2013, and *Chengjiangocaris kunmingensis* Yang *et al*. 2013), and the bivalved arthropod *Branchiocaris pretiosa* (Resser 1929). In order to reconcile a chelicerae homology with the „great-appendage" in taxa that clearly have antennae as well, a model was proposed wherein the antenna of these taxa was homologised with the „primary" (protocerebral) antenna of onychophorans, and would therefore be innervated from the protocerebral neuromere of the brain, anterior to the deutocerebral „great-appendages" (Scholtz and Edgecombe 2005, 2006). However, the putative „great-appendages" of *B. pretiosa* are unlike those of megacheirans, and the presence of such appendages in fuxianhuiid arthropods has until recently been controversial (Chen *et al*. 1995, Waloszek *et al*. 2005, Budd 2008, Yang *et al*. 2013). Herein the head structure is documented for selected bivalved arthropods from the Burgess Shale Lagerstätte (Cambrian, Series 3, Stage 5) of British Columbia, Canada. These taxa are notable in possessing possible „great-appendage"-like limbs, somewhat similar to those of megacheirans, in some cases associated with antenniform appendages. Although the head structure of these taxa has been mentioned elsewhere (Budd and Telford 2009, Legg *et al*. 2012b, supp.), they have yet to be described.

The contents of this chapter are currently under review in *Arthropod Structure and Development* (Legg *et al*. in review).

7.2. Materials

All described material is located in the Smithsonian Institution National Museum of Natural History (NMHM formerly USNM), Washington, D.C., USA. Specimens judged to show adequate preservation of the head appendages were selected; these include two specimens of *Perspicaris dictynna* (NMNH 189245, figured in Briggs 1977, Plate 68, figs. 6, 7; Text-fig. 10; and Budd and Telford 2009, fig. 3e; and NMNH 213804, figured in Briggs 1977, Plate 69, figs. 1, 2; Text-fig. 11), a single specimen of *Canadaspis perfecta* (NMNH 189019a, figured in Briggs 1978, Plate 7, fig. 83), and a single specimen of *Odaraia alata* (NMNH 213807, figured in Briggs 1981, figs. 29, Plate 4, figs. 33-35; and Budd 2008, figs. 7C, 9). All specimens are from the Cambrian (Series 3, Stage 5), *Pagetia bootes* Subzone of the *Bathyuriscus-Elrathia* Zone, Greater Phyllopod Bed (formerly USNM locality 35k), Walcott Quarry

Shale Member, Burgess Shale Formation, located in Yoho National Park, British Columbia, Canada (Fig. 5.1).

7.3. Terminology

The specialized head appendages of stem-group euarthropods have been referred to by numerous different names depending on their morphology and the identity of the taxa to which they belong. Perhaps the most commonly used term to refer to these appendages is as „*great-appendages*"; a term first coined by Raymond (1935) to refer to the appendages of *Leanchoilia superlata* Walcott 1912, and now used to describe the enlarged frontal appendages of megacheirans in general – hence their vernacular name „great-appendage" arthropods. The term „great-appendage" has also been used to describe the enlarged head appendages of other stem-group euarthropods such as those of anomalocaridids (Budd 2002) – originally termed „frontal appendages" (*cf*. Budd 1993) – and various Cambrian bivalved arthropods (e.g. *P. dictynna*, *in* Budd and Telford 2009). Because of the considerable morphological differences between the „great-appendages" of anomalocaridids and megacheirans (*see* **Chapter 6**), the frontal limbs of the latter are often referred to as „short-great-appendages" (*cf*. Chen *et al*. 2004).

Whether or not these appendages are all homologous is a question of considerable importance in arthropod phylogeny. The phylogenetic reconstruction of Budd (2002) implied that all of these „great-appendages", including those of anomalocaridids were homologous to the anterior-most appendages of the onychophorans and the labrum of extant arthropods, making them all protocerebral in origin, although this reconstruction has not been widely accepted. Stein (2010) provided an alternative view based on the morphology of the Sirius Passet taxon *Kiisortoqia soperi* Stein 2010, suggesting that the anomalocaridid frontal appendages are homologous to those of the deutocerebral first antenna of mandibulates (see also Chen *et al*. 2004, Haug *et al*. 2012c). As several authors have placed the „short-great-appendage" arthropods in the stem-group of the chelicerates (e.g. Chen *et al*. 2004, Cotton and Braddy 2004, Dunlop 2005, Haug *et al*. 2012c), it follows that the homology of all the „great-appendages" fails, whether at the level of morphology (they might all be homologous as deutocerebral appendages but not as „great-appendages"), or position (they may have mixed derivation from the protocerebrum and deutocerebrum). The situation has become more clouded recently with the description of purported nervous tissues in one of the key taxa, *F. protensa* (Ma *et al*. 2012b), suggesting a tritocerebral innervation for its „great-appendages".

To avoid nomenclatural confusion and *a priori* assumptions of homology between „great-appendages" and other similar limbs in the anterior of stem-group euarthropods, Yang *et al*. (2013) proposed the neutral term "*specialised post-antennal appendages*" (SPAs) to refer specifically to the second pair of head appendages in fuxianhiids, and potentially also applicable to those of Cambrian

bivalved arthropods, such as *B. pretiosa* and *P. dictynna*. This term, however, has some limitations in its applicability; although megacherians indeed have a set of specialized anterior appendages, most representatives lack antennae, and thus utilizing this terminology for describing the latter group would be a misnomer (at least for some species). For the sake of clarity, we restrict the term „great-appendage" to the anterior limbs that possess chelate spines on their distal podomeres (i.e. megacheirans), and use „SPAs" to refer to potentially homologous, although non-chelate, appendages in other stem-group euarthropods (i.e. Cambrian bivalved arthropods, fuxianhuiids).

7.4. Results

7.4.1. Head structure of Perspicaris dictynna

Examination of NMNH 189245 and NMNH 213804 reveals details of the structure and organization of the cephalic components in *P. dictynna* that were overlooked or misinterpreted in previous descriptions (Simonetta and Delle Cave 1975, Briggs 1977, *but see also* Budd 2008) (Fig. 7.1). The prominent ovoid eyes are attached to the anterior-most region of the head by well-developed eyestalks, which are themselves associated with the subcircular anterior sclerite (Fig. 7.1A-B). Since all of these structures are positioned just outside the anterior margin of the bivalved carapace, they represent the best-preserved components of the cephalic morphology. The preserved left antenna in NMNH 213804 indicates that the site of attachment lies within the carapace border (Fig. 7.1C-D), although it is not possible to ascertain the precise location. Briggs (1977) suggested that the antennae attach ventrally relative to the stalked eyes. Further comparisons with *Branchiocaris pretiosa* (*see* Budd 2008, figs. 1-2) suggest that the antennae were attached between the anterior sclerite and the hypostome. NMNH 189245 provides a clear view of the subrectangular hypostome in life position (Fig. 7.1A-B), which Briggs (1977) mistook for a muscle scar of the bivalved carapace. In the same specimen, the posterior border of the hypostome is associated with a discrete concentration of dark material, which likely indicates the position of the mouth. A distinct, but fragmentary, cuticular structure lying posterior to the anterior sclerite in NMNH 213804 might also represent the remains of the fragmented hypostome; in this case, however, the anterior sclerite, the eyes and the hypostome have experienced some disarticulation and thus shifted slightly forward from the original position.

Posterior to the antennae, it is possible to observe a pair of large limbs positioned either side of the hypostome (Fig. 7.1). The morphology of these appendages differs conspicuously from those of the antennae and the (post-oral) trunk limbs, the latter consisting of a homonomous series of paddle-like exopods. The specialized appendages are most obvious in NMNH 189245 owing to the ventral preservation of this specimen (*see also* Budd and Telford 2009, fig. 3e), and consists

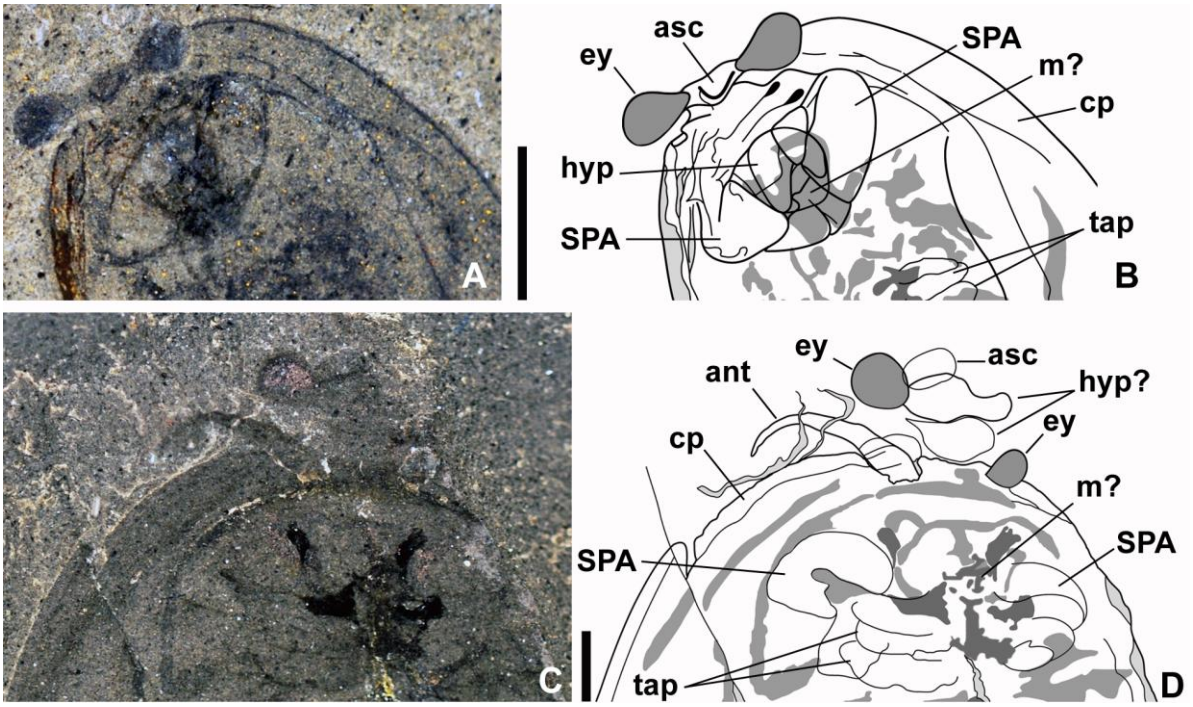


Fig. 7.1 | Structural organization of the head in *Perspicaris dictynna* (Simonetta and Delle Cave 1975). A, NMNH 189245, an articulated specimen preserved in ventral view, showing ventral components of the head region, with **B**, interpretive sketch; **C**, NMNH 213804, articulated specimen preserved in dorsal view, with **D**, interpretive sketch. Abbreviations: ant, antenna; asc, anterior sclerite; cp, carapace; ey, eye; hyp, hypostome; m, mouth; SPA, specialized post-antennal appendage; and, tap, trunk appendages. Scale bars = 2 mm. (Image produced by Javier Ortega-Hernández).

of posterior-facing, robust uniramous limbs seemingly composed of only a few podomeres. The flexure pattern of these limbs suggests the presence of at least three, but possibly four, podomeres (Fig. 7.1B). The most proximal podomere seems to attach directly to the body at either side of the hypostome, representing roughly half of the total length of the extended limb. The following podomere establishes a conspicuous articulation with the former one, allowing the strongest point of flexure for the limb. The distal parts of these appendages are not preserved in sufficient detail to unequivocally determine the exact number of terminal components, although NMNH 189245 suggests that the appendages include two additional podomeres, the most distal of which narrows into a blunt tip. In NMNH 213804, it is only possible to recognize the gross outline of these limbs as they lie underneath the carapace in this specimen preserved in dorsal view (Fig. 7.1C). However, the strong flexure point of the appendages that corresponds to the articulation between the putative first and second podomeres, as observed in NMNH 189245 (Fig. 7.1B), is evident and indicative of the same fundamental construction.

7.4.2 Head structure of Canadaspis perfecta

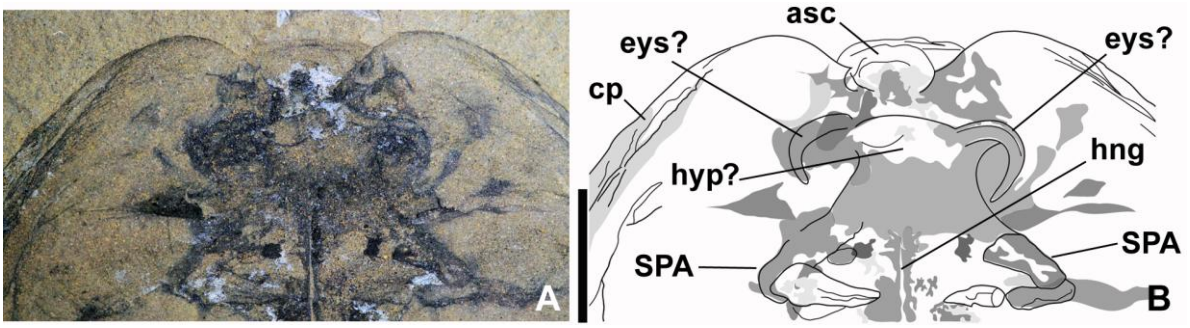


Fig. 7.2 | Structural organization of the head in *Canadaspis perfecta* (Walcott 1912). A, NMNH 18901a, articulated specimen preserved in dorsal view showing components of the head region, with **B**, interpretive sketch. Abbreviations: asc, anterior sclerite; cp, carapace; eys, eye stalk; hng, hinge; hypostome; and, SPA, specialized post-antennal appendage. Scale bar = 5 mm. (Image produced by Javier Ortega-Hernández).

Budd (2008) provided the most recent reconstruction of the anterior morphology of *C. perfecta* based on specimens NMNH 189019b (counterpart) and NMNH 207298. Budd (2008) interpreted the presence of a broad plate-like structure on the anterior margin of *C. perfecta* as an anterior sclerite, instead of an elongate hypostome as considered by Briggs (1978). Examination of NMNH 189019ba (part) (Fig. 7.2) confirms the observations made by Budd (2008) and provides new information on the associated appendages. In addition to the wide anterior sclerite, NMNH 189019a preserves the anterior margin of a large hypostome (Fig. 7.2B; *see also* Budd 2008, fig. 8a), although details on the posterior region of this structure are largely indistinct. Immediately behind the anterior sclerite, the anterior margin of the hypostome is associated with a pair of vaguely hook-shaped structures that point posteriorly. Although the elongate appearance of these structures could suggest a possible antennal identity, this cannot be possible as the antennae are well preserved in the counterpart NMNH 189019b (*see* Briggs 1978, fig. 81, Plate 7, fig. 84; Budd 2008, figs. 7a, 8a). With this in mind, and considering their position, these structures are interpreted as the proximal portion of the eyestalks. As in *P. dictynna*, the putative posterior margin of the hypostome in *C. perfecta* is associated with an accumulation of dark material; in this case, however, the dark material has a more widespread distribution within the axial region of the anterior body that extends to some of the limbs increasing their contrast within the carapace margins. A pair of slender, uniramous appendages can be discerned at either side of the hypostome. Although comparatively less robust in their overall appearance, these limbs closely resemble those described above for *P. dictynna* (Fig. 7.1B, D) in the possession of a distinctively posterior-facing inward flexure that indicates the presence of a functional articulation (Fig. 7.2B). The inner side of this articulation produces an acute angle of approximately 45 degrees. The preservation of the specialized appendages

underneath the carapace in NMNH 189019a does not allow resolution of the precise

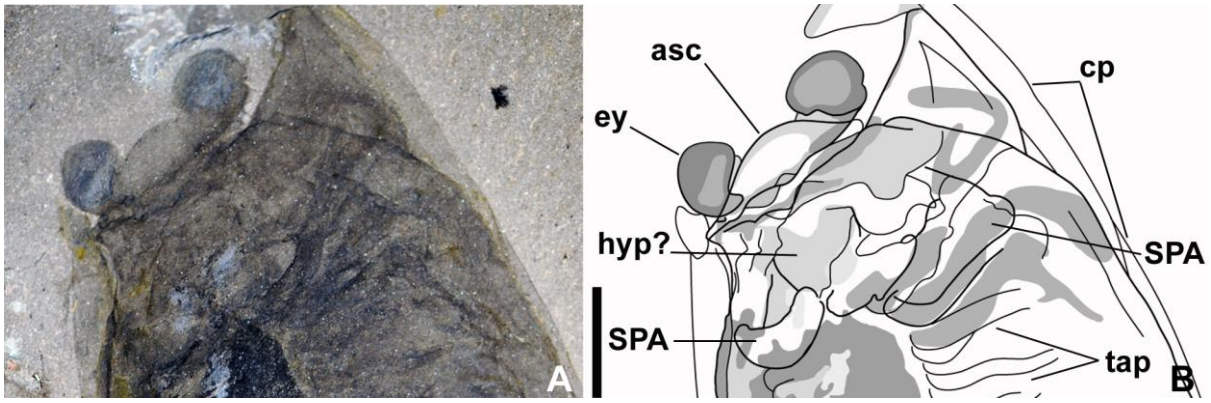


Fig. 7.3 | Structural organization of the head in *Odaraia alata* Walcott 1912. A, NMNH 213807, articulated specimen preserved in ventral view, with **B**, interpretive sketch. Abbreviations: asc, anterior sclerite; cp, carapace; ey, eye; hyp, hypostome; SPA, specialized post-antennal appendages; and tap, trunk appendages. Scale bar = 5 mm. (Image produced by Javier Ortega-Hernández).

number of podomeres, but the functional articulation indicates the presence of at least two. The most distal podomere in the right appendage indicates the presence of an additional podomere but it is not possible to ascertain whether this is a true feature or if the podomere is broken. The most distal portion of the last appendage is striated although it cannot be ascertained based on the available evidence if this striation is a genuine feature or a taphonomic artefact.

7.4.3. Head structure in Odaraia alata

Budd‟s (2008) reinterpretation of the anterior region of *O. alata* also recognized the presence of a prominent anterior sclerite that is associated with the large eyes. Budd (2008) utilized NMNH 213807 to make this assertion, as this specimen clearly shows the distinction between the borders of the anterior sclerite and the anterior margin of the body concealed within the bivalved carapace (Fig. 7.3). Similar to *P. dictynna* and *C. perfecta*, Briggs (1981) reported the presence of putative muscle scars in several specimens of *O. alata* (e.g. NMNH 189231, NMNH 189235, NMNH 189239, NMNH 202295, NMNH 213807, NMNH 213809, NMNH 34306). Examination of the putative muscle scars in NMHN 213807 (Fig. 7.3B) indicates that these structures are actually a pair of specialized uniramous appendages that also display the characteristic flexure observed in the specialized appendages of *P. dicynna* and *C. perfecta*. As in the other taxa, the preservation of these limbs under the bivalved carapace obscures much of the fine detail, including the precise location of the podomere boundaries. There are no clear traces of a hypostome associated with the specialized appendages, although the seemingly featureless space between the proximal portions of the limbs might be suggestive of its existence.

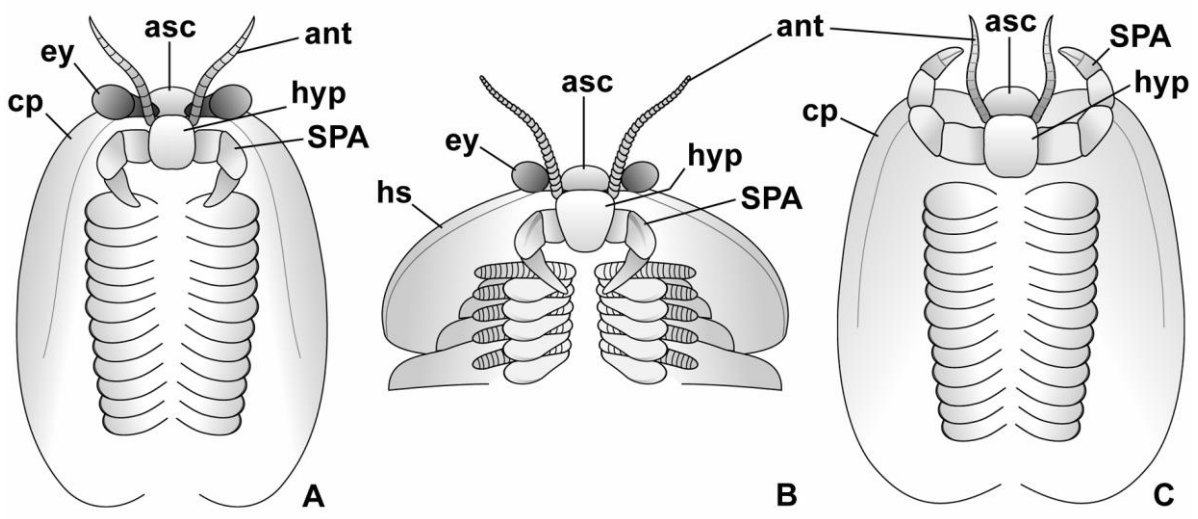


Fig. 7.4 | Fundamental structural organization of the head region in selected Cambrian bivalved arthropods and fuxianhuiids. A, Ventral reconstruction of *Perspicaris dictynna* showing distinct arrangement of antennae and (posterior-facing) specialized post-antennal appendages, in association with the eye-bearing anterior sclerite and hypostome; **B**, ventral reconstruction of the genus *Fuxianhuia* Hou 1987b (based on findings in Chen *et al*. 1995, Bergström *et al*. 2008, Budd 2008, and Yang *et al*. 2013); and **C**, ventral reconstruction of *Branchiocaris pretiosa* (Resser 1929). Abbreviations: ant, antennae; asc, anterior sclerite; cp, carapace; ey, eye; hyp, hypostome; and, SPA, specialized post-antennal appendage. (Image produced by Javier Ortega-Hernández).

7.5. Discussion

7.5.1. Summary of bivalved arthropod head structure

The head region of all Cambrian bivalved taxa described herein demonstrate a common structural organization, also shared by other bivalved arthropods described elsewhere (e.g. *Branchiocaris pretiosa*, *in* Budd 2008). The distinctive configuration consists of an anterior-most pair of antenniform appendages associated with an anterior sclerite, followed ventrally by a pair of SPAs that attach para-orally relative to the hypostome (Fig. 7.4). There are, however, some aspects that show an important degree of variability. For example, *B. pretiosa* shares a very similar antenna and SPA configuration with *P. dictynna* and *C. perfecta*, but lacks the prominent stalked eyes in the latter taxa (Fig. 7.4). Also unlike the later taxa, which possess a pair of posteriorly-directed SPAs composed of few (~ three) podomeres, the SPAs of *B. pretiosa* face anteriorly and contain at least five well-defined podomeres, the most distal of which is bulbous and tipped with a pair of claw-like terminals (Briggs 1976, Budd 2008). A conspicuous functional articulation, however, is still apparent in these limbs and thus indicates a similar structural organization (Fig. 7.4).

The appendages of *Loricicaris spinocaudatus* (**Chapter 5**) are similar to those of other bivalved forms in that they include a stout pair of antennae followed by a pair of SPAs, however, the SPAs of this taxon are notable in that they are directed anteriorly and seem to possess claws that originate from the terminal podomeres, comparable to those of *B. pretiosa* (Fig. 7.4). The distinctive organization of the pre-oral appendages suggests that the antennae and SPAs represent homologous structures across a disparate range of Cambrian bivalved arthropods. Under this scheme, the appendage morphology of *B. pretiosa* may represent either an intermediate morphology between a more pediform appendage and the SPAs of other arthropods, or a novel innovation within a clade that includes *B. pretiosa* and *L. spinocaudatus*.

A notable derivation from the head configuration observed in other bivalved arthropods is found in *O. alata*. This taxon clearly lacks antennae (Fig. 7.3). It is unlikely that this is an artefact of preservation as *O. alata* is known from several specimens with well-preserved anterior structures (Briggs 1981). It is interesting to note that apart from the absence of antennae, *O. alata* also stands out among bivalved arthropods by the large size of the stalked eyes, whose position allowed them to extend well beyond the anterior margins of the carapace. It may be possible that the enlarged stalked eyes and absence of antennae represent a trade-off in terms of sensorial structures in the head region of this arthropod.

7.5.2. Comparisons with contemporaneous non-bivalved arthropods

The head organization of Cambrian bivalved arthropods examined here shows notable similarities to other contemporaneous groups (Fig. 7.4), which allow us to infer potential segmental affinities for their pre-oral appendages. It is possible to draw morphological parallels between the structure of the SPAs in bivalved arthropods and fuxianhuiids, and the „great-appendage" of megacheirans. All of these limbs are distinctly geniculate with a distinctive point of flexure, located approximately halfway along the appendage, and generally possess a broad proximal attachment site that gradually tapers towards an acute distal tip. In megacheirans this morphology is further modified with the addition of chelate spines, although the overall morphology remains consistent with the previous description. The structural organization of the „great-appendages" is generally stable, although it can differ in the number of chelate segments, with forms such as *Yohoia tenuis* and *Fortiforceps foliosa* possessing four (Haug *et al*. 2012c) and more derived members such as *L. superlata* possessing three (Haug *et al*. 2012a). The exact number of podomeres in the SPAs of the bivalved arthropods described herein could not be determined with certainty, although the distal section of the appendage of *P. dictynna* appears to possess three, making them similar to the condition observed in the fuxianhuiid *Chengjiangocaris kunmingensis* (Yang *et al*. 2013). Although all these taxa appear to lack chelate podomeres, the appendages of *Canadaspis perfecta*

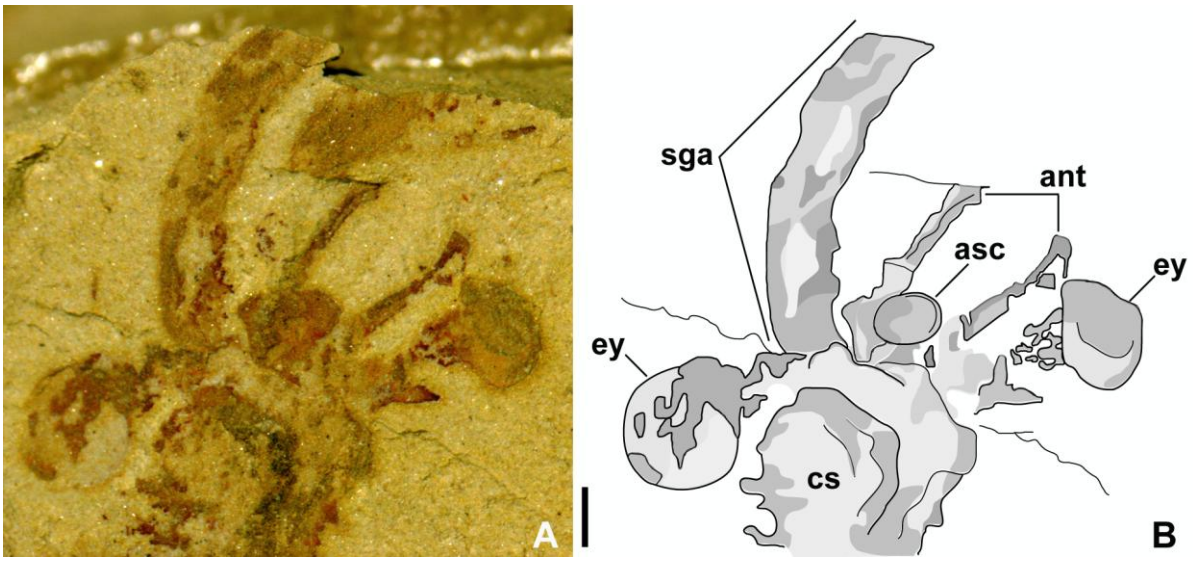


Fig. 7.5 | Structural organization of the head of *Fortiforceps foliosa* Hou and Bergström 1997. A, Specimen number unknown (image courtesy of Xiaoya Ma), nearly complete specimen preserved in ventral view, with **B**, interpretive sketch. Abbreviations: ant, antennae; asc, anterior sclerite; cs, cephalic shield; ey, eyes; and, ga, „great-appendage". Scale bar = 1 mm. (Image produced by Javier Ortega-Hernández).

show a noticeable distal striation that could represent a functional chela, however, this cannot be determined with certainty as it is not possible to distinguish individual podomere boundaries. The exact number of proximal podomeres could not be determined in any of the examined specimens, although megacheiran „great-appendages" always possess two (Haug *et al*. 2012a, c), a condition which is seemingly also expressed in the SPAs of *C. kunmingensis* (Yang *et al*. 2013).

Similar to Cambrian bivalved arthropods, the anteriormost appendages of some megacheirans, such as *F. foliosa* (Fig. 7.5) and *Kootenichela deppi* Legg 2013 (*see* **Chapter 7**), are antenniform, although it seems that these are not associated with a hypostome in the latter, or at least one is not preserved. The presence of antennae anterior to the great-appendages" in some megacheiran representatives increases the structural similarities between these taxa, Cambrian bivalved arthropods and fuxianhuiids, and provides clear evidence that there is a fundamental similarity in terms of structural organization of the head in stem-group euarthropods.

7.5.3. The segmental affinities of SPAs and 'great-appendages'

The morphological and positional parallels between SPAs and the „short-great-appendages" leads us to reconsider their potential segmental homology. There has been much debate regarding the segmental affinities of these head appendages. Traditionally the antennae of stem-group arthropods were considered to innervate from the deutocerebral neuromeres, whilst the „great-appendages" were considered to innervate from either the proto- (Budd 2002), or tritocerebral neuromere (Cotton

and Braddy 2004). This was partly based on comparisons with extant antennate arthropods (e.g. hexapods) that possess deutocerebral antennae (Averof and Akam 1995), and a misunderstanding of the neurological organization of chelicerates, which were thought to lack a deutocerebrum (*cf*. Weygoldt 1985). Under these models the „great-appendages" were considered precursors of the chelate appendages of pycnogonids and euchelicerates (Cotton and Braddy 2004) or novel appendages absent from crown-group arthropods (Budd 2002). Other studies noted the structural similarities between „great-appendages" and the chelicerae of chelicerates, but instead considered them deutocerebral (e.g. Chen *et al*. 2004, Dunlop 2005, Haug *et al*. 2012c), based on gene expression data from extant chelicerates (Damen *et al*. 2008, Telford and Thomas 1998). These studies often considered the antennae of megacheirans, such as *F. foliosa*, to be absent based on the reconstruction of Bergström and Hou (2005), or the SPAs of fuxianhuiids to represent gut diverticulae based on Waloszek *et al*. (2005), and Bergström *et al.* (2008), all of which are incorrect (this study, Chen *et al*. 1995, Yang *et al*. 2013). To accommodate these observations Scholtz and Edgecombe (2005, 2006) proposed that the antenna of stem-group euarthropods was instead homologous to the protocerebral antennae of onychophorans, which they termed „primary antennae", and thus not homologous to the deutocerebral antennae of mandibulate arthropods, which they termed the „secondary antennae". This view has recently been contradicted by new information on the neurological architecture of *F. protensa* (Ma *et al*. 2012b), and new fuxianhuiid species from the Xiaoshiba biota that provide insights into the segmental organization of the head of these stem-group euarthropods (Yang *et al*. 2013). All this information supports the interpretation that the SPAs at least, and possibly also the megacheiran „great-appendages", are associated with the tritocerebral neuromere of the brain (*cf*. Chen *et al*. 1995, Yang *et al*. 2013). In this scenario, neither the SPAs nor the „great-appendages" can be considered homologous to the deutocerebral chelicerae of chelicerates, and thus any structural similarities must be the result of convergent evolution.

8. Multi-segmented Cambrian arthropods from British Columbia

8.1. Introduction

Herein a „great-appendage" arthropod, *Kootenichela deppi* Legg 2013, is described, from the recently discovered (Caron *et al*. 2010) middle Cambrian (Series 3, Stage 5) Stanley Glacier exposure of the „thin" Stephen Formation in Kootenay National Park (British Columbia, Canada) (Fig. 5.1). This taxon shows a remarkable similarity to the putative annelid *Worthenella cambria* Walcott 1911a, from the nearby Walcott Quarry exposure of the Burgess Shale Formation in Yoho National Park (Fig. 5.1), which is herein reinterpreted as a „great-appendage" arthropod.

This chapter was published, in part, in the *Journal of Paleontology* (Legg 2013).

8.2. Systematic Palaeontology

Phylum ARTHROPODA Siebold 1848
Class "MEGACHEIRA" Hou and Bergström 1997
Family KOOTENICHELIDAE Legg 2013

Type genus. Kootenichela Legg 2013.

Included genera. Worthenella Walcott 1911a, and possibly *Pseudoiulia* Hou and Bergström 1998.

Diagnosis. Elongate arthropods with a trunk of at least 25 somites and subtriangular exopod flaps fringed with fine setae.

Remarks. The diagnosis of this family is based on shared characteristics of *Kootenichela* and *Worthenella*, the sister taxon relationship of which is supported by phylogenetic analysis (Legg 2013; **Chapter 9**). *Pseudoiulia cambriensis* Hou and Bergström 1998, from the lower Cambrian Chengjiang Lagerstätte, conforms to this familial diagnosis but due to its poor preservation is only tentatively assigned to Kootenichelidae.

Genus ***KOOTENICHELA*** Legg 2013

2013 *Kootenichela* Legg, p. 493.

Type species. *Kootenichela deppi* Legg 2013, by monotypy.

Etymology. After Kootenay National Park, where material referred to this taxon was discovered, and *chela* (Latin for “claw”), in reference to the raptorial frontal appendages.

Diagnosis. Distinguished from other kootenichelids by the presence anastomosing midgut glands, an elongate trunk with at least 29 segments and a short cephalon encompassing an ocular segment with a large pair of pedunculate lateral eyes, and a pair of “great-appendages” consisting of a bipartite proximal peduncle and three spine-bearing podomeres, the most proximal of which is recurved and accounts for 70 per cent of the total appendage length.

Kootenichela deppi Legg 2013
Figures 8.1-8.4

v.2010 "Great Appendage arthropod A" Caron, Gaines, Mángano, Streng and Daley, p. 813, fig. 3F.
v*2013 *Kootenichela deppi* Legg, p. 492-500, figs. 1-3.

Etymology. After the actor Johnny Depp for his portrayal of *Edward Scissorhands* in the 1990 film of the same name. The hands of which are reminiscent of this taxon.

Diagnosis. As for genus.

Specimens. Holotype, ROM 59948 (Figs. 8.1A-B, 8.2A-B, 8.3), a near complete specimen preserved in an oblique-lateral orientation, consisting of a cephalon and an elongate trunk, the posterior of which is missing. Paratypes ROM 61521 (Figs. 8.1C, 8.2E), a pair of isolated "great-appendages", and ROM 61520 (Figs. 8.1D-E, 8.2C-D), an isolated trunk with poorly preserved limbs and a possible telson.

Occurrence. Specimens were collected from the mudstone layers of Cycle 5 of the Waputik Member (Stephen Formation), Stanley Glacier locality, Kootenay National Park, British Columbia, Canada (Caron *et al*. 2010), stratigraphically equivalent to the Marpole Limestone Member of the Burgess Shale Formation in nearby Yoho National Park (Cambrian, Series 3, Stage 5; *Pagetia walcotti* subzone, *Bathyuriscus-Elrathia* zone).

Description.

The description refers to the holotype ROM 59948 (Figs. 8.1A-B, 8.2A-B, 8.3), except where otherwise noted. The cephalon is 4 mm long (< 10 per cent of the preserved body length), measured from the anterior-most margin to the postero-dorsal margin. This is best preserved in the part (Fig. 8.1A, 8.2A, 8.3) and consists of two distinct regions: a narrow anterior, i.e. an anterior sclerite, and an expanded posterior shield. The anterior region bears two large pedunculate eyes 0.9 mm in diameter; a small rounded stain within the cephalon is the right eye and appears to preserve individual lenses. Individual lenses can also be distinguished on the left eye (Fig. 8.3) and number c. 50 lenses per mm^2. The posterior margin of the cephalon curves antero-ventrally and encompasses at least the „great-appendages" and possibly an antenna-like appendage on the ocular segment. There are no other cephalic limbs although the posterior of the cephalon appears to overlap the first trunk tergites, which led to the previous misinterpretation that it possessed four limb-bearing segments (Legg *et al*. 2012b). Numerous striations in the posterior part of the cephalon (Fig. 8.3) may indicate that it was convex in life and was crushed post-mortem. The putative antenna is preserved as a narrow, almost filamentous staining

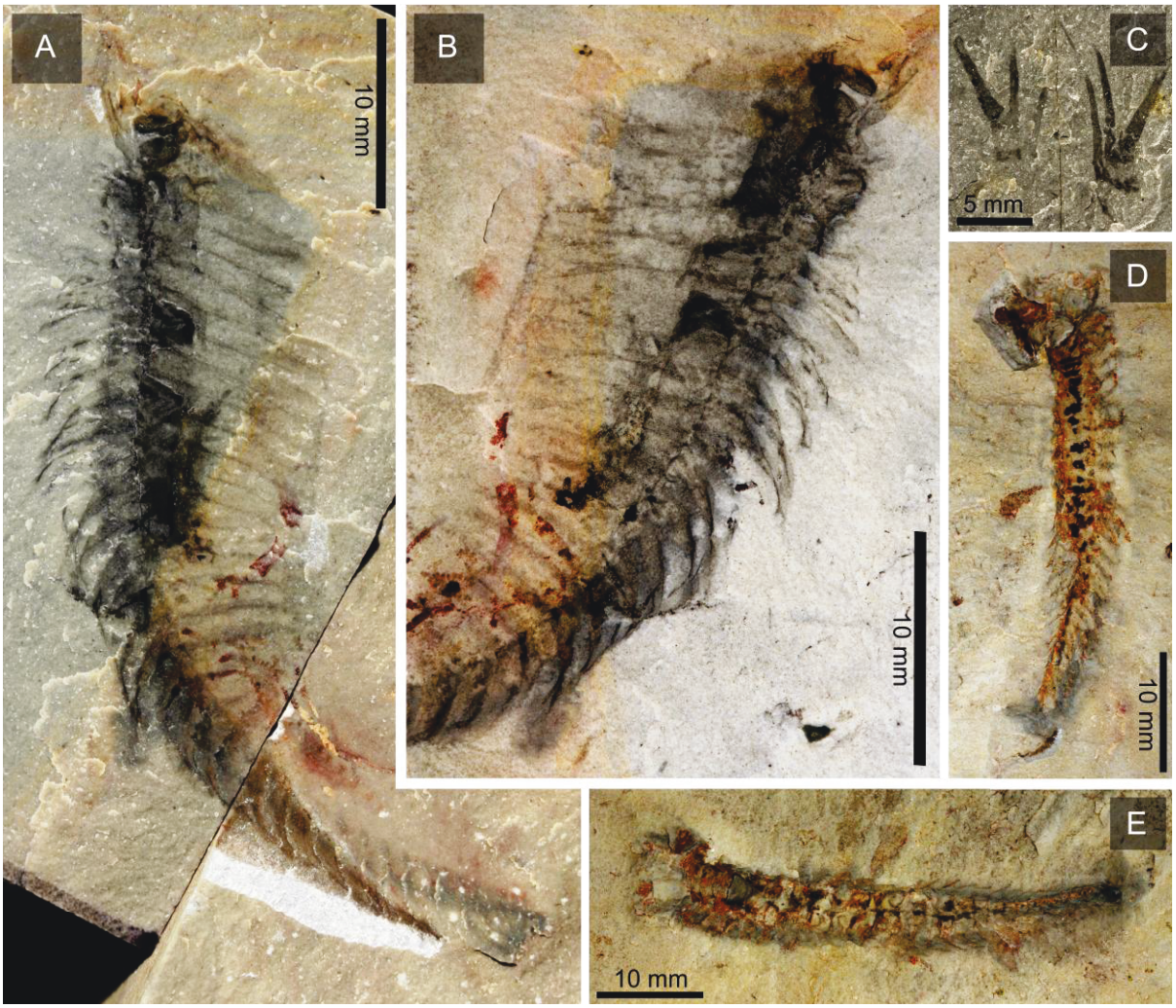


Fig. 8.1 | Specimens of *Kootenichela deppi* Legg 2013. A, part; and **B**, counterpart of the holotype ROM 59948; **C**, ROM 61521, an isolated pair of „great-appendages"; and **D**, part; and **E**, counterpart of ROM 61520.

with little structural detail. This structure is interpreted as a true biological structure rather than abiogenic staining, which is not found elsewhere in material from this horizon. Gaps in the staining may represent antennal segmentation. The „great-appendages" are composed of a bipartite proximal peduncle and three distal spine-bearing podomeres. Although poorly preserved in the holotype, the spines have similar proportions and degree of recurvature to those in a well-preserved isolated pair of co-occurring „great-appendages" that are herein considered conspecific (ROM 61521; Figs. 8.1C, 8.2E). The most proximal spine-bearing podomere has the longest spine, 11.1 mm in length (roughly 70 per cent of total appendage length), less robust than the others and slightly recurved.

An anterior gut trace is preserved; this documents a ventrally directed mouth (Fig. 8.3) and extends into the anterior cephalic region (Figs. 8.1A-B, 8.2A-B), where the dark staining may result from gut rupturing. Midgut glands extend from the gut into the posterior cephalon and trunk (Fig. 8.1A-B, 8.2A-B). The preserved part of the trunk in the holotype is 43.5 mm long and consists of 29 segments. The posterior of

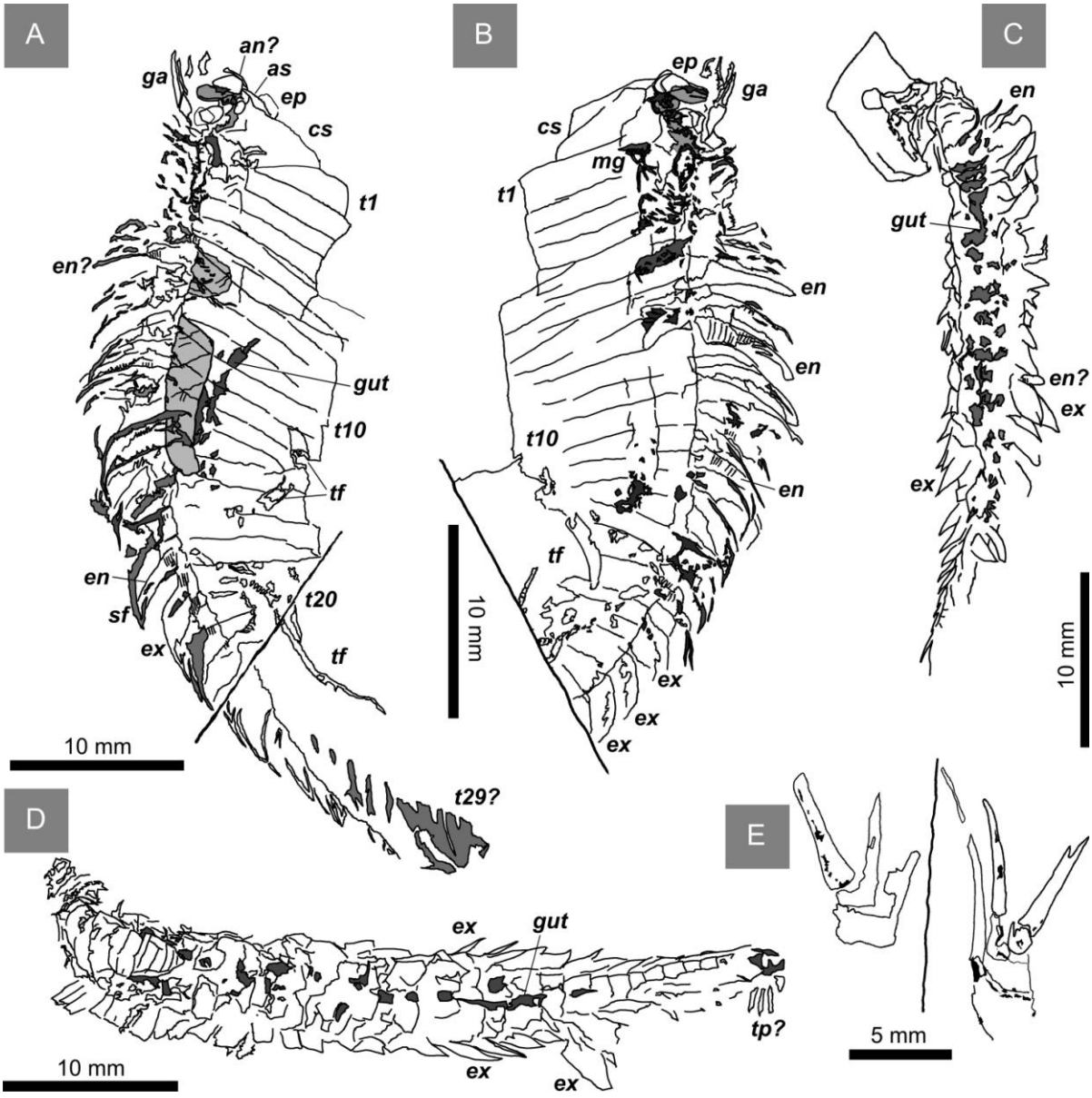


Fig. 8.2 | Interpretive camera lucida drawings of *Kootenichela deppi* Legg 2013. A, part; and **B**, counterpart of the holotype ROM 59948; **C**, part; and **D**, counterpart of ROM 61520; and **E**, ROM 611521. Abbreviations: an, antenna; as, anterior sclerite; cs, cephalic shield; en, endopod; ep, eye peduncle; ex, exopod; ga, „great-appendage"; gut, gut; mg, midgut glands; sf, setal fringe; t1-t29; tergites 1-29; tf, trace fossil; and, tp, telson processes.

the trunk is missing in the holotype but may be preserved in ROM 61520 (Figs. 8.1D-E, 8.2C-D) where possible lateral projections are preserved at the posterior of the specimen. The latter is a dorso-ventrally preserved trunk section consisting of at least 29 segments, tapering posteriorly. Each segment bears a single pair of limbs.

The limbs are poorly preserved in all specimens making identification difficult, however in the holotype stout, multi-annulated endopods are preserved underneath triangular exopods, the latter evident by their dark setal fringe (Fig. 8.1A, 8.2A). There is no evidence of a gnathobasic protopodite and given the extent of the annulations in the endopod it is unlikely this animal possessed them.

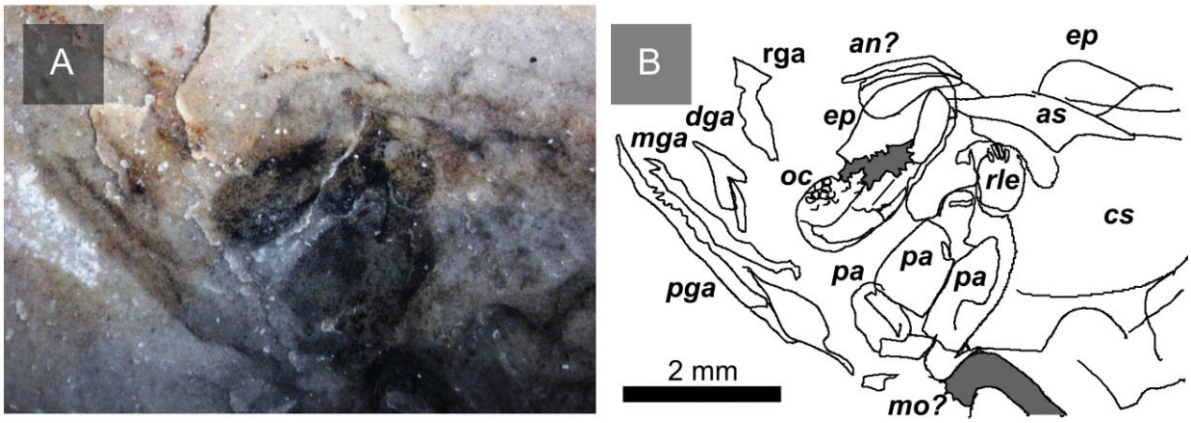


Fig. 8.3 | The head region of *Kootenichela deppi* Legg 2013. A, the head region of the holotype ROM 59948; with **B**, interpretive camera lucida drawing. Abbreviations: an, antenna; as, anterior sclerite; cs, cephalic shield; dga, distal „great-appendage" article; ep, eye peduncle; mga, medial „great-appendage" article; oc, ocelli; pa, peduncle article; pga, proximal „great-appendage" article; rga, right „great-appendage and, rle, right lateral eye.

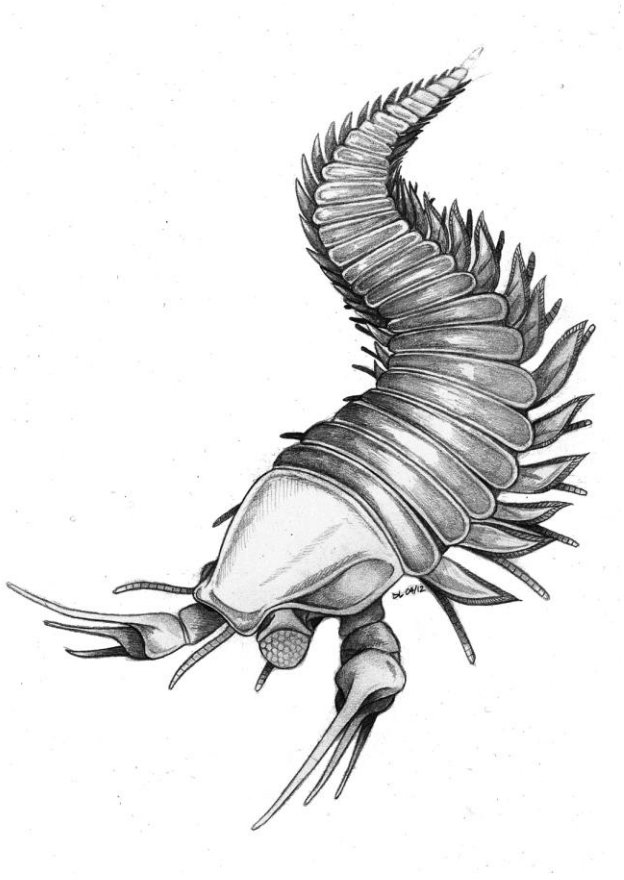


Fig. 8.4 | Reconstruction of *Kootenichela deppi*.

Remarks.

The presence of a short raptorial frontal appendage in *Kootenichela* (Fig. 8.4) clearly indicates affinities with megacheiran arthropods. Among this group *Kootenichela* shows most similarities to the Chegjiang megacheirans *Fortiforceps foliosa* Hou and Bergström 1997, and *Jianfengia multisegmentalis* Hou 1987a. All taxa possess a long, homonomous trunk (20 segments in *Fortiforceps*, 25 in *Jianfengia*), with multi-podomerous appendages consisting of > 10 segments. The Chengjiang taxa also posess telsons with modified lateral processes (Hou and Bergström 1997, Strausfeld 2012), making their possible presence in *Kootenichela* more plausible. *Kootenichela* differs from these taxa in possessing only three spine-bearing articles in its „great-

appendage", whereas the others have four (Haug *et al*. 2012c). In this regard the appendages are more like those of *Haikoucaris* (Chen *et al*. 2004) or *Leanchoilia* (Liu *et al*. 2007, Haug *et al*. 2012c), although few other features are common to these taxa.

WORTHENELLA Walcott 1911a

1911a *Worthenella* Walcott, p. 125.
1927 *Worthenella*; Walton, p. 240, 243, 248.
1974 *Worthenella*, Ushakov, p. 59.
1986 *Worthenella*; Briggs and Conway Morris, p. 179.
1989 *Worthenella*; Conway Morris, fig. 1.
2013 *Worthenella* Walcott; Legg, p. 494.

Type species. Worthenella cambria Walcott 1911a, by monotypy.

Diagnosis. Kootenichelid with an elongate trunk composed of 50 segments, each bearing an anterior ridge and lacking extensive tergal pleura (emended from Legg 2013).

Remarks. The diagnosis presented herein reflects the placement of the genus in the family Kootenichelidae.

Worthenella cambria Walcott 1911a
Figures 8.5-8.6

v*1911a *Worthenella cambria* Walcott, p. 125, 153, Pl. 22, fig. 2.
1916 *Worthenella cambria*; Osborn, p. 1225, fig. 25.
1927 *Worthenella cambria* Walcott; Walton, p. 240, 243, figs. 4, 6.
1942 *Worthenella cambria*; Miller, p. 123, fig. 69B.
1979 *Worthenella cambria*; Conway Morris, p. 336.
1986 *Worthenella cambria*; Briggs and Conway Morris, p. 179, fig. 16.
1994 *Worthenella cambria* Walcott; Briggs, Erwin and Collier, p. 221.
2013 *Worthenella cambria* Walcott; Legg, p. 495-497, figs. 5-6.

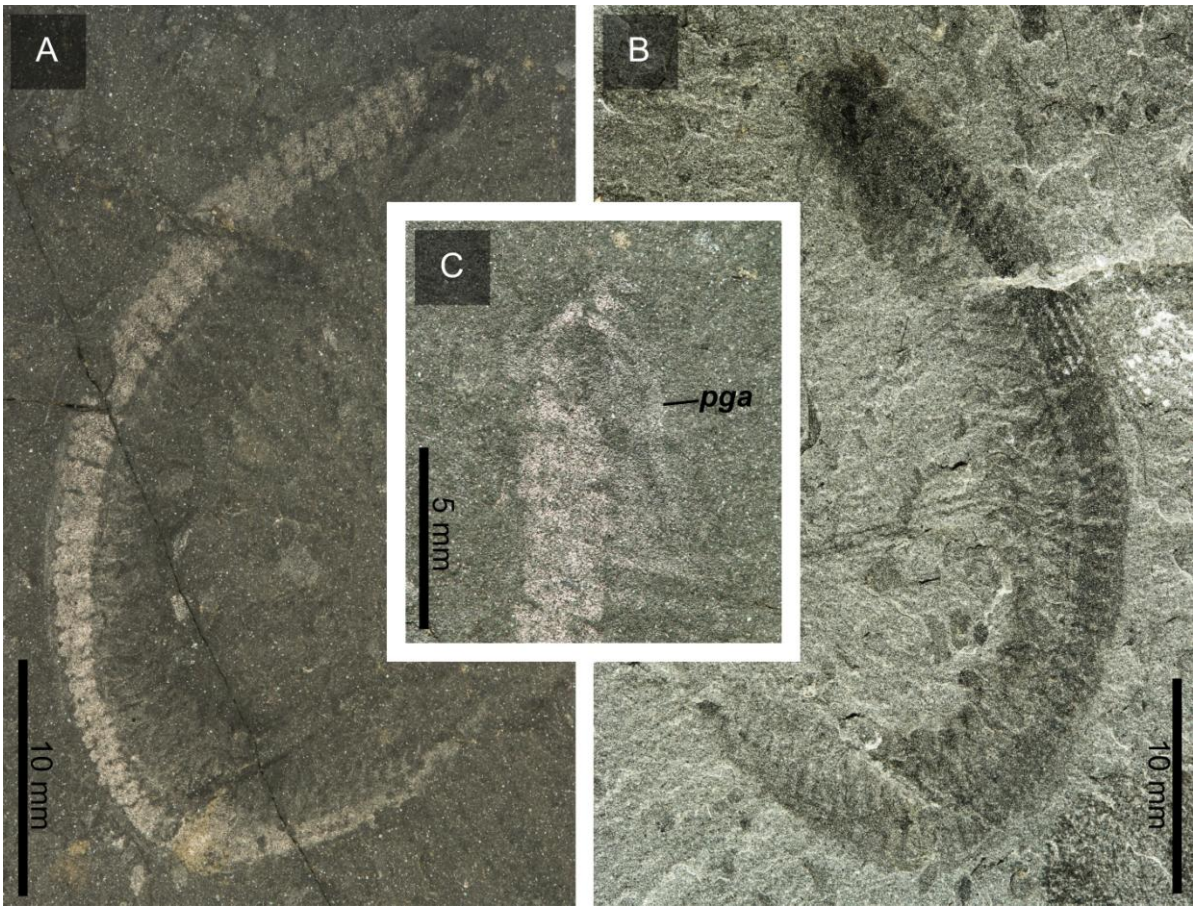


Fig. 8.5 | The type and only specimen of *Worthenella cambria* Walcott 1911a, NMNH 57643. A, part, in direct light; **B**, counterpart, in cross-polarized light; and **C**, detailed view of the cephalic region of the part showing possible proximal great-appendage article (pga).

Diagnosis. As for genus.

Specimens. Type and only specimen, NMNH 57643 (Figs. 8.5-8.6), a near complete specimen preserved in lateral orientation.

Occurrence. The only known specimen of *Worthenella* was collected from the middle Cambrian (Series 3, Stage 5; *Pagetia bootes* subzone of the *Bathyuriscus-Elrathia* Biozone) Walcott Quarry Shale Member of the Burgess Shale Formation, exposed along Fossil ridge, between Mount Wapta and Mount Field in Yoho National Park, British Columbia, Canada.

Description and morphological reinterpretation.

NMHN 57643 (Figs. 8.5-8.6) has a preserved length of 59.6 mm. The cephalic region accounts for just 5 per cent of the entire body length (3.2 mm). In the original

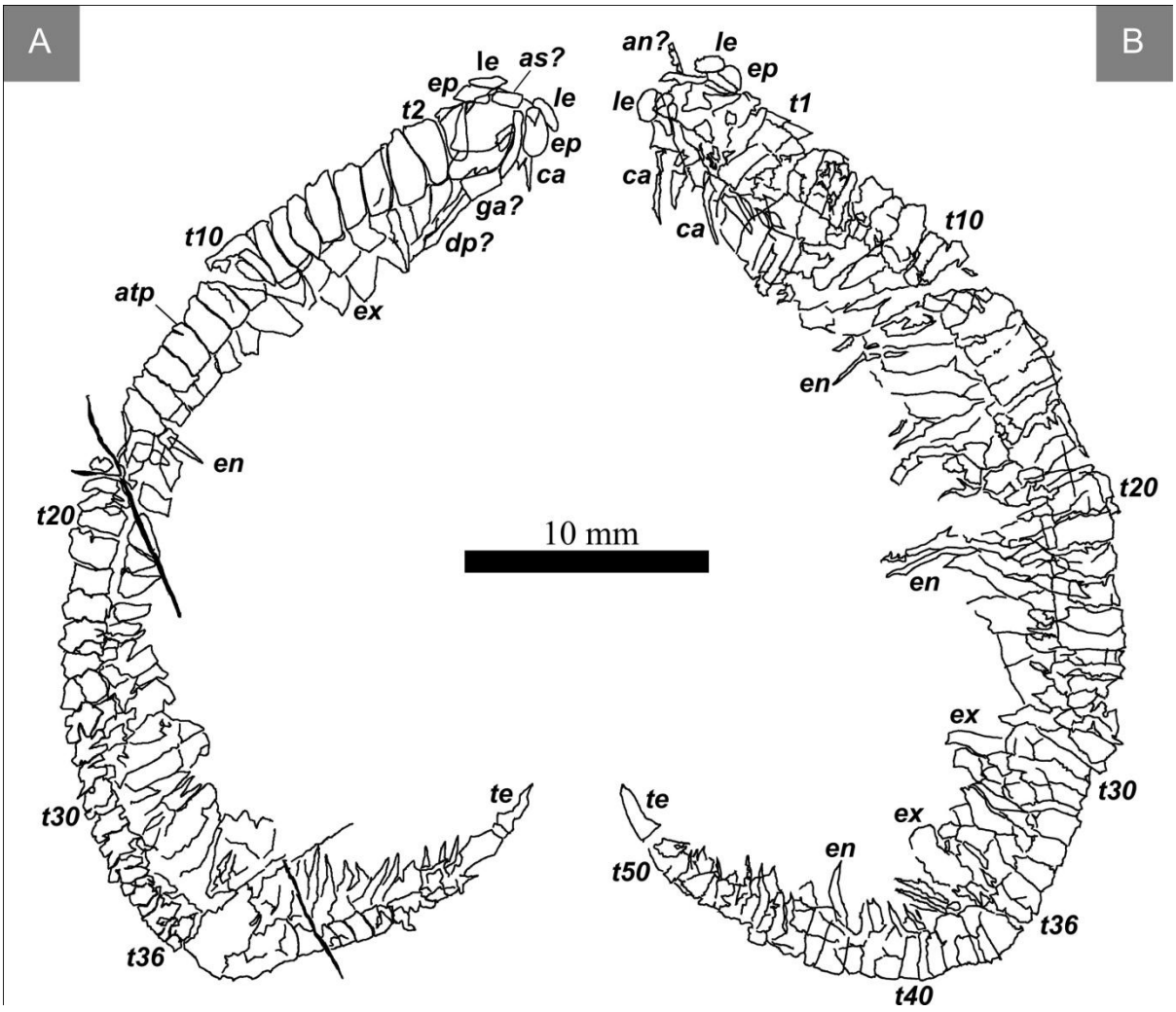


Fig. 8.6 | Interpretive camera lucida drawings of *Worthenella cambria* Walcott 1911a. **A**. part; and **B**, counterpart of NMNH 57643. Abbreviations: as, anterior sclerite; atp, anterior tegal process; ca, cephalic appendage; dp, distal podomere of „great-appendage"; en, endopod; ep, eye peduncle; ex, exopod; ga, „great-appendage"; le, lateral eye; t1-t50, trunk somites 1-50; te, telson.

description of this taxon, Walcott (1911a) noted the presence of a reflective spot as possibly indicative of an eye. Under direct light a single reflective spot is present on the left antero-lateral margin of the cephalon (Fig. 8.5A, C). A second eye on the right antero-lateral margin of the cephalon, approximately 2 mm in diameter, is observable under polarized light (Fig. 8.5B). A small rectangular area between the eyes may represent an anterior sclerite (Figs. 8.5-8.6). Walcott (1911a) noted the presence of two limb types in the head region which he interpreted as an anterior pair of jointed tentacles, and a posterior pair of long filamentous palps. The latter structure, best observed under direct lighting, is here interpreted as part of a „great-appendage" (Figs. 8.5C, 8.6A). Although individual segments are indistinguishable, a distinct rounded segment may represent the proximal spinose article. Definitive structures anterior to this antenniform appendage could not be distinguished,

although a fragment of cuticle, possibly representing the basal segment of the right antenna, could be observed using cross-polarized light (Fig. 8.5B).

The trunk of this taxon is clearly split into discrete articles separated by soft-tissue, i.e. arthrodized somites (Figs. 8.5-8.6). Such segmentation is very distinct from that of annelids which lack discrete sclerotized plates. Fifty trunk segments could be distinguished (Figs. 8.5A-B, 8.6), four more than indicated by Walcott (1911a). Some somites possess distinctive ridges. There structures can best be seen on somites 3 and 4 (Figs. 8.5A, C, 8.6). The trunk tapers towards the posterior with the anterior somites (represented by somite 6) measuring 4.6 mm high and 1.5 mm long, and the posterior somites (represented by somite 39) measuring 1.07 mm by 0.71 mm.

The structure formerly identified as bipartite parapodia on somites 9-35 are clearly evident under direct light; under polarized light however these can be seen to represent the most proximal elements of arthropodized limbs. Each appendage is tapered, indicative of trunk endopods. Reflective areas at the posterior of the trunk may represent exopods (Fig. 8.5A-B, 8.6). If so they are subtriangular, almost fin-shaped, and reminiscent of *Kootenichela*.

A gap between the trunk somites and the trunk limbs was originally interpreted as an enteric canal. This structure has the same composition as the surrounding matrix (Fig. 8.5B) and most likely represents a preservational artefact.

Remarks.

Worthenella cambria was originally considered a polychaete annelid of uncertain affinities (Walcott 1911a). The ventrolateral appendages were interpreted as bipartite parapodia, an interpretation followed by subsequent workers (e.g. Walton 1927). Osborn (1916) compared *W. cambria* to the extant polychaetes *Nereis virens* and *Arabella opalina* and speculated that it may have lived in a similar habit to these taxa. This species was largely ignored in subsequent works except for the occasional reference to miscellaneous polychaetes from the Burgess Shale (e.g. Miller 1942, Ushakov 1974). Conway Morris (1979) rejected polychaete affinities for this taxon, instead considering it a vermiform organism of uncertain affinities, or a possible uniramous arthropod (Briggs and Conway Morris 1986) although later stating that it has a body plan prohibiting assignment to any known phylum (Conway Morris 1989).

The segmentation of the body axis into discrete plates, i.e. arthrodization, is instead indicative of arthropod affinities and is the interpretation favoured herein. The long multi-segmented trunk of *W. cambria* is reminiscent of a number of Cambrian arthropod taxa, such as *Pseudoiulia cambriensis* Hou and Bergström 1998, and *Xanthomyria spinosa* Budd *et al*. 2001. There taxa have been allied to the Myriapoda (Budd *et al*. 2001), based on the shared presence of a long body with homonymous segments. This interpretation has been questioned because these taxa lack autapomorphies of Myriapoda (Edgecombe 2004). Furthermore, a large number of

segments appears to be a common feature among Cambrian arthropods, with many taxa possessing over 20 segments, e.g. *Fuxianhuia protensa* Hou 1987b, *Jianfengia multisegmentalis* and *Fortiforceps foliosa*. In this regard *W. cambria* is unlike any other taxon from the Burgess Shale Formation, except *Kootenichela deppi*; both taxa possess a tapered, elongate and multisegmental trunk, subtriangular exopods and large pedunculate eyes. This morphology is common among taxa from the earlier Chengjiang biota of southwest China. A long, slender and tapering trunk is prevalent in the so called „short-great-appendage" arthropods such as *Fortiforceps*, *Tnaglangia*, and *Jianfengia* (Hou *et al.* 2004a). Among them, *W. cambria* most closely resembles *Jianfengia multisegmentalis*. Both taxa possess trunk somites which appear to lack extensive pleura and possess ridged tergites.

8.3. Modes of life

The presence of well-developed midgut glands in *Kootenichela* indicates either a predatory or scavenging mode of life (Butterfield 2002). In extant arthropods midgut glands act as phosphate storage organs. The midgut glands of *Kootenichela* are poorly phosphatised in the holotype which may indicate that this individual had gone a considerable time without food and had used its phosphate stores (García-Bellido and Collins 2007). Other evidence for a predatory lifestyle in megacheirans includes the possession of robust gnathobasic trunk appendages and well developed eyes. Although the latter are present in *Kootenichela*, the former appear absent. Instead the enlarged frontal appendages may have been used to grasp and manipulate prey items, although how food was moved to the mouth is unclear.

Although megacheirans have traditionally been considered benthic (e.g. Bruton and Whittington 1985) many later workers have considered them nekto-benthic and capable of prolonged periods of swimming (e.g. García-Bellido and Collins 2007, Haug *et al*. 2012c). Many extant benthic arthropods employ short bursts of swimming as an escape mechanism but spend the majority of time among the benthos. This was also likely the case for the kootenichelids which show little if any adaptations for a nektonic lifestyle, but in the absence of any direct evidence, hypotheses regarding lifestyle will remain speculative.

9. Results of phylogenetic analyses

9.1. Introduction

This chapter contains the results of the phylogenetic analyses produced using the methodology outlined in **Chapter 3**. Topologies resolved using implied character weightings with a concavity constant of two and three are described in detail; all subsequent topologies (produced using alternative methodologies) are compared to the results of these preferred analyses. This approach was applied because topologies produced using a more-linear concavity function are thought to produce a more accurate depiction of evolutionary events (Goloboff *et al*. 2008a, Legg *et al*. 2012b, Ortega-Hernández *et al*. 2013, **Chapter 3**).

Character optimization was performed using TNT v.1.1. (Tree analysis using New Technology; Goloboff *et al*. 2008b). TNT does not distinguish between accelerated (ACCTRAN), or delayed character transformation (DELTRAN), instead resolving ambiguous branches as such, therefore only unambiguous character transformations are mapped on to the resultant trees. Only synapomorphies present in all most parsimonious trees (MPTs) used to produce the strict-consensus are discussed.

9.2. Implied weighted analyses (k = 2 and 3)

Analysis of the data set (**Appendix 3**) using implied character weighting with a concavity constant of three produced 45 MPTs of 139.87601 steps with a weighted character fit of 592 (Ensemble consistency index [CI] = 0.520; Ensemble Retention index [RI] = 0.873). The strict consensus tree is shown in Figure 9.1.

The strict-consensus topology produced using a concavity constant of two is identical to that produced using a concavity constant of three (Fig. 9.1), and

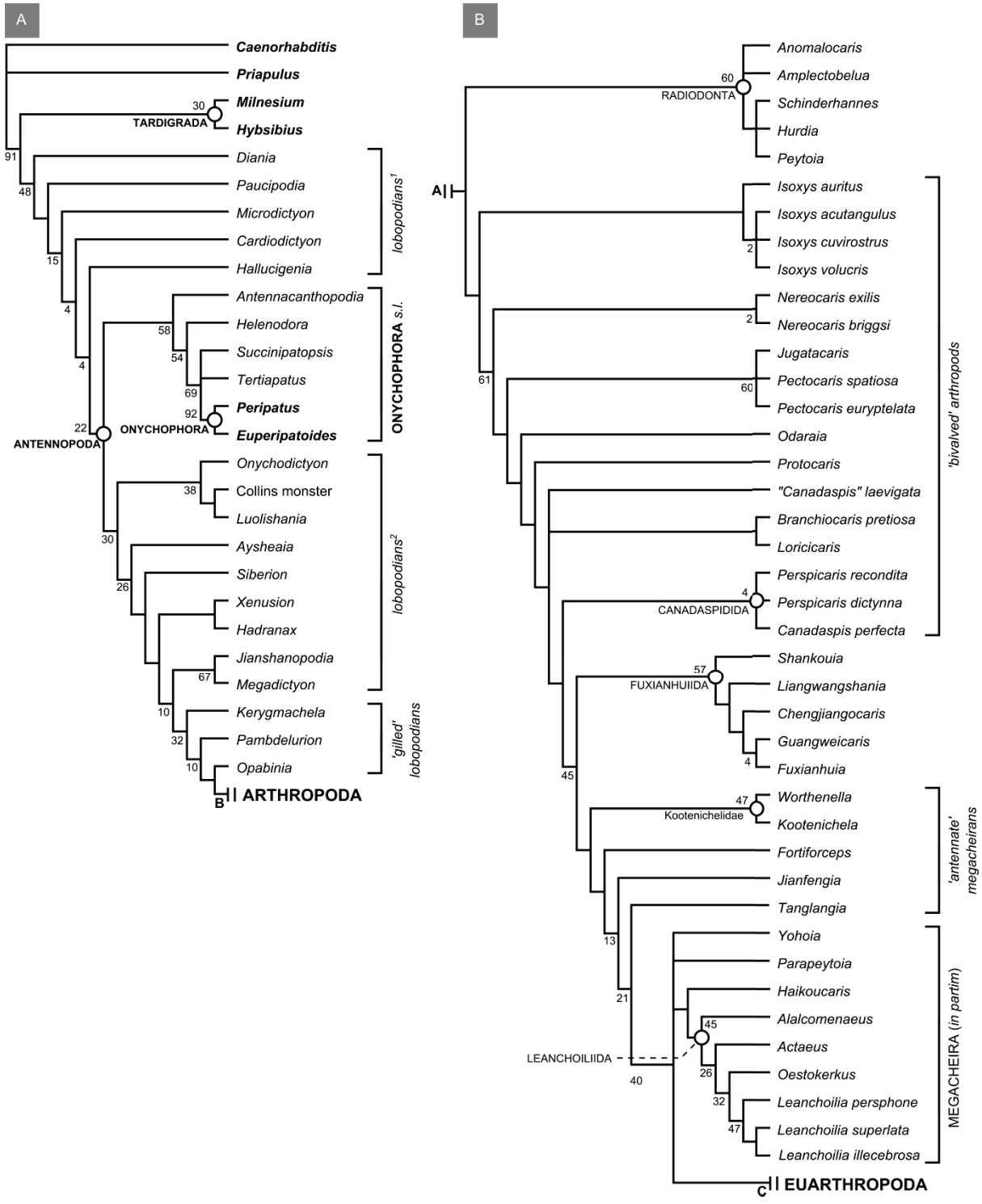


Fig. 9.1 (part 1) | Phylogeny of Panarthropoda. Strict-consensus of 45 MPTs of 139.87601 steps (weighted character fit = 592; CI = 0.520; RI = 0.873), produced using implied character weighting (k = 3). Numbers associated with nodes are GC support values. **A**, non-arthropod panarthropods; and **B**, radiodontans and upper stem-group euarthropods.

character optimization remained consistent. Analysis of the data set using implied character weighting with a concavity constant of two produced 48 MPTs of 173.05712 steps with a weighted character fit of 559 (CI = 0.519; RI = 0.872).

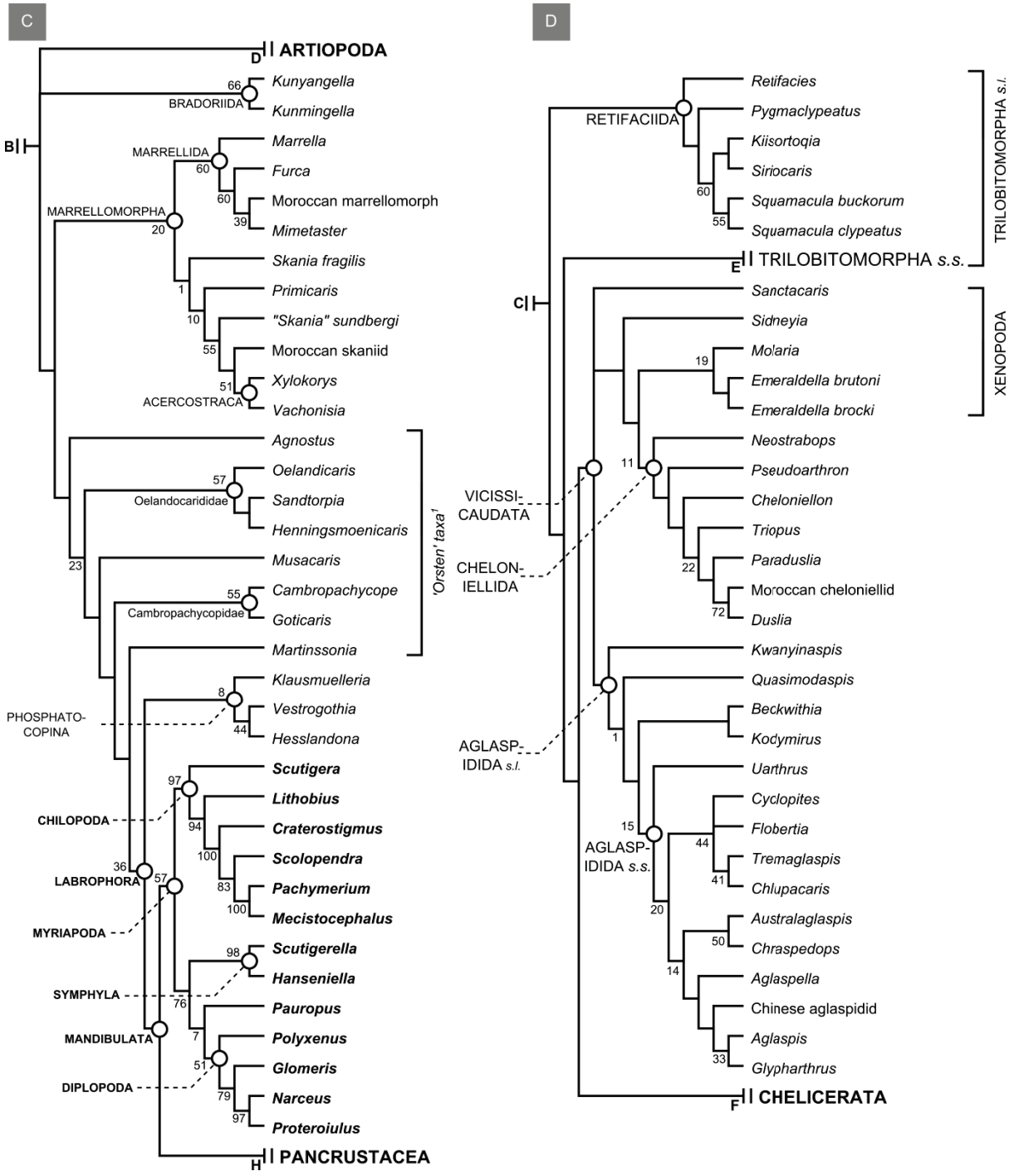


Fig. 9.1 (part 2) | Phylogeny of Panarthropoda. C, Total-group Mandibulata and Bradoriida; **D**, stem-group chelicerates (Artiopoda).

9.2.1. The extant sister-taxon of Euarthropoda

The current analysis supports a monophyletic Panarthropoda Nielsen 1995, with tardigrades (*Milnesium* Doyère 1840, plus *Hypsibius* Ehrenberg 1848), resolving as sister taxon to all other panarthropods. The monophyly of Panarthropoda is supported by three synapomorphies: the external expression of discrete segments

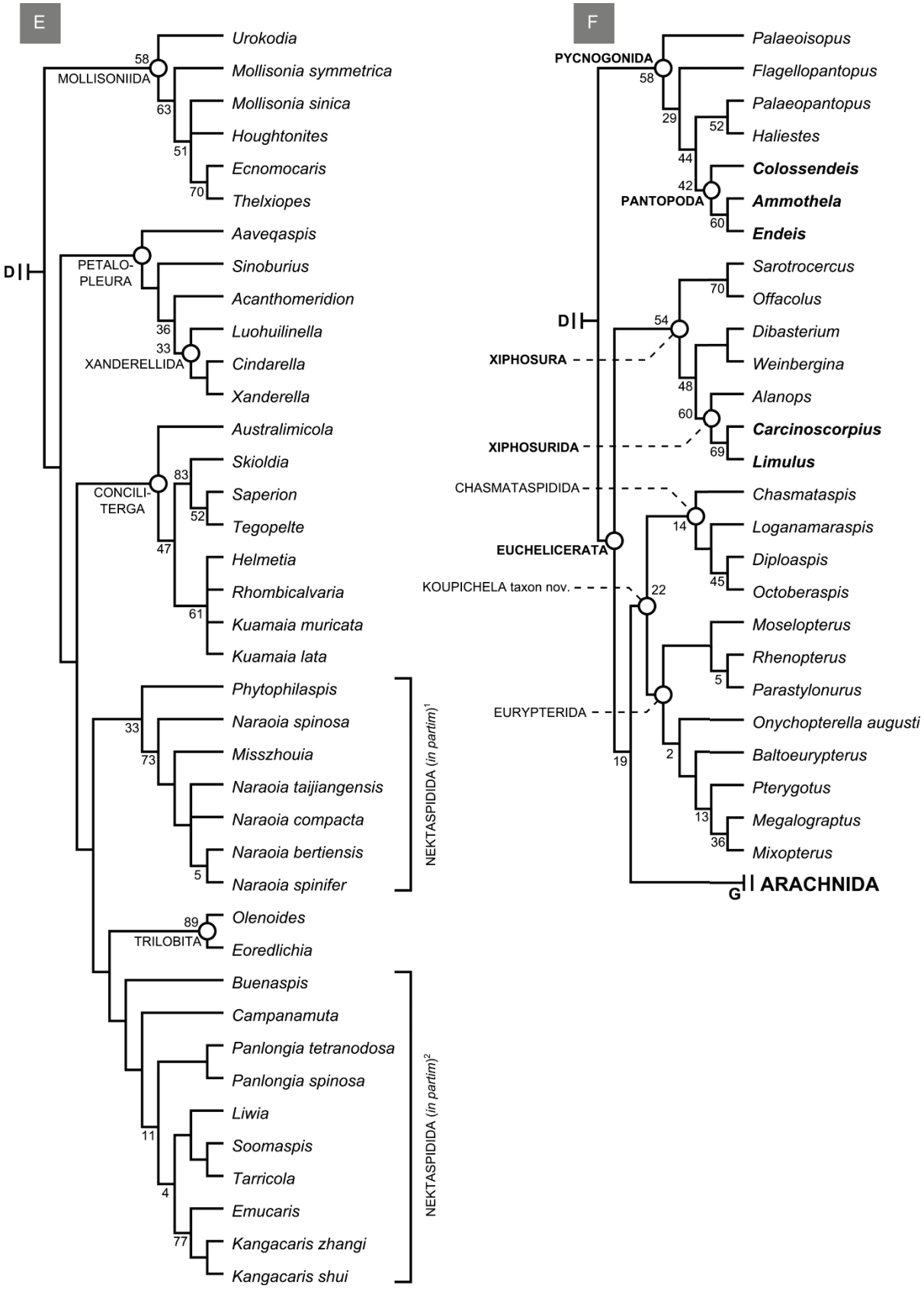


Fig. 9.1 (part 3) | Phylogeny of Panarthropoda. E, Trilobitomorpha *sensu stricto*; and **F**, Chelicerata (including Xiphosura and stem-group Arachnida).

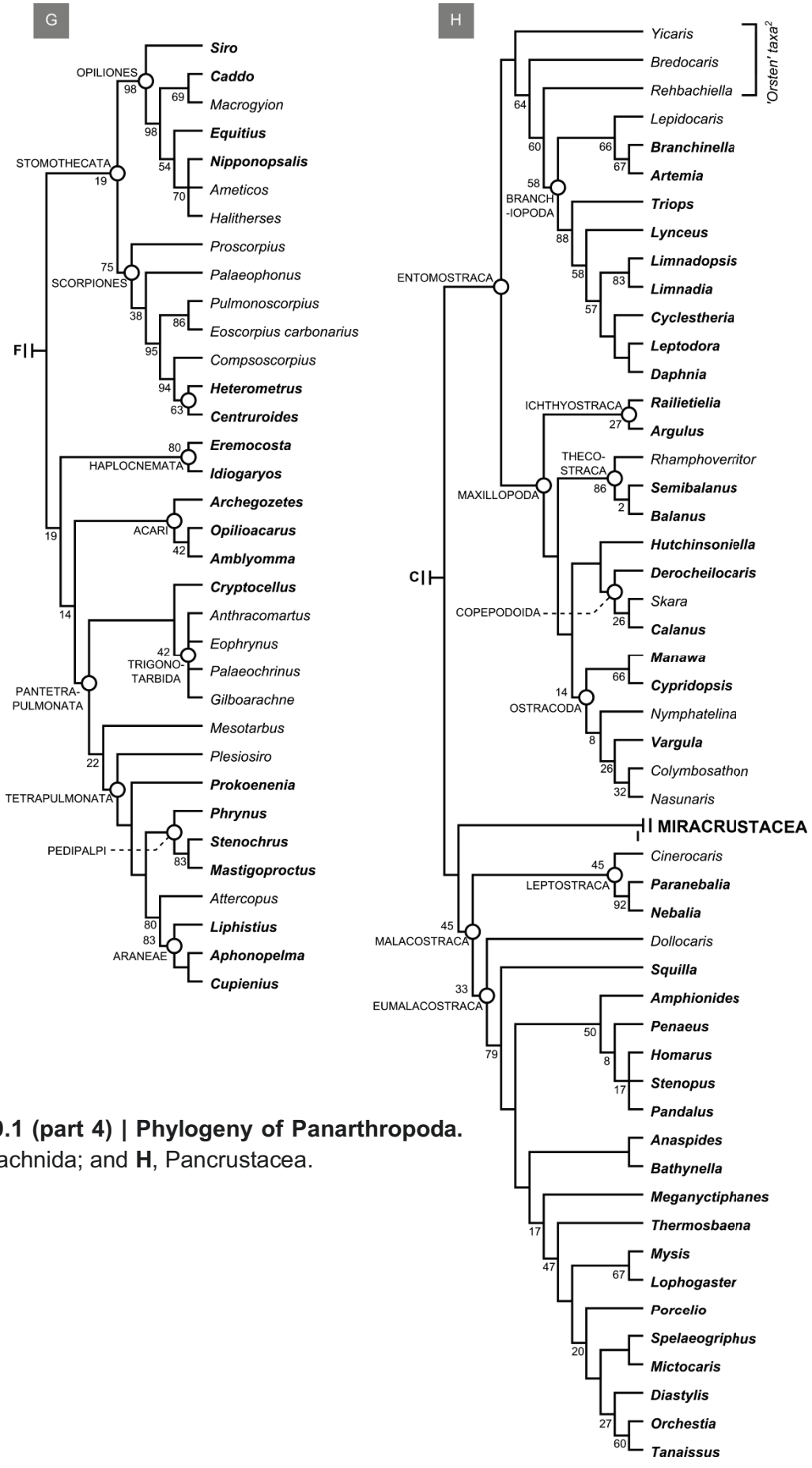


Fig. 9.1 (part 4) | Phylogeny of Panarthropoda.
G, Arachnida; and **H**, Pancrustacea.

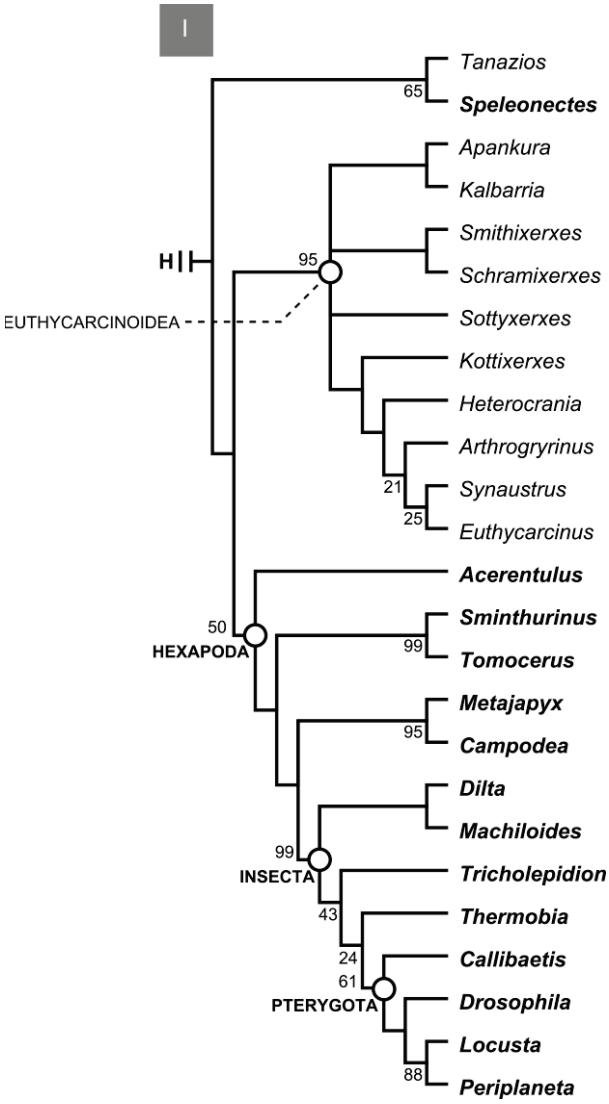


Fig. 9.1 (part 5) | Phylogeny of Panarthropoda. I, Miracrustacea.

(**ch. 3:1**), paired ventrolateral appendages (**ch.199:1**), and the presence of a radially arranged circumoral structure (**532:1**); the latter is differentiated into a flexible buccal tube and stylet apparatus (**ch. 555:1**) in Tardigrada Doyère 1840, and serves a unique synapomorphy supporting the monophyly of this clade.

Onychophorans (*Peripatus* Guilding 1926, plus *Euperipatoides* Reid 1996), resolved as the extant sister taxon to Euarthropoda Lankester 1904. The least inclusive clade including onychophorans and euarthropods, termed Antennopoda De Haro 1998, is supported by three synapomorphies: the presence of more than two sclerites or nodes on each trunk segment (**ch.6:1**); the presence of differentiated uniramous anterior appendages (**ch. 201:1**); and the presence of locomotory limbs with spinules or papillae (**ch. 392:1**). Differentiated uniramous anterior appendages (**ch. 201:1**) are common amongst antennopods and demonstrate a variety of morphologies and segmental affinities (Scholtz and Egdecombe 2006). Comparative morphology indicates that the anterior appendages of lobopodians and dinocaridids likely originate from the protocerebal somite (**Chapter 6**), whereas those of euarthropods originate from the deutocerebral somite (**Chapter 7**); the optimization of character 201 further supports that they are not homologous, although the appearance of this character in the euarthopod stem-lineage cannot be unambiguously determined using the current taxon sampling (*see* section 9.2.3.4). Crown-group euarthropods lack multiple sclerotized nodes as well as papillae on their locomotory appendages, however they are present in their-stem lineage members, e.g. the dinocaridid *Pambdelurion* Budd 1997.

The monophyly of Onychophora Grube 1853, is supported by two synapomorphies: the presence of pads on their lobopodous appendages (**ch. 211:1**), and the possession of numerous spiracles scattered over the body (**ch. 628:6**).

Other ‗typical' onychophoran characters, such as jaws associated with the deutocerebral somite (**ch. 236:1**), and tritocerebral slime papillae (**ch. 257:1**) (Wright 2012), evolved successively within the onychophoran stem-lineage; jaws appear at the least inclusive node including onychophorans and *Helenodora* Thompson and Jones 1980, and slime papillae are present in *Succinipatopsis* Poinar 2000, *Tertiapatus* Poinar 2000, and extant onychophorans. Poinar (2000) proposed the Class Udeonychophora, within the Subphylum Onychophora, for terrestrial onychophorans with a ventral mouth, including *Helenodora*, *Succinipatopsis*, *Tertiapatus*, and extant onychophorans. The former three taxa were assigned to the Order Ontonychophora Poinar 2000, and extant onychophorans restricted to the Order Euonychophora Hutchinson 1930. The current analysis indicates that ontonychophorans represent a paraphyletic assemblage (Fig. 9.1A). For the sake of taxonomic stability Onychophora is restricted to the crown-group (= Euonychophora *sensu* Poinar 2000), and the most inclusive group including onychophorans but not euarthropods or tardigrades as Onychophora *sensu lato*. The latter clade also includes *Antennacanthopoda* Ou and Shu *in* Ou *et al*. 2011, and is supported by two synapomorphies: a lack of multi-facetted lateral eyes (**ch. 472:0**), and the possession of a ventrally placed mouth (**ch. 529:1**); however, both characters have a low consistency (ch. 472, CI = 0.25; ch. 529, CI = 0.4), and may not be reliable indicators of relationships.

9.2.2. Interrelationships of extant euarthropods

Analyses recovered a fundamental split in the arthropod crown-group between chelicerates and mandibulates (Fig. 9.1C). Both have a diverse stem-lineage (Fig. 9.1C-D), the contents of which are discussed in section 9.2.3.

The monophyly of Chelicerata Heymons 1901 (Fig. 9.1F), the least inclusive clade including Pycnogonida Latreille 1810, and Euchelicerata Weygoldt and Paulus 1979, is supported a single synapomorphy: the presence of chelate deutocerebral appendages (**ch. 236:2**), but each of its constituent clades is supported by numerous synapomorphies. A monophyletic Pycnogonida, including *Palaeoisopus* Broili 1928, *Flagellopantopus* Poschmann and Dunlop 2006, *Palaeopantopus* Broili 1929, *Haliestes* Siveter *et al*. 2004, and crown-group pycnogonids (= Pantopoda Gerstaecker 1863), is supported by 10 synapomorphies: a lack of a fused cephalic shield (**ch.23:0**); a lack of tergal overlap (**ch. 87:0**); a lack of extensive lateral tergal pleurae (**ch. 88:0**); modification of the tritocerebral appendages into palps (**ch. 258:3**); the presence of ovigers (**ch. 283:1**); an absence of lateral eyes (**ch. 473:0**); the presence of four median eyes (**ch. 506:3**), the latter positioned on an ocular tubercle (**ch. 516:1**), the presence of an extensive proboscis (**ch. 531:1**), and an absence of a visible labrum (**ch. 537:1**). The placement of Pycnogonida within Euarthropoda and Chelicerata suggests that many of the character absences supporting its monophyly are the result of secondary reduction, rather than a primary (primitive) absence.

The monophyly of Euchelicerata is supported by five synapomorphies: a reduction or absence of trunk endopods (**ch. 399:0**), the fusion of the post-oral appendicular ganglia into a single nerve mass (**ch. 452:1**), the fusion of the ventral tendons into a prosomal endosternum (**ch. 588:1**), intralecithal cleavage (**ch. 704:1**), and epimorphic development (**ch. 719:1**). The majority of these characters cannot be verified in fossil exemplars, although other characters support the placement of these taxa on either the xiphosurid or arachnid stem. Xiphosura Latreille 1802, defined herein as the most inclusive clade including xiphosurids, but not arachnids, is composed of a paraphyletic assemblage of synziphosurans (*Sarotrocercus* Whittington 1981, *Offacolus* Orr *et al*. 2000, *Dibasterium* Briggs *et al*. 2012, and *Weinbergina* Richter and Richter 1929), the xiphosurid *Alanops* Racheboeuf *et al*. 2002, and the crown-group xiphosurids *Carcinoscorpius* Pocock 1902, and *Limulus* Linnaeus 1758. The monophyly of Xiphosura is supported by four synapomorphies: reduction of the first trunk tergite (**ch. 80:1**), the presence of a telson more than half the length of the trunk (**ch. 188:1**), chelate walking legs (**ch. 391:1**), and the incorporation of the seventh metamere into the cephalic tagmata (**ch. 401:1**); and the monophyly of Xiphosurida [= *Alanops* plus *Limulus* and *Carcinoscorpius*] is defined by the possession of a single synapomorphy: the fusion of all opisthosomal somites into a thoracetron (**ch. 119:1**). The sister-taxon to Xiphosura, Dekatriata Lamsdell 2013, includes a monophyletic group of eurypterids and chasmataspidids (Fig. 9.1D), designated **Koupichela** herein, and Arachnida Lamarck 1801. Dekatriata is supported by four synapomorphies: the possession of a post-oral sternum (**ch. 67:1**), limited coxal movement (coxal swing) (**289:0**), the division of the tarsus into a basitarsus and telotarsus (**ch. 299:1**), and the possession of a sclerotized spermatophore (**ch. 646:1**). The name Koupichela nom. nov., derives from the Greek ~~-~~*koupi*" meaning ~~-~~oar" and *"chela"*, Latin for ~~-~~claw", in reference to the paddle-like sixth appendages, a unique synapomorphy of this clade (**ch. 388:1**).

Mandibulata Snodgrass 1935, is defined as the least inclusive group including Myriapoda Latrielle 1802, Hexapoda Latrielle 1802, and Crustacea Brunnich 1771. This clade is supported by two synapomorphies: the presence of maxillae on the fourth (**ch. 331:1**) and fifth (**ch. 340:1**) metameres. Mandibles (**ch. 307:2**), the feature from which the clade name is derived, resolved as a synapomorphy of Labrophora Siveter *et al*. 2003b, the least inclusive clade including Phosphatocopida Müller 1964, and Mandibulata; a group also supported by three additional synapomorphies: the presence of a coxa on both the first post-antennal appendages (**ch. 262:1**) and the third post-antennal appendages (**ch. 278:1**); and the presence of a sclerotized sternum formed by the antennal to maxillary sternites (**ch. 546:1**).

The crustaceans were recovered as paraphyletic with regard to Hexapoda in the current analysis (Fig. 9.1H); the name Pancrustacea Zrvarý and Štys 1997 [=Tetraconata Dohle 2001], is hence preferred to Crustacea for this clade. The monophyly of Pancrustacea is supported by 11 synapomorphies: the presence of neural cells with asymmetrical division (**ch. 437:1**), an anterior pair of serotonergic neurons with neurites that cross to contralateral sides (**ch. 441:1**), a fan-shaped body in the brain (**ch. 454:1**), morphogenetic front-type eye formation (**ch. 475:2**),

the possession of two corneagenous cells (**ch. 487:1**), the restriction of segmental glands to the second antennal and maxillary segments (**ch. 572:2**), the location of ovary germarium in the terminal part of each egg tube (**ch. 693:1**), the location of a presumptive mesoderm anterior to the midgut; (**ch. 716:1**) [later changed in Hexapoda, where the mesoderm is diffuse throughout the ectoderm (**ch. 716:3**)], the absence of nauplius larvae or egg-nauplii (**ch. 720:0**) [later developed within certain crustacean lineages], the relocation of $tRNA^{L(UUR)}$ between COI and COII (**ch. 744:1**), and the relative position of $tRNA^{L(CUN)}$ (**ch. 745:1**).

Hexapoda resolved as sister-taxon to euthycarcinoids, within a more inclusive clade that contains a Remipedia Yager 1981, plus *Tanazios* Siveter *et al*. 2007c, clade (Fig. 9.1I). This more inclusive clade, corresponding to Miracrustacea Regier *et al*. 2010, apart from the exclusion of Cephalocarida from the group, and is supported by three synapomorphies pertaining to the ovaries: subdivision of the ovary into a well-defined anterior germarium and an elongate vitellarium (**ch. 694:1**), localization of the germaria within the trunk and/or head region of the body (**ch. 695:1**), and the accommodation of germline cells by unpolarized somatic cells (**696:1**).

9.2.3. Relationships of fossil taxa

9.2.3.1. The mandibulate stem-lineage

Both the mandibulates and the chelicerates possess a diverse stem-lineage. Successive plesions of Mandibulata include phosphatocopids, ‗Ostencrustaceomorphs', *Agnostus* Linnaeus 1758, and marrellomorphs (Fig. 9.1B). Total-group Mandibulata is supported by two synapomorphies: the possession of cephalic exopods which are longer than the cephalic endopods (**ch. 220:1**), and the absence of rhabdometric lateral eyes: (**ch. 473:0**). The latter character has the lowest consistency of any character in the data set (CI = 0.03), and is therefore an unreliable indicator of relationships. Character 220, however, is optimally consistent (CI = 1).

Marrellomopha

The marrellomorphs resolved as the sister-taxon to all other total-group mandibulates. Marrellomorpha Beurlen 1930, includes Marrellida Raymond 1935, Acercostraca Lehmann 1955, and a paraphyletic assemblage of taxa previously assigned to Parvancorinomorpha Lin *in* Lin *et al*. 2006 (namely *Skania* Walcott 1931, *Primicaris* Zhang *et al*. 2003, and an undescribed skaniid from the Ordovician of Morocco [Van Roy *et al*. 2010]) (Fig. 9.1B). The monophyly of Marrellomorpha is supported by a single synapomorphy: the presence of a tritocerebral exopod that is longer than the other cephalic appendages (**ch. 275:1**).

Marrellid monophyly is supported by three synapomorphies: the possession of elongate mediolateral spines (**ch. 30:1**), and elongate genal spines on the cephalic shield (**ch. 58:1**), and a lack of extensive lateral tergal pleurae (**ch. 88:0**). An undescribed marrellomorph from the Ordovician of Morroco (Van Roy *et al*. 2010), which was previously referred to *Furca* Fritsch 1908 (Van Roy 2006), resolved as sister-taxon to *Mimetaster* Gürich 1932, rather than *Furca bohemica* Fritsch 1908, casting doubt on its previous assignment. The latter relationship is supported by the possession of elongate anterolateral spines (**ch. 29:1**).

Parvancorinomorphs resolved as paraphyletic with regards to Acercostraca [= *Vachonisia* Lehmann 1956, and *Xylokorys* Siveter *et al*. 2007a]. This clade, containing parvancorinomorphs and acercostracans, is supported by two synapomorphies: the possession of an extensive dorsal shield (**ch. 102:1**) with a marginal doublure, which is coded as homologous to the cephalic doublure of other taxa (**ch. 40:1** *see* **Appendix 2** for further discussion). The undescribed Moroccan skaniid, *Skania sundbergi* Lin *in* Lin *et al*. 2006, *Primicaris larvaformis* Zhang *et al*. 2003, and *Skania fragilis* Walcott 1931, resolved as successive plesions of Acercostraca. The position of *S. sundbergi* may indicate it is not referable to *Skania*.

Agnostus

Agnostus resolved as the most-basal member of a paraphyletic assemblage of ‗Orsten' taxa (Fig. 9.1C). This placement is supported by a single synapomorphy: the possession of multisegmented post-antennal exopods with inward pointing setae: (**ch. 306:1**). This may be an example of long-branch attraction however, as *Agnostus* possesses numerous autapomorphies, namely: the possession of a calcified cuticle (**ch. 13:1**), an extensive cephalic doublure (**ch. 40:1**), a cephalon encompassing four appendage-bearing segments (**ch. 44:2**), a glabella (**ch. 52:1**), genal spines (**ch. 58:1**), a raised axial region (**ch. 112:1**), with axial furrows (**ch. 113:1**), a pygidium (**ch. 154:1**), and the absence of a telson (**ch. 181:1**); all of which are also present in trilobites (*sensu stricto*). *Agnostus* resolved as sister-taxon to Trilobita Walch 1771 during jackknife resampling, albeit with low GC frequency values (GC = 2).

„Orsten" crustaceomorphs

The so-called ‗Orsten' crustaceomorphs, *Martinssonia* Müller and Walossek 1986, Cambropachycopidae Walossek and Müller 1990, *Musacaris* Haug *et al*. 2010b, and Oelanocarididae Haug *et al*. 2010a; resolved as successive plesions of Labrophora (*see* section 9.2.2) (Fig. 9.1C). Each node is supported by a singular synapomorphy. The entire clade is supported by the possession of an enlarged proximal endite on the mandibular somite (**ch, 307:1**); the next node (excluding Oelandocarididae) is supported by the possession of a proximal endite on the first post-antennal appendages during early larval development (**ch. 260:1**); the successive nodes

(Cambropachycopidae, *Martinssonia* and Labrophora) by the possession of a multi-annulated exopod on the third post-antennal appendages (**ch. 280:1**); and a sister-taxon relationship between *Martinssonia* and Labrophora is supported by the possession of a proximal endite on the third post-antennal appendages in adults (**ch. 279:1**).

Bradoriida

The position of the bradoriids was unresolved in the strict-consensus tree (Fig. 9.1C), the group resolving in a polytomy with the mandibulate total-group and the chelicerate total-group. The majority-rule consensus resolved bradoriids as the most basal member of the mandibulate stem-lineage in 73 per cent of trees, however, no unambiguous synapomorphies support this placement.

9.2.3.2. The chelicerate stem-lineage

The chelicerate stem-lineage includes vicissicaudates and a paraphyletic assemblage of taxa traditionally included in Trilobitomorpha Størmer 1944 (Fig. 9.1D). This clade, termed Artiopoda Hou and Bergström 1997, is supported by a single synapomorphy: the presence of an expansive cephalic doublure (**40:1**).

Trilobitomorpha

The trilobitomorphs resolved as paraphyletic with regards to a clade consisting of Vicissicaudata Ortega-Hernández *et al*. 2013, and Chelicerata, termed Cheliceromorpha Boudreaux 1979. A clade including retifaciids, *Siriocaris* Lagebro *et al*. 2009, and *Kiisortoqia* Stein 2010, for which the clade name Retifaciida Hou and Bergström 1997 is employed, resolved as the most basal artiopods (Fig. 9.1D). A single synapomorphy, the presence of a segmented telson (**ch. 189:1**), supports this clade, although a telson is absent (**ch. 181:0**) in derived members of this clade, namely *Siriocaris*, *Kiisortoqia* and *Squamacula* Hou and Bergström 1997.

Trilobitomorpha *sensu stricto*, a name applied herein to a monophyletic group of all non-retifaciid trilobitomorphs, resolved as sister-taxon to Cheliceromorpha (Fig. 9.1D); a relationship supported by a single synapomorphy: the presence of imbricated lamellar setae (**ch. 229:1**). A monophyletic Trilobitomorpha *s.s.* is supported by two synapomorphies: the absence of a telson (**ch. 181:0**), and the possession of a bilobate exopod shaft (**ch. 225:1**). This clade includes the mollisoniids, petalopleurans, concilitergans, trilobites, and a paraphyletic assemblage of nektaspids (Fig. 9.1D). *Phytophilaspis* Ivantov 1999, resolved as sister-taxon to naraoiids, a relationship supported by three synapomorphies: the absence of distinct thoracic boundaries (**ch. 106:1**), a reduction in thorax length (**ch. 110:1**), and the possession of a pygidium more than half the length of the entire

body (**ch. 163:1**). This clade resolved as sister-taxon to a clade containing other nektaspids, and trilobites. Trilobita resolved as sister-taxon to a clade containing the nektaspids *Buenaspis* Budd 1999b, *Campanamuta* Budd 2011, *Panlongia* Liu *et al*. 2006, Liwiidae Dzik and Lendzion 1988, and Emucarididae Paterson *et al*. 2010. This more inclusive clade is supported by the presence of articulating half-rings on the thoracic segments (**ch. 111:1**).

The enigmatic arthropod *Acanthomeridion* Hou *et al*. 1989, resolved as sister-taxon to Xandarellida Chen, Ramsköld, Edgecombe and Zhou *in* Chen *et al*. 1996 (Fig. 9.1D); a relationship supported by three synapomorphies: an absence of a distinct glabella (**ch. 52:0**), posterior curvature of the posterior tergites (**ch. 149:1**), and reduction of the pygidium (**ch. 156:1**).

Vicissicaudata

A sister-taxon relationship between vicissicaudates and chelicerates is supported by two synapomorphies: the possession of dorsally positioned (**ch. 479:1**) and un-stalked lateral eyes (**ch. 478:0**), although both characters are later reversed in the vicissicaudate *Sidneyia* Walcott 1911c. A monophyletic Vicissicaudata (Fig. 9.1D), consisting of *Sanctacaris* Briggs and Collins 1988, *Sidneyia*, *Emeraldella* Walcott 1912, *Molaria* Walcott 1912, Cheloniellida Broili 1933, and Aglaspidida Raymond Walcott 1911c, is supported by three synapomorphies: an abdomen consisting of three segments (**ch. 140:2**), defined by a lack of appendages (**ch. 138:1**); and the presence of posteriorly curving tergites on the posterior thoracic segments (**ch. 149:1**).

Sanctacaris resolved in a polytomy with aglaspidids and a xenopod—cheloniellid clade, in the strict consensus tree (Figs. 9.1D, 9.2A), although in the constituent trees it resolved as either sister-taxon to all other vicissicaudates (Fig. 9.2B), or as sister-taxon to the xenopod plus chelonielliid clade (Fig. 9.2C). The latter is present in 53 per cent of trees and is supported by a single synapomorphy: the possession of elongate setiferous endopod endites differentiated into primary (short) and secondary (elongate) sets (**419:1**). The alternative topology, with *Sanctacaris* as sister-taxon to all other vicissicaudates (Fig. 9.2B), was supported by the presence of a single synapomorphy uniting non-*Sanctacaris* vicissicaudates: the possession of a pair of flaps lateral to the telson (**ch. 178:1**).

The xenopod plus cheloniellid clade is supported by a single synapomorphy: the presence of uniramous tritocerebral appendages (**ch. 259:1**). The xenopods (*Sidneyia*, *Emeraldella* and *Molaria*) resolved as paraphyletic with regards to Cheloniellida (Fig. 9.1D). A polytomous clade including *Emeraldella brocki* Walcott 1912, *E. burtoni* Stein *et al*. 2011, and *Molaria spinifera* Walcott 1912, resolved as the immediate sister-taxon of Cheloniellida, a grouping supported by a single synapomorphy: an abdomen consisting of a single segment (**ch. 140:0**).

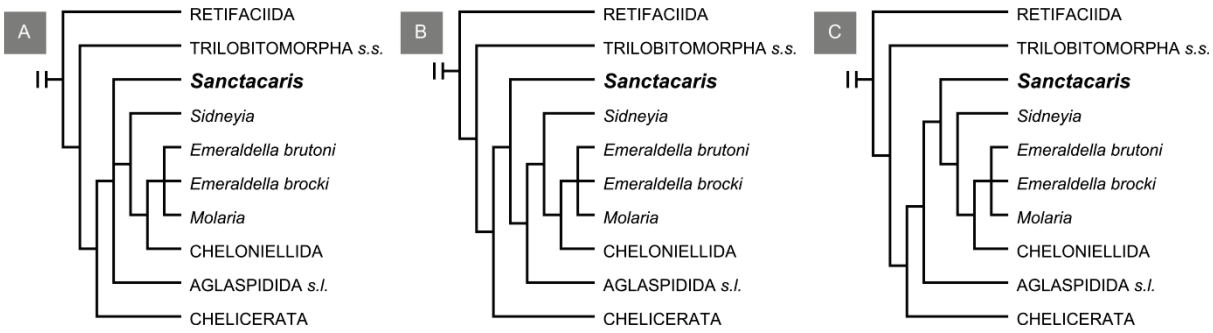


Fig. 9.2 | Divergent position of *Sanctacaris* Briggs and Collins 1988. A, Strict-consensus topology; **B**, *Sanctacaris* as sister-taxon to all other vicissicaudates; and **C**, *Sanctacaris* as basal-most member of a Xenopoda plus Cheloniellida clade.

9.2.3.3. The arthropod stem-lineage

The euarthropods possess a diverse stem-lineage including lobopodians, dinocaridids and upper stem-group euarthropods (Fig. 9.1A-B). Upper stem-group euarthropods are discussed in detail in section 9.2.3.4.

Lobopodians

The euarthropod total-group is supported by a single synapomorphy: the presence of a restricted number of complete annulations per segment/somite (**ch. 9:0**).The lobopodian *Aysheaia* Walcott 1911a resolved as the most basal stem-group euarthropod, with its sister-node defined by the presence of a distinct head (**ch. 19:1**). Successive nodes consist of *Siberion* Dzik 2011; a *Hadranax* Budd and Peel 2008, plus *Xenusion* Pompecki 1927 clade, and a *Jianshanopodia* Liu *et al*. 2006, plus *Megadictyon* Luo and Hu *in* Luo *et al*. 1999 clade, and a paraphyletic Dinocaridida Collins 1996 (Fig. 9.1A). Important character acquisitions include the modification of the anterior appendages into grasping appendages (**ch. 204:1**; present in the *Siberion*, plus Euarthropoda clade), and midgut glands (**ch. 566:1**; present in the *Megadictyon* plus Euarthropoda clade).

Dinocaridids and the definition of Arthropoda

Dinocaridida, including Radiodonta Collins 1996, *Opabinia* Walcott 1912, *Pambdelurion* and *Kerygmachela* Budd 1997, resolved as paraphyletic with regards to upper stem-group euarthropods (Fig. 9.1A-B). The base of this assemblage is defined by four synapomorphies: the presence of lateral flaps: (**ch. 82:1**), a posterior tagmata with elongate lateral processes (**ch. 164:1**), the loss of papillae on the trunk appendages (**ch. 392:0**), and the possession of respiratory exites (**ch. 618:1**). The next node (*Pambdelurion* plus Euarthropoda) is supported by two synapomorphies: a

ventrally orientated mouth (**ch. 529:1**), and an oral cone consisting of overlapping plates (**ch. 536:1**); and the successive node (*Opabinia* plus Euarthropoda) by six synapomorphies: the absence of prominent, unsclerotized (**ch. 11:0**) nodes (**ch. 6:0**) on the trunk, the presence of longitudinal wrinkles on the lateral flaps (**ch. 83:1**), the loss of a bulbous, post-appendicular flap (**ch. 153:0**), and basal fusion (**ch. 210:1**) of the ventrally placed anterior-most appendages (**ch. 202:1**).

The least inclusive node including Radiodonta and Euarthropoda is supported by two synapomorphies: the possession of strongly sclerotized and arthropodized limbs (**ch. 213:1**) with pivot joints and intrinsic muclulature (**ch. 212:1**). This topology indicates a singular origin for arthropodization, a defining feature of Arthropoda Siebold 1848, hence the radiodontans are here assigned to this clade (Fig. 9.1B). An arthrodized trunk, another diagnostic arthropod characteristic, resolved as an autapomorphy of *Schinderhannes* Kühl *et al*. 2009, although the appearance of this character in the euarthropod stem-lineage cannot be determined with accuracy due to its uncertain distribution in the basal-most bivalved arthropods (see below).

9.2.3.4. Upper stem-group euarthropods

Bivalved arthropods

A paraphyletic assemblage of bivalved arthropods resolved as the basal-most upper stem-group euarthropods (Fig. 9.1B). The most inclusive clade including euarthropods, but not dinocaridids, is supported by five synapomorphies: a loss of lateral flaps (ch. 82:0), modification of the posterior tagmata into a fluke (**ch. 167:1**), sclerotization and arthropodization of the trunk appendage (**ch. 214:1**), biramy in the post-antennal limbs (**ch. 215:1**), and the loss of a sclerotized oral cone (**ch. 532:0**). Although a bivalved carapace is prevalent in the most basal arthropods its appearance could not be optimized on the strict consensus tree due to the uncertain homology of the lateral plates in the dinocaridid *Hurdia* Walcott 1912 (Daley *et al*. 2009, in press).

Isoxys resolved as the most-basal bivalved arthropod (Fig. 9.1B), its monophyly supported by the possession of antero- and posterolateral spines on the carapace (**ch. 34:1**). Its sister-node is supported by five synapomorphies: the sclerotization of the cuticle into an arthrodized tergal exoskeleton (**ch. 12:1**), an elongate limb-less abdomen (**ch. 138:1**), recurving of the lateral telson processes (**ch. 171:1**), and the loss of arthropodized (**ch. 205:0**) grasping appendages (**ch. 204:0**). Synapomorphies of successive nodes mostly pertain to morphology of the telson, however, the presence of specialized tritocerebral appendages (specialized post-antennal-appendages and ‗great-appendages') (**ch. 258:1**), supports a clade including *Odaraia* Walcott 1912, and Euarthropoda. The appearance of specialized deutocerebral appendages could not be adequately optimized in this analysis as they are unequivocally present in a clade including *Canadaspis laevigata* Hou and Bergström 1991, a *Branchiocaris* Briggs 1976, plus *Loricicaris* Legg and Caron in

press, clade, and Euarthropoda, but the sister-taxon of this clade – *Protocaris* Walcott 1884 – is not adequately preserved to determine their presence or absence.

A clade composed *Canadasips perfecta* (Walcott 1912), *Perspicaris dictynna* (Simonetta and Delle Cave 1975) and *Perspicaris recondite* Briggs 1977, termed Canadaspidida Novozhilov 1960, resolved as sister-taxon to a Fuxianhuiida Bousfield 1995, plus Euarthropoda clade (Fig. 9.1B). The monophyly of Canadaspidida is supported by a single synapomophy: the presence of posterior spines on the abdominal segments (**ch. 141:1**), although this feature is also present in *Loricicaris*. The disparate positions of *Canadaspis perfecta* and *C. laevigata* may indicate that the latter should be referred to a distinct genus.

Fuxianhuiids

The least inclusive clade containing Fuxianhuiida and Euarthropoda is supported by six synapomorphies: the possession of a true cephalic shield (**ch. 23:1**), the loss of a bivalved (**ch. 33:0**) free cephalic shield (**ch. 32:0**), differentiation of the trunk somites into distinct tergites and sternites (**ch. 75:1**), the extension of the tergal pleurae into paratergal folds (**ch. 88:1**), and the possession of flap-like telson processes (**ch. 173:1**). The monophyly of Fuxianhuiida is supported by the possession of a cephalon composed of a small anterior plate and a posteriorly expansive shield (**ch. 39:1**).

Megacheirans and the plesiomorphic condition of Euarthropoda

Megacheirans resolved as the paraphyletic plesion of Euarthropoda (Fig. 9.1B). The least inclusive clade containing megacheirans and euarthropods is supported by three synapomorphies: a lack of significant overlap of the cephalon and the anterior trunk somites (**ch. 64:0**), the loss of a posteriorly differentiated abdomen (**ch. 138:0**), and the presence of a ‘great-appendage‘ with a bipartite peduncle (**250:0**). The most basal megacheiran clade, Kootenichelidae Legg 2013 (Fig. 9.1B), are united by their shared possession of triangular, fin-shaped, exopods (**ch. 231:3**).

In the strict consensus tree both *Parapeytoia* Hou *et al*. 1995, and *Yohoia* Walcott 1912, resolved as part of a polytomy including a Leanchoillida Størmer 1944, plus *Haikoucaris* Chen *et al*. 2004, clade, and Euarthropoda (Fig. 9.1B). This clade is supported by two synapomorphies: the possession of a rigid protopodite (**ch. 216:1**), and an exopod with strong setae (**ch. 224:1**). The strict consensus position of *Parapeytoia* and *Yohoia* is the consensus of three alternative topologies (Fig. 9.3). A polytomy including *Parapeytoia*, *Yohoia*, leanchoiliids and euarthropods (Fig. 9.3A) is only present in 27 per cent of the constituent trees and an alternative topology favouring a position within the *Haikoucaris* plus Leanchoiliida clade (Fig. 9.3C) is more common (present in 38 per cent of trees recovered). The latter topology is supported by three synapomorphies: the possession of a paddle-shaped telson (**ch.**

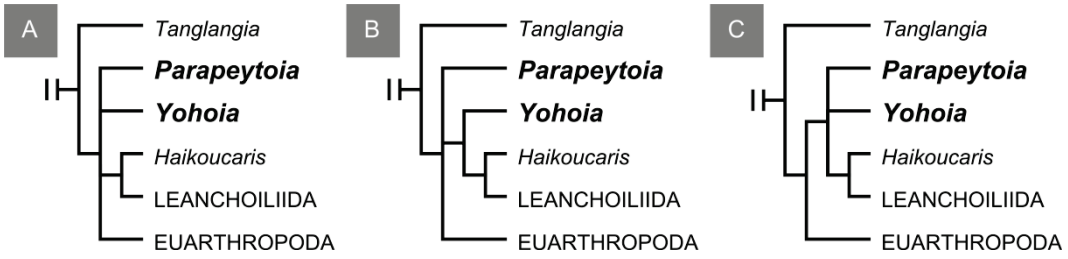


Fig. 9.3 | Divergent positions of *Parapeytoia* Hou *et al*. 1995, and *Yohoia* Walcott 1912. **A**, Strict-consensus topology, also present in 27 per cent of constituent tree; **B**, *Yohoia* as sister-taxon of a *Haikoucaris* Chen *et al*. 2004, plus Leanchoiliida Størmer 1944 clade, present in 35 percent of constituent trees; and **C**, *Parapeytoia* and *Yohoia* as sister-taxon of a *Haikoucaris* plus Lenchoiliida clade, present in 38 per cent of constituent trees.

183:1) that is fringed with setae (**ch. 191:1**), and the possession of long, flattened and tapered exopod setae (**ch. 430:1**).

A monophyletic Euarthropoda is supported by two synapomorphies: the modification of the ‗great-appendage' into an unspecialized ramus (**ch. 258:0**) and the sclerotization of the labrum (**ch. 538:1**). This analysis indicates that many features characteristic of euarthropods, such as paratergal folds and gnathobasic appendages (Boudreaux 1979), evolved successively within the euarthropod stem-lineage.

9.3. Other weighted analyses (k = 10)

Analysis of the data set using implied character weighting with a concavity constant of 10 produced 39 MPTs of 62.72580 steps with a weighted character fit of 669 (CI = 0.522; RI = 0.74). These trees are discussed in the following section.

9.3.1. Variations and common topological features

The topology produced using a concavity constant of 10 was identical to the topology produced using a concavity constant of three, except for the internal relationships of Pancrustacea (Fig. 9.4); which is divided into hexapods and a euthycarcinoid plus monophyletic Crustacea clade. Synapomorphies which linked euthycarcinoids and hexapods in other implied weighted analyses, e.g. uniramous appendages (**ch. 205:0**) and an intercalary segment (**ch. 258:2**) resolved as symplesiomorphies of Pancrustacea and their reversal supports a monophyletic Crustacea. The euthycarcinoid plus crustacean clade is supported by three synapomorphies: the presence of a limbless abdomen (**ch. 138:1**), the possession of a posteriorly-facing mouth (**ch. 530:2**), and the presence of a fleshy labrum (**ch. 542:1**). A monophyletic Crustacea is supported by three synapomorphies: the presence of articulated furcal rami (**ch. 176:1**), biramy in post-antennal appendages (**ch. 215:1**), and presence of

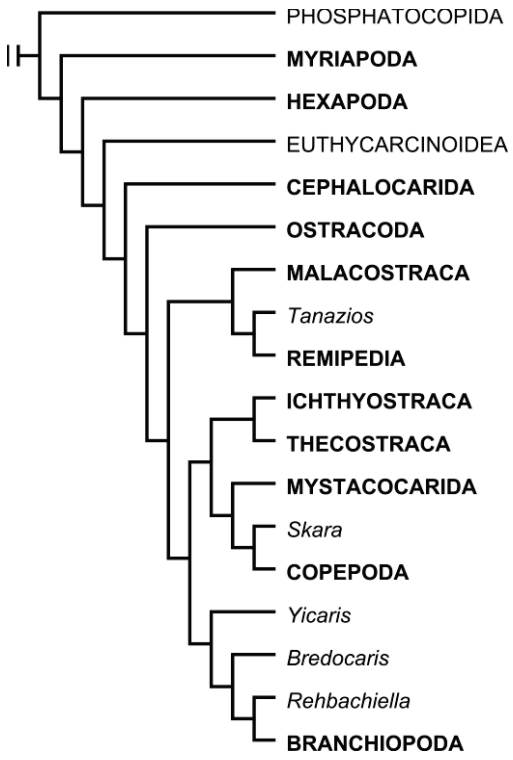


Fig. 9.4 | The internal relationships of mandibulate arthropods. Based on a strict-consensus of 39 MPTs produced using Implied character weighting (*k* = 10). Relationships within supra-generic clades are consistent with those resolved using implied weighting with a concavity constant of three (see Fig. 9.1C, H-I).

a pair of second antennae on the tritocerebral head segment (**258:1**). The cephalocarid *Hutchinsoniella macracantha* Sanders 1955, resolved as sister-taxon to all other crustaceans, which are united by a single synapomorphy: the possession of a nauplius larva (**ch. 720:1**). Ostracods resolved as sister-taxon to all other crustaceans, the internal topology of the latter is consistent with all previous analyses and is supported by a single synapomorphy: the relocation of $tRNA^{L(UUR)}$ between COI and COII (**ch. 744:1**).

9.4. Equally weighted analysis

Analyses utilizing equally weighted characters produced 37 MPTs of 1829 steps, with a weighted character fit of 588 (CI = 0.522, RI = 0.874). Few novel clades (i.e., those not also found under implied weights) were obtained using equal character weighting, the majority of which were limited to Crustacea (discussed below). The only novel clade outside of Crustacea was a sister-taxon relationship between *Agnostus* and Trilobita, supported by three synapomorphies: calcification of the cuticle (**ch. 13:1**), the presence of genal spines (**ch. 58:1**), and the possession of axial furrows (**ch. 113:1**). The equally weighted topology does not differ significantly from those produced using implied character weighting except that many nodes are collapsed into polytomies in the equally weighted strict-consensus. To better understand the underlying topology of the equally weighted tree an ensemble agreement subtree was produced (Fig. 9.5). This topology is compared to those produced using implied character weighting in the next section.

9.3.1. Agreement subtrees

During the calculation of the agreement subtree topology 110 taxa were pruned including *Onychodictyon*; Loulishaniidae Hou and Bergström 1995 (*sensu* García-

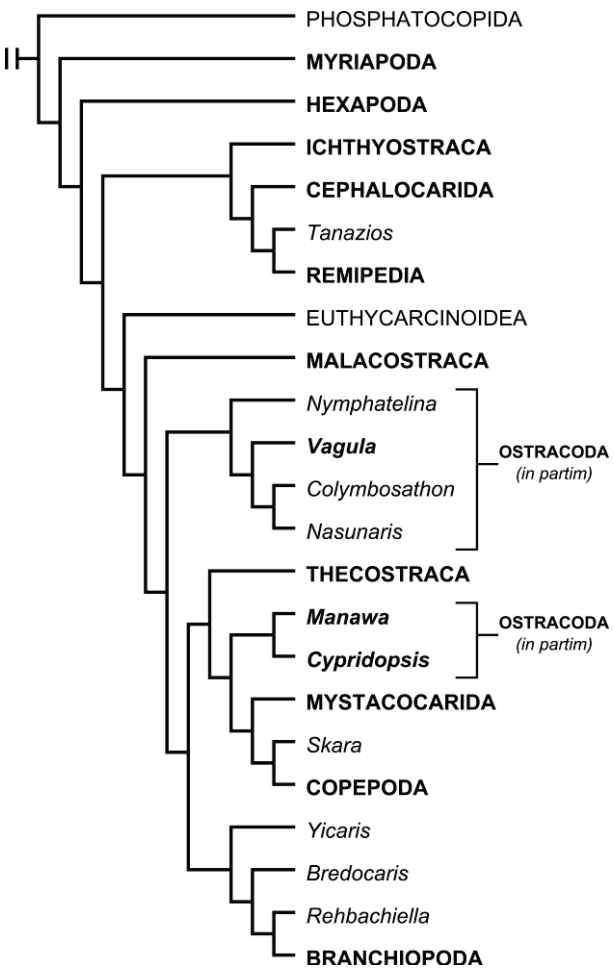


Fig. 9.5 | Agreement subtree consensus of pancrustacean relationships. Produced using equal character weighting. Note the polyphyly of Ostracoda.

Bellido *et al*. 2013); Radiodonta; the bivalved arthropods *Isoxys acutangulus* Walcott 1908, *Nereocaris* Legg *et al*. 2012b, and *Pectocaris eurypetala* (Hou and Sun 1988); the megacheirans *Parapeytoia* and *Yohoia*; all trilobitomorphs, vicissicaudates, chasmataspidids and bradoriids; *Sarotrocercus*; *Mesotarbus* Petrunkevitch 1949; *Plesiosiro* Pocock 1911; the extant arachnids *Prokoenenia* Börner 1901, and *Cryptocellus* Westwood 1874; the ‗Osten' crustaceomorphs *Sandtorpia* Haug *et al*. 2010a, *Musacaris*, and *Martinssonia*; the euthycarcinoids *Apankura* Vaccari *et al*. 2004, and *Kalbarria* McNamara and Trewin 1993; and the extant malacostracan *Pandalus* Leach 1814.

A clade including icthyostracans, the cephalocarid *Hutchinsoniella*, *Tanazios*, and the remipede *Speleonectes* Yager 1981, resolved as sister-taxon to all other crustaceans (Fig. 9.5). This clade is supported by a single synapomorphy: the relative position of tRNA-R and tRNA-N (**ch. 746:1**). Relationships amongst the remaining crustaceans, including euthycarcinoids, are consistent with the topologies produced using implied weighting with a concavity constant of 10 (Fig. 9.4), except with regards to ostracods. Although the a clade composed of the extant ostracods *Manawa* Hornibrook 1949, and *Cypridopsis* Brady 1867, resolved as sister-taxon to Copepodoida Haug *et al*. 2011b (Fig. 9.5), as per previous analyses, the remaining ostracods resolved outside of a clade composed of non-malacostracan crustaceans (Fig. 9.5). This latter clade is supported by a single synapomorphy: the possession of three median eyes (**ch. 506:2**).

10. Discussion

10.1. Introduction

Phylogenies represent hypotheses by which we can elucidate patterns and processes within evolutionary lineages. In this chapter the phylogenetic hypotheses obtained in **Chapter 9** are compared to selected previous hypotheses of arthropod relationships; and explanations are sought for similarity or differences. Current topologies are also used to make inferences about the origin of arthropods and the symplesiomorphic condition of Euarthropoda and its constituent clades.

Aspects of section 10.2.2. were published in *Proceedings of the Royal Society B* (Legg *et al.* 2012b), and aspects of section 10.2 and 10.3 are currently under review in *Nature Communications* (Legg *et al*. in review). Parts of section 10.2.2. were published in the *Journal of Paleontology* (Legg 2013).

10.2. Comparisons with previous hypotheses

It would be unfeasible to compare the results of this study to all prior hypotheses; instead discussion will focus on significant topological variations and the potential causes of disparate phylogenies.

10.2.1. Perturbation of the data set

To aid comparison and to determine the impact of both characters and taxa on the data set a number of subsets of taxa and/ or characters (Table 10.1) were analysed using the methods outlined in **Chapter 3**. The primary focus of these experiments was to determine what factors influenced the position of Hexapoda, however, these tests were also used to explore the relationships of other taxa particularly pycnogonids (section 10.2.2).

10.2.2. 'Great-appendage' arthropods and the origin of chelicerae

Data set	Included taxa	Deactivated characters	Relationships
DS-I	All taxa	None	Chelicerata paraphyletic Crustacea
DS-II	Extant only	None	Cormogonida monophyletic Crustacea
DS-III	Cba, Fx and Mc removed	None	Cormogonida paraphyletic Crustacea
DS-IV	Extant only	215, 258, 323, 328, 628 (terrestrial characters)	Cormogonida paraphyletic Crustacea
DS-V	Extant only	Higher-order jackknifing	Cormogonida monophyletic Crustacea
DS-VI	All taxa	Non-morphological characters	Chelicerata paraphyletic Crustacea

Table 10.1 | Comparison of data sets analysed in this study. Numbers refer to character descriptions in **Appendix 2**. Deactivated characters during higher order jackknifing were selected using a random number generator. Abbreviations: Cba, Cambrian bivalved arthropods, Fx, fuxianhuiids, and Mc, megacherians.

The analysis detailed in **Chapter 9** placed Pycnogonida within Chelicerata; however during perturbation of the data set a sister-taxon relationship between pycnogonids and all other euathropods (= Cormogonida Zrvarý *et al*. 1998), was frequently recovered. Selective taxon-deletion (DS-III) revealed that the upper stem-group euarthropods, e.g. Cambrian bivalved arthropods, fuxianhuiids, and megacheirans, were the most important taxa with regards to determining pycnogonid affinities; when they were removed from the data set Cormogonida was recovered instead of Chelicerata. A possible explanation is that these fossil taxa alleviate long-branch attraction effects caused by character losses in pycnogonids. Cormogonida is supported in both the extant only topologies and those excluding upper stem-group euarthropods by four synapomorphies: the presence of a fused cephalic shield (**ch. 23:1**), the lateral extension of the tergites into paratergal folds (**ch. 88:1**), the presence of a labrum (**ch. 537:1**), and the possession of intersegmental tensons (**ch. 595:1**). These features are absent from non-arthropods, such as onychophorans, but are present in upper stem-group euarthropods. Therefore any analysis excluding the latter will most likely favour a close relationship between pycnogonids and non-arthropods and recover these features as symplesiomorphic for Euarthropoda, whereas analyses including upper stem-group euarthropods are likely to resolve these features as convergently acquired and autapomorphic for Pycnogonida (e.g. Legg *et al*. 2012b, Legg 2013), as was found in the original analyses.

The megacheirans have played a central role in discussions of basal arthropod systematics (see section 4.6), being variously regarded as stem-group chelicerates (Chen *et al* 2004, Cotton and Braddy 2004, Dunlop 2005, Haug *et al*. 2012a, c), or upper stem-group euarthropods (Budd 2002, Daley *et al*. 2009, Liu *et al*. 2011). Much of the discussion regarding their affinities is focussed on the segmental affinities and putative homologies of their 'great-appendages' (Scholtz and Edgecombe 2006 and references therein), which are considered by many to represent precursors of the chelate frontal appendages of chelicerates (Chen *et al* 2004, Cotton and Braddy 2004, Dunlop 2005, Haug *et al*. 2012a, c). Evidence to the contrary was presented in **Chapter 7**.

Previous cladistic analyses that have resolved megacheirans as basal-chelicerates (e.g. Cotton and Braddy 2004), have tended to root their phylogenies using either trilobitomorphs (Edgecombe *et al*. 2011) or marrellomorphs (Cotton and Braddy 2004), a notable exception being Lamsdell (2013), who used the upper stem-group euarthropod *Fuxianhuia* Hou 1987b. In contrast, those that have resolved megacheirans as upper-stem group euarthropods (e.g Daley *et al* 2009) have tended to employee a much wider sampling of panarthropods and root their phylogenies using lobopodians (Budd 2002) or cycloneuralians (Daley *et al*. 2009, Liu *et al*. 2011, Legg *et al*. 2012b, Legg 2013). Rooting a phylogeny including megacheirans using crown-group euarthropods, such as marrellomorphs or trilobitomorphs, will inadvertently resolve megacheirans as ingroup euarthropods, regardless of their actual affinities. Including megacheirans in the chelicerate stem-lineage, particularly taxa such as *Fortiforceps* Hou and Bergström 1997, and *Kootenichela* Legg 2013, would require a number of unparsimonious assumptions of character evolution. For instance, in the topology proposed by Haug *et al*. (2012c) typical euarthropod characters such as reduction in the number of walking leg podomeres would need to be independently acquired by chelicerates and mandibulates.

The problem of resolving megacheiran affinities is also confounded by assumptions of homology regarding the 'great-appendages'. Any analysis which codes great-appendages' and chelicerae as homologous is likely to resolve megacheirans and chelicerate as closely related. This means that any analysis employing such a coding and rooting using a euarthropod ingroup is liable to resolve megacheirans as stem-chelicerates, and by extension support a monophyletic Chelicerata. Studies using a non-euarthropod outgroup have a greater potential to resolve a non-monophyletic Chelicerata (e.g. Legg *et al* 2012b).

Earlier versions of the current data set (Legg *et al*. 2012b, Legg 2013), followed Scholtz and Edgecombe (2006) in considering 'great-appendages' to originate from the deutocerebral somite, and the antennae of 'great-appendage'-bearing arthropods to originate from the protocerebral somite. Under this scheme the megacheirans resolved as successive plesions of Euarthropoda and a chelate deutocerebral appendage optimized as a symplesiomorphy of euarthropods (Fig. 10.1). As a consequence, chelicera-bearing arthropods resolved as the most basal arthropods, either as monophyletic, or with pycnogonids as sister-taxon to all other

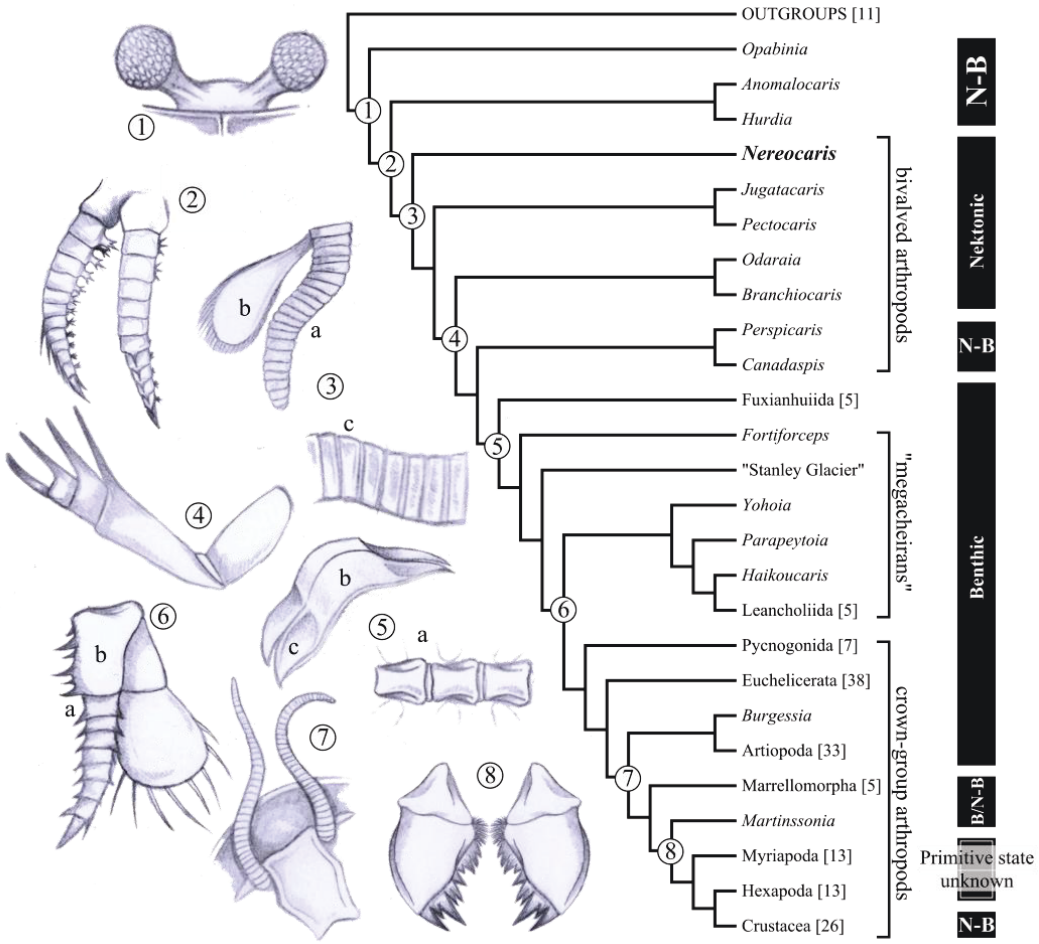


Fig. 10.1 | The origin of key innovations in Arthropoda. Reproduced from Legg *et al*. 2012b. Summary of three most parsimonious trees (MPTs) of 91.98 steps (implied character weighting, *k* = 3; CI = 0.565; RI = 0.863). Numbers in parentheses are the number of terminal taxa within supra-generic clades. Column at right is locomotory habit (B, benthic; N-B, nekton-benthic). Key innovations include: 1, compound eyes (as figured for *Odaraia*); 2, arthropodized limbs (*Anomalocaris*); 3, (a) arthropodization and (b) biramy of trunk limbs (*Fuxianhuia*), and (c) arthrodization of trunk exoskeleton (*Nereocaris*); 4, specialization of the cephalic appendages into 'great-appendages' (*Yohoia*); 5, (a) division of trunk somites into distinct ventral sternites (*Misszhouia*) and (b) dorsal tergites with (c) paratergal folds (*Shankouia*); 6, (a) reduction in the number of trunk limb podomeres associated with (b) the acquisition of a rigid gnathobasic protopodite (*Alalcomenaeus*); 7, modification of the anterior (deutocerebral) appendages into antennae (*Olenoides*); and 8, the origin of mandibular mastification (*Locusta*).

euarthropods. Additionally, taxa bearing secondary (deutocerebral) antennae, including trilobitomorphs and mandibulates, resolved as a clade.

Preserved neural tissues in *Fuxianhuia protensa* Hou 1987b (Ma *et al*. 2012b) indicate unambiguously that the antennal neurons are derived from the deutocerebum, and are therefore homologous to the secondary antennae of trilobites and mandibulates (Scholtz and Edgecombe 2005). The specialized post-antennal appendages must therefore derive from the tritocerebral somite. Given the structural

and organizational similarities of the heads of fuxianhuiids, various Cambrian bivalved arthropods, and megacheirans, the 'great-appendages' of these taxa likely also derive from the tritocerebral somite, and are unlikely to be homologous to the chelicerae of chelicerates (see **Chapter 7**). This homology model was followed in the current data set, analysis of which resolves a paraphyletic assemblage of megacheirans as successive plesions of Euarthropoda.

If 'great-appendages' and chelicerae are not homologous then another model for the origin of chelicerae must be sought. The current analysis resolves chelierates as a derived clade within an assemblage of antennate arthropods, including trilobitomorphs and vicissicaudates; here a deutocerebral antennae resolves as a symplesiomophic feature of Euarthropoda. This topology suggests that chelicerae are derived from an antennate appendage. The recently described *Dibasterium* Briggs *et al*. 2012 and *Offacolus* Orr *et al*. 1998, both from the Silurian Herefordshire *Konservat-Lagerstätte*, possess elongate chelicerae, and while the exact number of podomeres cannot be precisely determined, in *Dibasterium* it is demonstrably more than the three found in other chelicerates. These taxa resolved as basal eucheliceratates (synziphosurids) and may therefore illustrate the plesiomorphic condition of the chelicerate chelicerae.

10.2.3. Trilobitomorphs as stem-chelicerates

The resolution of trilobitomorphs (including trilobites) and vicissicuadates in the chelicerate stem-lineage is contrary to many recent analyses which have instead considered these taxa stem-lineage mandibulates (Scholtz and Edgecombe 2006, Paterson *et al*. 2010, 2012, Ortega-Hernández *et al*. 2013). The close affinities of chelicerates and trilobites, and by extension trilobitomorphs, were recognized for a long time prior to the publication of Scholtz and Edgecombe (2005, 2006), with few exceptions (e.g. Boudreaux 1979). Scholtz and Edgecombe (2005) reviewed putative synapomorphies of a clade uniting trilobites and chelicerates, termed Arachnomorpha Heider 1913 or Arachnata Lauterbach 1980, including trilobation, lamellate gills, dorsal eyes and a widened head shield with genal spines. They concluded that such characters were either likely to be convergent, or were limited to selected members of this clade, instead preferring to unite trilobites with mandibulates based on the shared possession of secondary antennae. This was further supported by a phylogenetic analysis which resolved trilobites as part of the mandibulate stem-lineage (Scholtz and Edgecombe 2006).

Although it is true that some of the characters linking chelicerates and trilobites are absent from many included taxa, these absences are largely restricted to pycnogonids and arachnids. The arachnids have experienced numerous character reversals, such as a loss of lamellate gills, as the result of terrestrialization (Dunlop and Webster 1999), and pycnogonids have also undergone such major specialization, losing many characters indicative of euarthropod affinities. Other

marine chelicerates, such as xiphosurans and eurypterids, possess most putative synapomorphies of Arachnomorpha.

Besides secondary antennae, trilobites share few features with mandibulate arthropods, which lack lamellate gills, trilobation, or extensive paratergal folds (except in some derived lineages). Another character potentially linking mandibulates and trilobites, a cephalon possessing a pair of antennae and three post-oral segments, has been considered a putative symplesiomorphy of Euarthropoda (Lauterbach 1980, Walossek 1993, Vilpoux and Waloszek 2003, Dunlop 2005). The distribution of this character in the current data set indicates this character is a potential synapomorphy of Euarthropoda, however, it could not be unambiguously optimized due to the uncertain presence of this character in basal artiopodans.

10.2.3.1. Trilobite affinities of Agnostus *and the status of 'Orsten' crustaceans*

Although the agnostids have traditionally been regarded as trilobites (e.g. Fortey 1997), the discovery of juvenile specimens of *Agnostus pisiformis* Linnaeus 1758 with phosphatised limbs cast doubt on its affinities, with Müller and Walossek (1987) instead regarding it as a stem-lineage crustacean. This was mainly based on the large number of differences between agnostid and trilobite limbs, such as a lack of lamellate exopod setae in agnostids (*see* Bergström and Hou 2005 for a complete list of differences). This has resulted in agnostids being excluded from phylogenetic analyses of trilobitomorph taxa (e.g. Paterson *et al*. 2010, 2012), and likewise analyses that have included *Agnostus* have tended to exclude trilobites (e.g. Haug *et al*. 2010b). Many of the features listed by Bergström and Hou (2005) that apparently refute trilobite affinities for agnostids may be autapomorhies of agnostids, e.g. the possession of a simple prismatic exoskeleton (Wilmot 1990), or symplesiomorphies of Trilobita, e.g. a lack of ecdysial sutures.

A sister-taxon relationship between *Agnostus* and trilobites was recovered in prior analyses based on earlier versions of the current data set (e.g Legg *et al*. 2012b), and in some trees obtained in this work (*see* **Chapter 9**). Many of the characters thought to support trilobite affinities for *Agnostus*, e.g. genal spines, a raised axial region, a pygidium, etc., (Cotton and Fortey 2005), resolved as synapomorphies of more inclusive clades including trilobites in some of the analyses performed in the present study (**Chapter 9**). Meanwhile, features supporting the placement of *Agnostus* in the mandibulate stem-lineage, such as the possession of filamentous exopod setae, are also present in other 'Orsten' juveniles, including *Martinssonia* Müller and Walossek 1986, and *Skara* Müller 1983. The latter resolved as a crown-group crustacean, allied to copepods (Fig. 9.1H), which may indicate that the presence of multi-segmented exopods with inward pointing exopod setae is a juvenile characteristic (possibly for euarthropods as a whole) and therefore of little utility in resolving relationships. The position of *Agnostus* in the crustacean stem-lineage should therefore be treated with caution. The recovery of *Agnostus* as the sister-taxon to trilobites in some of analyses performed herein (**Chapter 9**) suggests

that the recovery of this taxon on the mandibulate stem-lineage may therefore be the result of long-branch attraction. The addition of additional trilobites, particularly eodiscids - which Cotton and Fortey (2005) considered the paraphyletic sister-taxon of agnostids – may help to resolve this issue.

10.2.4. Mandibulata vs. Paradoxopoda

A monophyletic Mandibulata was recovered in all analyses regardless of character weighting criteria. The current data set includes those characters that have been proposed as potential synapomorphies of a Chelicerata plus Myriapoda clade [= Paradoxopoda Mallet *et al*. 2004, or Myriochelata Pisani *et al*. 2004], including: the immigration of clusters of post-mitotic cells during neurogenesis (**ch. 435:1**), the segmental invaginations of neuroectoderm giving rise to ventral organs (**ch. 436:1**), and the exclusive generation of neurons in the central neuroectoderm (**ch. 438:1**) (Stollewerk and Chipman 2006, Mayer and Whitington 2009); as well as the expression patterns of leg gap genes *extradenticle* (**ch. 751:1**) and *homothorax* (**ch. 752:1**). These characters were either found to be convergently acquired in chelicerates and myriapods (**ch. 435:1**), symplesiomorphies of Euarthropoda (**ch. 436:1** and **ch. 438:1**), or poorly resolved due to insufficient taxon sampling (**ch. 751:1** and **ch. 752:1**). Further studies may find additional support for Paradoxopoda, however, it is not supported by the current data set. Rather the current pattern of character distribution corroborates analyses which indicate Paradoxopoda is a long-branch artefact (e.g. Rota-Stabelli *et al*. 2011).

10.2.5. Hexapods as derived crustaceans

Diverse molecular data sources support a close relationship between hexapods and crustaceans, either as sister-taxa (Friedrich and Tautz 1995), a result also favoured by some morphological evidence (Bitsch and Bitsch 2004, Giribet *et al*. 2005), or more typically with hexapods within a paraphyletic Crustacea. The latter position is supported by a number of independent lines of evidence including nuclear ribosomal genes (Mallet *et al*. 2004, von Reumont *et al*. 2009), mitochondrial genomes and gene order, nuclear protein-coding genes (Regier *et al*. 2010), and transcriptomics (Rota-Stabelli *et al*. 2011, von Reumont *et al*. 2012, Oakley *et al*. 2013). It has, however, remained elusive in morphological phylogenies apart from those based solely on neural characters (Strausfeld and Andrew 2011), which resolve malacostracans closer to hexapods than to branchiopods. The crustaceomorph phylogeny of Schram and Koenemann (2004), which resolved insects as the sister-taxon of branchiopods rather than malacostracans, is another notable exception – although they did not sample other extant euarthropods, such as myriapods, and their data set remains unpublished.

A paraphyletic Crustacea, with regards to hexapods, was recovered in this study when implied character weighting with a greater concavity (*k* = 2 and 3) was implemented. However a monophyletic Crustacea was recovered in analyses with a lesser concavity (*k* = 10). This suggests that hexapod affinities in morphological data sets are susceptible to the influence of homoplastic characters. The low GC support values associated with this clade (Fig. 9.1H) are also indicative of character conflict. This was explored by performing a number of perturbation tests on the data set.

In the first round of perturbation tests all fossil taxa were removed from the data set (DV-II). The topology produced (Fig. 10.2) included a monophyletic Crustacea with Hexapoda as its sister-taxon. This indicates that the inclusion of fossils is responsible for the paraphyly of crustaceans in the original analyses with a complete data set (DV-I). The monophyly of Crustacea may therefore be the result of long-branch attraction. This was confirmed by further perturbation of the data set (DV-IV and DV-V) which indicate there is an attraction between myriapods and hexapods.

A close relationship between myriapods and hexapods was commonly recovered in earlier phylogenetic analyses of arthropods, including those involving fossil taxa (e.g. Wheeler *et al*. 1993, Wills *et al*. 1995, 1998). Many of the characters previously considered to support close affinities of myriapods and hexapods, such as the presence of a limbless intercalary segment (**ch. 258:2**), uniramous appendages (**ch. 215:0**), pleural spiracles (**ch 628:1**), Malpighian tubules as ectodermal extensions of the hindgut (**ch. 578:1, 2**), and a tentorial endoskeleton (e.g. **ch. 323:1**), resolved in the current study either as symplesiomorphies of Mandibulata, or their absence resolved as synapomorphies of a monophyletic Crustacea (e.g. **ch. 215:1**). These characters are commonly associated with a terrestrial habit (Garwood and Edgecombe 2011), and are also found in other terrestrial arthropods, e.g. arachnids, and so may not be a reliable indicator of relationships. When they were removed from the data set (DV-IV), a paraphyletic Crustacea was recovered instead. Likewise, when myriapods were removed from the data set a paraphyletic Crustacea was also recovered. Further higher-level jackknifing of taxa and characters (DV-V) showed that other taxa and characters have little impact on the position of Hexapoda.

The perturbations of the data set performed above suggest that the position of hexapods and the monophyly of crustaceans are the result of long-branch attraction (between hexapods and myriapods), which is moderated by the inclusion of fossil taxa. In the current analyses the close affinities of euthycarcinoids and hexapods were consistently recovered (Figs. 9.1I, 9.4, 9.5), as was a close association between this clade and a Remipedia Yager 1981 plus *Tanazios* Siveter *et al*. 2007c, clade. Both *Tanazios* and euthycarcinoids possess characters associated with a terrestrial habit, e.g. an intercalary segment (present in both euthycarcinoids [Ortega-Hernández *et al*. 2010c], and *Tanazios* [Boxshall 2007]), and uniramous trunk appendages (present in euthycarcinoids only [Ortega-Hernández *et al*. 2010c]). They also possess unequivocal crustacean features, such as caudal furcae (in *Tanazios* [Siveter *et al*. 2007c]) and a fleshy labrum (in euthycarcinoids [Racheboeuf

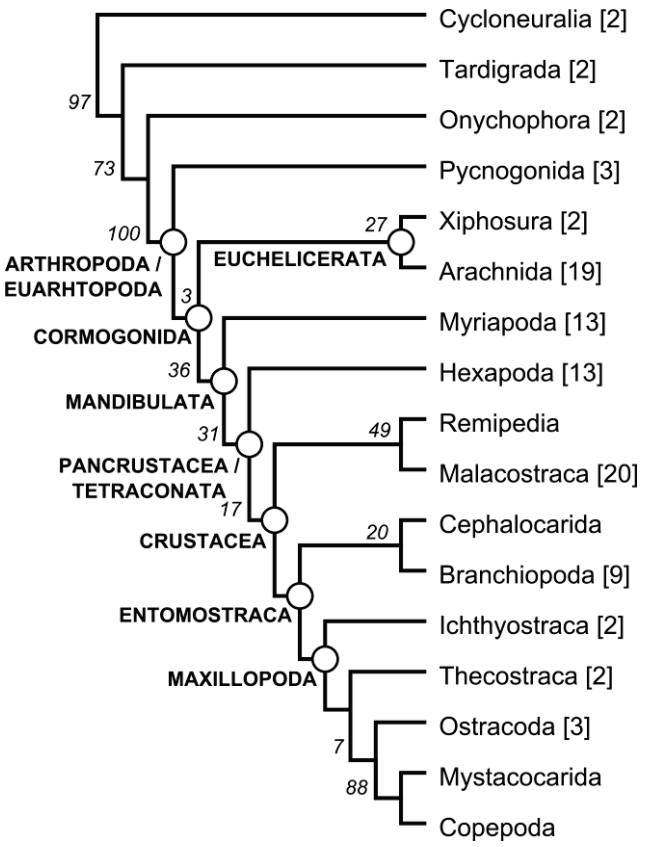


Fig. 10.2 | Relationships of major panarthropod taxa when fossils were removed from the data set. Numbers associated with nodes are selected GC support values, based on analyses using implied weighting (k = 3).

et al. 2008]). The position and effect of these taxa provides a clear example of the importance of fossils in demonstrating intermediate character combinations, and hence in mitigating long-branch attraction (Gauthier *et al*.1988, Bergsten 2005).

10.2.6. Impact of data inclusion

The results obtained herein are not heavily biased by the inclusion of characters with little or no fossilisation potential, such as embryonic development, behaviour, gene order and gene expression; when these characters were removed from the data set and morphology was analyzed in isolation (DS-VI), higher-level topologies remained stable, with variation restricted to smaller extant subclades. For example, cephalocarids grouped with remipedes and *Tanazios*, a grouping consistent with some molecular analyses (this grouping was named as Xenocarida by Regier *et al*. 2010), however most other relationships within Pancrustacea remain consistent with previous analyses.

10.3. Congruence with molecular hypotheses

When compared to other morphology-based phylogenetic analyses of arthropods, the current data set demonstrates a greater level of congruence with broadly sampled molecular phylogenies of arthropods (e.g. Regier *et al*. 2010), particularly in the placement of Hexapoda within a paraphyletic Crustacea, with remipedes their closest extant relatives (see above), as well as the resolution of Chelicerata in favour of Cormogonida. However, the internal relationships of the major euarthropod subclades, e.g. Euchelicerata and Entomostraca are more comparable to 'traditional' morphological results. For example, scorpions and opilions resolved as sister-taxa on a basal node of Arachnida Lamarck 1801 (Fig. 9.1G), consistent with other

morphological studies of arachnid relationships (Shultz 1990, 2007, Dunlop and Braddy 2001), but divergent from molecular analyses, such as Regier *et al*. (2010), which resolved scorpions as sister-taxon to Tetrapulmonata Shultz 1990, and opilions as sister-taxon to a clade including parasitiform mites and pseudoscorpions. This example may be due to the weak support for the conflicting nodes in the molecular phylogeny and/or a paucity of fossils near the time of cladogenesis. Many arachnid orders are well established in the Carboniferous with some showing remarkable similarities to extant taxa (Garwood *et al*. 2011). Terrestrialisation likely occurred in the late Cambrian or earliest Ordovician (Rota-Stabelli *et al*. 2013), but the fossil record prior to the Devonian is poor, with the earliest unequivocal arachnid recorded from the mid Silurian (Dunlop and Selden 2013), and hence it can contribute few informative character combinations to analyses.

11. Conclusions

Numerous empirical studies have demonstrated the utility of fossils in phylogenetic analyses. Evidence to the contrary is usually anecdotal. By sampling extinct morphologies that date close to cladogenesis times of major nodes, fossils can negate the influence of long-branch attraction (**Chapter 2**).

The arthropods have a long evolutionary history, with morphological and molecular evidence indicating that the five major subclades (subphyla) - pycnogonids, euchelicerates, myriapods, hexapods and crustaceans - originated and diversified before or during the early to mid Cambrian. Although relationships amongst these clades have been hotly debated, frequently recovered topologies are compatible with a single unrooted network, demonstrating that it is the position of the root and not the topology that is in dispute (Fig. 1.3).

To explore the potential impact of fossils on arthropod phylogeny, numerous fossils, particularly from lower and middle Palaeozoic Konservat-Lagerstätten, were coded into an extensive data set that included representatives from all major extant arthropod groups (**Chapters 3** and **4**).

An extensive study of potential upper stem-group arthropods from the middle Cambrian Burgess Shale Formation and coeval Stephen Formation in Yoho and Kootenay National Park in British Columbia, Canada, was undertaken. Specimens from the lowest members of the Burgess Shale Formation previously curated as *Branchiocaris* were systematically studied and assigned to two new genera and three new species: *Nereocaris exilis* Legg *et al*. 2012b, *N. briggsi* Legg and Caron in press, and *Loricicaris spinocaudatus* Legg and Caron in press (**Chapter 5**). *Nereocaris* Legg *et al*. 2012b demonstrates a number of features indicative of a nektonic mode of life, such as a laterally compressed carapace with a medial keel and an elongate abdomen tipped with a fluke-like telson.

A re-examination of the cosmopolitan Cambrian arthropod *Isoxys* Walcott 1890, recognized numerous similarities between this taxon and dinocaridids, particularly *Anomalocaris* Whiteaves 1892, such as elongate frontal appendages with perpendicularly orientated spines, and a posterior tagmata with tripartite, dorsally orientated lateral processes (**Chapter 6**). These shared features contribute to the resolution of bivalved Cambrian arthropods in a basal position within the upper euarthropod stem-lineage.

Further examination of Cambrian bivalved arthropods from the Walcott Quarry Shale Member of the Burgess Shale Formation revealed previously undescribed specialized post-antennal appendages in three taxa: *Canadaspis perfecta* (Walcott 1912), *Perspicaris dictynna* (Simonetta and Delle Cave 1975) and *Odaraia alata*

Walcott 1912 (**Chapter 7**). These taxa demonstrate a conserved pattern of head organization in upper stem-group euarthropods, including Cambrian bivalved arthropods, fuxianhuiids and megacheirans. The common cephalic organization of upper stem-group euarthropods, which are herein interpreted as possessing a pair of deutocerebral antennae and tritocerebral 'great-appendages', based on comparisons with specimens of *Fuxianhuia protensa* Hou 1987b with preserved neural tissues, reveals the plesiomorphic possession of a pair of deutocerebral antennae in crown-group arthropods [= Euarthropoda Lankester 1904] (Fig. 11.1).

Megacheirans are typically considered either stem-lineage chelicerates or upper stem-group euarthropods. An examination of two megacheirans, *Kootenichela deppi* Legg 2013, and *Worthenella cambria* Walcott 1911a (**Chapter 8**), from the 'thin' Stephen Formation and Burgess Shale Formation, respectively, favours a more basal positon for megacheirans, based, in part, on the possession of multipodomerous walking legs, a short cephalon with an anterior sclerite, and the possession of a pair of 'pre-great-appendage' antennae.

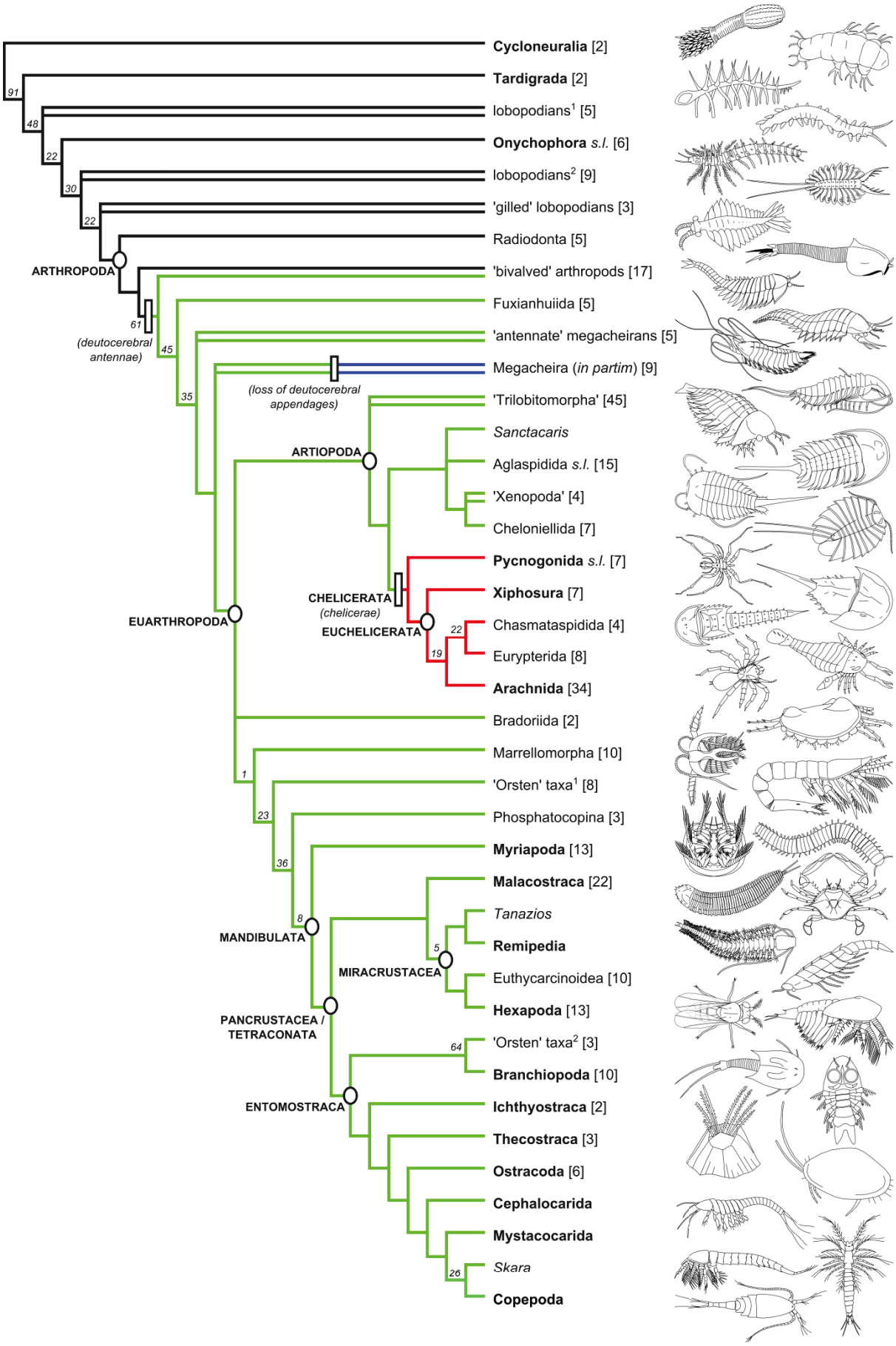
The revelation that deutocerebral antennae are part of the symplesiomorphic condition of Euathropoda belies hypotheses that have considered this feature a unique synapomorphy of trilobite-like taxa and mandibulates. This calls into question the purported phylogenetic position of trilobites and trilobite-like taxa, e.g. vicissicaudates, which are herein resolved as stem-group chelicerates. Such features as lamellar gills, trilobation, and the possession of genal spines optimize as synapomorphies of trilobite-like taxa and chelicerates, contrary to concerns that their absences in pycnogonids and arachnids render them phylogenetically unreliable.

The reassignment of antenna-bearing taxa to the chelicerate stem-lineage suggests an antennate origin for the chelicerae of chelicerates. Basal chelicerate taxa such as *Dibasterium* Briggs *et al*. 2012, possess elongate, almost antenniform chelicerae, which may demonstrate an intermediate morphology between antennae and 'typical' chelicerae.

Pertubation of the data set reveals that the inclusion of fossil taxa contributes to positioning pycnogonids as sister-taxon to euchelicerates in the present data set, bringing morphological trees into line with molecular trees. Fossils were also found to underpin the position of hexapods as most closely related to remipedes within a paraphyletic Crustacea. These hypotheses were anticipated by molecular phylogenetic analyses but until now had been absent from large scale morphological analyses of arthropods, which generally favoured crustacean monophyly.

A sister-taxon relationship between hexapods and a monophyletic Crustacea is a long-branch artefact caused by the attraction of hexapods and myriapods, drawn

Fig. 11.1 (*overleaf*) | Summary of relationships amongst major arthropod taxa as resolved in this study. A summary of results based on analyses using Implied weighting (*k* = 3). Paraphyletic taxa are indicated with a double line, groups containing extant taxa are bold and numbers in parentheses indicate the number of terminal taxa analyzed within each group. Colours on branches show the transformation between antennae and chelicerae. Numbers associated with nodes are selected GC support values.


Cycloneuralia [2]
Tardigrada [2]
lobopodians[1] [5]
Onychophora s.l. [6]
lobopodians[2] [9]
'gilled' lobopodians [3]
Radiodonta [5]
'bivalved' arthropods [17]
Fuxianhuiida [5]
'antennate' megacheirans [5]
Megacheira (in partim) [9]
'Trilobitomorpha' [45]
Sanctacaris
Aglaspidida s.l. [15]
'Xenopoda' [4]
Cheloniellida [7]
Pycnogonida s.l. [7]
Xiphosura [7]
Chasmataspidida [4]
Eurypterida [8]
Arachnida [34]
Bradoriida [2]
Marrellomorpha [10]
'Orsten' taxa[1] [8]
Phosphatocopina [3]
Myriapoda [13]
Malacostraca [22]
Tanazios
Remipedia
Euthycarcinoidea [10]
Hexapoda [13]
'Orsten' taxa[2] [3]
Branchiopoda [10]
Ichthyostraca [2]
Thecostraca [3]
Ostracoda [6]
Cephalocarida
Mystacocarida
Skara
Copepoda
ARTHROPODA
(deutocerebral antennae)
(loss of deutocerebral appendages)
ARTIOPODA
CHELICERATA
(chelicerae)
EUCHELICERATA
EUARTHROPODA
MANDIBULATA
MIRACRUSTACEA
PANCRUSTACEA / TETRACONATA
ENTOMOSTRACA
91
48
22
30
22
61
45
35
22
19
1
23
36
8
5
64
26

together by ‘terrestrial characters’ such as the possession of tracheae and uniramous appendages. This attraction is exacerbated by the paucity of stem-group (marine) representatives of these clades.

Some relationships within major clades are incongruent with molecular hypotheses and tend to favour ‘traditional’ morphological patterns of relationships. This is attributed to the paucity of ‘intermediate’ morphologies amongst extant orders, which is particularly acute in the Arachnida Lamarck 1801, which rapidly established morphological stasis in its constituent clades.

Increased congruence with molecular results when compared to an analysis of extant-only taxa provides clear evidence that the addition of fossils improves the results of morphological parsimony analysis, as intermediate morphologies break up long branches and provide a root for character polarization. Fossil taxa are therefore not only helpful but integral to large scale phylogenetic analyses of morphological data.

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Appendix 1. Taxa and coding

A1.1. Introduction

This appendix contains a complete list of all 311 taxa employed in the phylogenetic analyses (**Chapter 3**) and sources of coding. Extant taxa are given in bold. Sources of coding are not given for extant taxa, as these taxa are rarely comprehensively described in singular sources, with articles usually focussed on individual organ systems. Instead sources of character coding for these taxa are provided in the character descriptions of **Appendix 2** (and references therein). Unless stated otherwise the original descriptions of fossil taxa were used to code these taxa. In some instances other workers were consulted for assistance in coding including Allison Daley (AD), Derek Siveter (DS), Javier Ortega-Hernández (JOH), Jean Vannier (JV), Jakob Vinther (JKV), Martin Stein (MS), Peter Van Roy (PVR), Tom Hegna (TH), and Xiaoya Ma (XM). Additional references refer to museum collection, the abbreviations of which are present on page **xv**.

A1.2. Taxa and coding

Taxa	Source of coding
Aaveqaspis inesoni Peel and Stein 2009	-----
Acanthomeridion serratum Hou *et al*. 1989	Hou *et al*. 1989, Hou and Bergström 1997
Acerentulus sp. (Berlese 1908)	-----
Actaeus armatus Simonetta 1970	Whittington 1981, NMNH
Aglaspella granulifera Raasch 1939	Hesselbo 1992, JOH
Aglaspis spinifer Raasch 1939	Briggs *et al*. 1979, Hesselbo 1992
Agnostus pisiformis Linnaeus 1758	Müller and Walossek 1987
Alalcomenaeus cambricus Simonetta 1970	Briggs and Collins 1999, ROM
Alanops magnificus Racheboeuf *et al*. 2002	-----
Amblyomma americanum Linnaeus 1758	-----
Ameticos scolos Garwood *et al*. 2011	-----
Ammothella sp. (Verrill 1900)	-----
Amphionides reynaudii (Milne-Edwards 1833)	-----

Amplectobelua symbrachiata Hou *et al*. 1995	-----
Anaspides sp. Thomson 1894	-----
Anomalocaris canadensis Whiteaves 1892	AD
Antennacanthopodia gracilis Ou and Shu *in* Ou *et al*. 2011	-----
Anthracomartus hindi Pocock 1911	Garwood and Dunlop 2011
Apankura machu Vaccari *et al*. 2004	-----
Aphonopelma sp. (Pocock 1911)	-----
Archegozetes longisetosus Aoki 1965	-----
Argulus sp. (Müller 1785)	-----
Artemia salina (Linnaeus 1758)	-----
Arthrogyrinus platyurus Wilson and Anderson 2001	-----
Attercopus fimbriungius (Shear *et al*. 1987)	Shear *et al*. 1987, Selden *et al*. 1991, 2008
Australaglaspis stonyensis Ortega-Hernández *et al*. 2010a	-----
Australimicola spriggi Paterson *et al*. 2012	-----
Aysheaia pedunculata Walcott 1911a	Whittington 1978, NMNH, ROM
Balanus balanus (Linnaeus 1758)	-----
Baltoeurypterus tetragonophthalmus (Fischer 1839)	Selden 1981, NHM, PMU
Bathynella sp. (Vejdovsky 1882)	-----
Beckwithia typa Resser 1931	Hesselbo 1989, JOH
Branchinella sp. Sayce 1903	-----
Branchiocaris pretiosa (Resser 1929)	Briggs 1976, NMNH, ROM
Bredocaris admirabilis Müller 1983	-----
Buenaspis forteyi Budd 1999b	-----
Caddo agilis Banks 1892	-----
Caenorhabditis elegans Maupas 1900	-----
Calanus sp. (Leach 1819)	-----
Callibaetis sp. (Eaton 1881)	-----
Cambropachycope clarksoni Walossek and Müller 1990	Haug *et al*. 2009
Campanamuta mantonae Budd 2011	-----
Campodea Westwood 1842	-----
Canadaspis laevigata Hou and Bergström 1991	Hou and Bergström 1997
Canadaspis perfecta (Walcott 1912)	Briggs 1978, NMNH (**Chapter 7**), ROM
Carcinoscorpius rotundicaudata (Latreille 1802)	-----
Cardiodictyon catenulum Hou *et al*. 1991	Hou *et al*. 1991, Ramsköld and Chen 1998
Centruroides sp. (Marx 1890)	-----
Chasmataspis laurencii Caster and Brooks 1956	Dunlop *et al*. 2004
Cheloniellon calmani Broili 1932	Stürmer and Bergström 1978, Moore *et al*. 2008
Chengjiangocaris kunmingensis Yang *et al*. 2013	-----
Chinese aglaspidid (Fortey and Theron 1994)	JOH, DS
Chlupacaris dubia Van Roy 2006a	-----
Chraspedops modesta Raasch 1939	Hesselbo 1992, JOH
Cindarella eucalla Chen *et al*. *in* Chen *et al*. 1996	Ramsköld *et al*. 1997
Cinerocaris magnifica Briggs *et al*. 2004	Briggs *et al*. 2004, OUMNH (SP)
Collins monster (Collins 1986)	Collins 1986, XM
Colossendeis sp. (Jarzinsky 1870)	-----
Colymbosathon ecplecticos Siveter *et al*. 2003a	Siveter *et al*. 2003a, OUMNH (SP)
Compsoscorpius buthiformis (Pocock 1911)	Legg *et al*. 2012a
Craterostigmus tasmanianus Pocock 1902b	-----
Cryptocellus Westwood 1874	-----
Cupiennius salei (Keyserling 1877)	-----
Cyclestheria hislopi (Baird 1859)	-----

Cyclopites vulgaris Raasch 1939	Hesselbo 1992, JOH
Cypridopsis sp. (Brady 1867)	-----
Daphnia sp. (Müller 1785)	-----
Derocheilocaris typicus Pennak and Zinn 1943	-----
Diania cactiformis Liu *et al*. 2011	Ma *et al*. in press
Diastylis sp. (Say 1818)	-----
Dibasterium durgae Briggs *et al*. 2012	Briggs *et al*. 2012, OUMNH (SP)
Dilta sp. (Strand 1911)	-----
Diploaspis casteri Størmer 1972	Dunlop *et al*. 2001
Dollocaris ingens van Straelen 1923	RG, JV
Drosophila sp. (Fallén 1823)	-----
Duslia insignis Jahn 1893	Chlupáč 1988
Ecnomocaris spinosa Conway Morris and Robison 1988	-----
Emeraldella brocki Walcott 1912	Stein and Selden 2012, NMNH, ROM
Emeraldella brutoni Stein *et al*. 2011	-----
Emucaris fava Paterson *et al*. 2010	-----
Endeis sp. (Philippi 1843)	-----
Eophrynus prestvicii Buckland 1837	Garwood *et al*. 2009, Dunlop and Garwood in press
Eoredlichia intermedia (Lu 1940)	Hou *et al*. 2008
Eoscorpius carbonarius (Meek and Worthen 1868)	FMNH
Equitius sp. (Simon 1880)	-----
Eremocosta sp. (Roewer 1934)	-----
Euperipatoides kanangrensis Reid 1966	-----
Euthycarcinus kessleri Handlirsch 1914	TH
Flagellopantopus blocki Poschmann and Dunlop 2006	-----
Flobertia kochi Hesselbo 1992	Hesselbo 1992, JOH
Fortiforceps foliosa Hou and Bergström 1997	Hou and Bergström 1997, XM (**Chapter 7**)
Furca bohemica Fritsch 1908	Rak *et al*. in press
Fuxianhuia protensa Hou 1987b	Bergström *et al*. 2008, Ma *et al*. 2012b
Gilboarachne griersoni Shear 1987	-----
Glomeris marginata (Villers 1789)	-----
Glypharthrus thomasi (Walter 1924)	Hesselbo 1992, JOH
Goticaris longispinosa Walossek and Müller 1990	Haug *et al*. 2009
Guangweicaris spinatus Luo *et al*. *in* Luo *et al*. 2007	Luo *et al*. 2007, Yang *et al*. 2008
Hadranax augustus Budd and Peel 1998	-----
Haikoucaris ercaiensis Chen *et al*. 2004	-----
Haliestes dasos Siveter *et al*. 2004	Siveter *et al*. 2004, OUMNH (SP)
Halitherses grimaldii Giribet and Dunlop 2005	-----
Hallucigenia fortis Hou and Bergström 1995	Hou and Bergström 1995, Ma *et al*. 2012a
Hanseniella sp. (Bagnall 1913)	-----
Helenodora opinata Thompson and Jones 1980	-----
Helmetia expansa Walcott 1918	NMNH
Henningsmoenicaris scutula (Walossek and Müller 1990)	Haug *et al*. 2010a
Hesslandona angustata Maas *et al*. 2003	-----
Heterocrania rhyniensis (Hirst and Maulik 1926)	Anderson and Trewin 2003
Heterometrus sp. (Ehrenberg 1828)	-----
Homarus gammarus (Linnaeus 1758)	-----
Houghtonites gracilis (Walcott 1912)	Raymond 1931
Hurdia victoria Walcott 1912	Daley *et al*. 2009, in press
Hutchinsoniella macracantha Sanders 1955	-----
Hypsibius dujardini (Doyère 1840)	-----

Idiogaryops sp. (Hoff 1963)	-----
Isoxys acutangulus Walcott 1908	García-Bellido *et al*. 2009b, ROM (**Chapter 6**)
Isoxys auritus Jiang 1982	JV (**Chapter 6**)
Isoxys cuvirostratus Vannier and Chen 2000	Vannier and Chen 2000, Fu *et al*. 2011 (**Chapter 6**)
Isoxys volucris Williams *et al*. 1996	Stein *et al*. 2010, MS
Jianfengia multisegmentalis Hou 1987a	Hou *et al*. 2004b, Haug *et al*. 2012c, XM
Jianshanopodia decora Liu *et al*. 2006	-----
Jugatacaris agilis Fu and Zhang 2011	-----
Kalbarria brimmellae McNamara and Trewin 1993	-----
Kangacaris shui Zhang *et al*. 2012b	-----
Kangacaris zhangi Paterson *et al*. 2010	-----
Kerygmachela kierkegaardi Budd 1993	Budd 1998, JKV
Kiisortoqia soperi Stein 2010	-----
Klausmuelleria salopensis Siveter *et al*. 2003	Siveter *et al*. 2001, 2003
Kodymirus vagans Chlupáč and Havlíček 1965	Chlupáč and Havlíček 1965, JOH
Kootenichela deppi Legg 2013	Legg 2013 (**Chapter 8**)
Kottixerxes gloriosus Schram 1971	-----
Kuamaia lata Hou 1987b	Hou and Bergström 1997
Kumaia muricata Hou and Bergström 1997	-----
Kunmingella douvillei (Mansuy 1912)	Hou *et al*. 2010
Kunyangella cheni Hou 1965	Hou *et al*. 2010
Kwanyinaspis maotianshanensis Zhang and Shu 2005	Zhang and Shu 2005, JOH
Leanchoilia illecebrosa Hou 1987a	Liu *et al*. 2007
Leanchoilia persephone Simonetta 1970	García-Bellido and Collins 2007
Leanchoilia superlata Walcott 1912	García-Bellido and Collins 2007, Haug *et al*. 2012a
Lepidocaris rhyniensis Scourfield 1926	Scourfield 1926, 1940
Leptodora kindti (Focke 1844)	-----
Liangwangshania biloba Chen 2005	-----
Limnadia lenticularis (Linnaeus 1761)	-----
Limnadopsis sp. (Spencer and Hall 1896)	-----
Limulus polyphemus Linnaeus 1758	-----
Liphistius sp. (Schiødte 1849)	-----
Lithobius sp. (Leach 1814)	-----
Liwia plana (Lendzion 1975)	Dzik and Lenzion 1988
Locusta migratoria (Linnaeus 1758)	-----
Loganamaraspis dunlopi Tetlie and Braddy 2004	-----
Lophogaster typicus Sars 1857	-----
Loricicaris spinocaudatus Legg and Caron in press	Legg and Caron in press (**Chapter 5**)
Luohuilinella rarus Zhang *et al*. 2012a	-----
Luolishania longicruris Hou and Chen 1989	Ma *et al*. 2009
Lynceus sp. (Müller 1776)	-----
Machiloides sp. (Silvestri 1904)	-----
Macrogyion cronos Garwood *et al*. 2011	-----
Manawa tryphena Hornibrook 1949	-----
Marrella splendens Walcott 1912	García-Bellido and Collins 2006, ROM
Martinssonia elongata Müller and Walossek 1986	Haug *et al*. 2010b
Mastigoproctus sp. (Pocock 1894)	-----
Mecistocephalus sp (Newport 1843)	-----
Megadictyon haikouensis Luo and Hu *in* Luo *et al*. 1999	-----
Megalograptus ohioensis Caster and Kjellesvig-Waering 1955	-----

Meganyctiphanes norvegica (Sars 1857)	-----
Mesotarbus peteri Dunlop and Horrocks 1997	-----
Metajapyx sp. (Silvestri 1933)	-----
Microdictyon sinicum Chen *et al*. 1989	Chen *et al*. 1995c, Ramsköld and Chen 1998
Mictocaris halope Bowman and Iliffe 1985	-----
Milnesium tardigradum Doyère 1840	-----
Mimetaster hexagonalis (Gürich 1931)	Kühl and Rust 2010
Misszhouia longicaudata (Zhang and Hou 1985)	Chen *et al.* 1997, Zhang *et al*. 2007
Mixopterus kiaeri Størmer 1934	-----
Molaria spinifera Walcott 1912	Whittington 1981, Stein *et al*. 2011, ROM
Mollisonia sinica Zhang *et al*. 2002	-----
Mollisonia symmetrica Walcott 1912	Walcott 1912, Simonetta and Delle Cave 1975, ROM
Moroccan Cheloniellid (Van Roy 2006b)	Van Roy 2006b, Van Roy *et al*. 2010, PVR
Moroccan marrellomorph (Van Roy 2006b)	Van Roy 2006b, Van Roy *et al*. 2010, PVR
Moroccan skaniid (Van Roy *et al*. 2010)	Van Roy *et al*. 2010, PVR
Moselopterus ancylotelson Størmer 1974	-----
Musacaris gerdgeyeri Haug *et al*. 2010b	-----
Mysis sp. (Latrielle 1802)	-----
Naraoia bertensis Caron *et al*. 2004	-----
Naraoia compacta Walcott 1912	Whittington 1977
Naraoia spinifer Walcott 1931	Whittington 1977
Naraoia spinosa Zhang and Hou 1985	Zhang *et al*. 2007
Naraoia taijiangensis Peng *et al*. 2012	-----
Narceus americanus (Palisot de Beauvois, 1817)	-----
Nasunaris flata Siveter *et al*. 2010	Siveter *et al*. 2010, OUMNH (SP)
Nebalia sp. (Leach 1814)	-----
Neostrabops martini Caster and Macke 1952	-----
Nereocaris briggsi Legg and Caron in press	Legg and Caron in press (**Chapter 5**)
Nereocaris exilis Legg *et al*. 2012b	Legg *et al*. 2012b (**Chapter 5**)
Nipponopsalis abei (Sato and Suzuki 1939)	-----
Nymphatelina gravida Siveter *et al*. 2007b	Siveter *et al*. 2007b, OUMNH (SP)
Octoberaspis ushakovi Dunlop 2002	-----
Odaraia alata Walcott 1912	Briggs 1981, NMNH (**Chapter 7**)
Oelandocaris oelandica Müller 1983	Stein *et al*. 2005, 2008
Oestokerkus megacholix Edgecombe *et al*. 2011	-----
Offacolus kingi Orr *et al*. 2000	Orr *et al*. 2000, Sutton *et al*. 2002, OUMNH (SP)
Olenoides serratus (Rominger 1887)	Whittington 1980
Onychodictyon ferox Hou *et al*. 1991	Ou *et al*. 2012
Onychopterella augusti Braddy *et al*. 1995	Braddy *et al*. 1995, 1999
Opabinia regalis Walcott 1912	Whittington 1975, Budd 1996, Budd and Daley 2012
Opilioacarus sp. (With 1902)	-----
Orchestia sp. (Leach 1814)	-----
Pachymerium sp. (Koch 1847)	-----
Palaeocharinus sp. (Hirst 1923)	Fayers *et al*. 2005
Palaeoisopus problematicus Broili 1928	Bergström *et al*. 1980
Palaeopantopus maucheri Broili 1929	Bergström *et al*. 1980
Palaeophonus nuncius Thorell and Lindström 1884	PMU

Pambdelurion whittingtoni Budd 1997	Budd 1997, JKV
Pandalus sp. (Leach 1814)	-----
Panlongia spinosa Liu *et al*. 2006	-----
Panlongia tetranodusa Liu *et al*. 2006	-----
Paraduslia tailmaae Dunlop 2002	-----
Paranebalia longipes (Willemoes-Suhm 1875)	-----
Parapeytoia yunnanensis Hou *et al*. 1995	DS
Parastylonurus ornatus (Laurie 1892)	Waterston 1979
Paucipodia inermis Chen *et al*. 1995b	Hou *et al*. 2004c
Pauropus longiramus Zhang and Chen 1988	-----
Pectocaris euryptelata (Sun and Hou 1988)	Hou *et al*. 2004b
Pectocaris spatiosa Hou 1999	-----
Penaeus sp. (Fabricius 1798)	-----
Peripatus juliformis Guilding 1826	-----
Periplaneta sp. (Linnaeus 1758)	-----
Perspicaris dictynna Simonetta and Delle Cave 1975	Briggs 1977, NMNH (**Chapter 7**), ROM
Perspicaris recondita Briggs 1977	Briggs 1977, NMNH, ROM
Peytoia nathorsti Walcott 1911b	Collins 1996, Daley and Bergström 2012
Phrynus sp. (Lamarck 1801)	-----
Phytophilaspis pergamena Ivantov 1999	-----
Plesiosiro madeleyi Pocock 1911	Dunlop 1999
Polyxenus fasciculatus Say 1821	-----
Porcellio sp. (Latreille 1804)	-----
Priapulus caudatus Lamarck 1816	-----
Primicaris larvaformis Zhang *et al*. 2003	-----
Prokoenenia sp. (Börner 1901)	-----
Proscorpius osborni (Whitfield 1885)	Dunlop *et al*. 2008b
Proteroiulus fuscus (Am Stein 1857)	-----
Protocaris marshi Walcott 1884	NMNH
Pseudoarthron whittingtoni Selden and White 1984	-----
Pterygotus anglicus Agassiz 1844	BGS
Pulmonoscorpius kirktonensis Jeram 1994	-----
Pygmaclypeatus daziensis Zhang *et al*. 2000	Zhang *et al*. 2000, Xu 2004
Quasimodaspis brentsae Waggoner 2003	-----
Railietiella sp. (Sambon 1910)	-----
Rehbachiella kinnekullensis Müller 1983	Walossek 1993
Retifacies abnormalis Hou *et al*. 1989	Hou and Bergström 1997
Rhamphoverritor reduncus Briggs *et al*. 2005	-----
Rhenopterus macrotunerculatus Størmer 1974	-----
Rhombicalvaria acantha Hou 1987b	-----
Sanctacaris uncata Briggs and Collins 1988	Briggs and Collins 1988, ROM
Sandtorpia vestrogothiensis Haug *et al*. 2010a	-----
Saperion glumaceum Hou *et al*. 1991	Hou and Bergström 1997
Sarotrocercus oblita Whittington 1981	Whittington 1981, Haug *et al*. 2011a, ROM
Schinderhannes bartelsi Kühl *et al*. 2009	-----
Schramixerxes geram (Schram and Rolfe 1982)	Racheboeuf *et al*. 2008
Scolopendra sp. (Linnaeus 1758)	-----
Scutigera sp. (Linnaeus 1758)	-----
Scutigerella immaculata (Newport 1844)	-----
Semibalanus balanoides (Linnaeus 1758)	-----
Shankouia zhenghi Waloszek *et al*. 2005	-----
Siberion lenaicus Dzik 2011	-----
Sidneyia inexpectans Walcott 1911c	Bruton 1981, NMNH, ROM, MS

Sinoburius lunaris Hou *et al*. 1991	Hou and Bergström 1997
Siriocaris trollae Lagebro *et al*. 2009	-----
Siro sp. (Latreille 1796)	-----
Skania fragilis Walcott 1931	NMNH, ROM
Skania sundbergi Lin *in* Lin *et al*. 2006	Lin *et al*. 2006
Skara anulata Müller 1983	Müller and Walossek 1985, Haug *et al*. 2011b
Skioldia aldna Hou and Bergström 1997	-----
Sminthurinus sp. (Börner 1901)	-----
Smithixerxes juliarum Schram and Rolfe 1982	-----
Soomaspis splendida Fortey and Theron 1994	-----
Sottyxerxes multiplex Schram and Rolfe 1982	Racheboeuf *et al*. 2008
Spelaeogriphus lepidops Gordon 1957	-----
Speleonectes sp. (Yager 1981)	-----
Squamacula buckorum Paterson *et al*. 2012	-----
Squamacula clypeata Hou and Bergström 1997	-----
Squilla mantis (Linnaeus 1758)	-----
Stenochrus sp. (Chamberlin 1922)	-----
Stenopus sp. (Latreille 1819)	-----
Succinipatopsis balticus Poinar 2000	-----
Synaustrus brookvalensis Reik 1964	Edgecombe and Morgan 1999
Tanaissus sp. (Norman and Scott 1906)	-----
Tanazios dokeron Siveter *et al*. 2007b	Siveter *et al*. 2007b, Boxshall 2007, OUMNH (SP)
Tanglangia caudatus Luo and Hu *in* Luo *et al*. 1999	Luo *et al*. 1999, Hou *et al*. 2004b
Tarricoia arrusensis Hammann *et al*. 1990	-----
Tegopelte gigas Simonetta and Delle Cave 1975	Whittington 1985, Ramsköld et al. 1996, Minter *et al*. 2012
Tertiapatus dominicanus Poinar 2000	-----
Thelxiope palaeothalassia Simonetta and Delle Cave 1975	-----
Thermobia domestica Packard 1873	-----
Thermosbaena mirabilis Monod 1924	-----
Tomocerus sp. (Nicolet 1842)	-----
Tremaglaspis unite Fortey and Rushton 2003	Fortey and Rushton 2003, 2009
Tricholepidion gertschi Wygodzinsky 1961	-----
Triops cancriformis (Bosc 1801)	-----
Triopus draboviensis Barrande 1872	Ortega-Hernández *et al*. 2010b
Uarthrus instabilis Raasch 1939	Hesselbo 1992, JOH
Urokodia aequalis Hou *et al*. 1989	Hou *et al*. 1989, 2004b
Vachonisia rogeri Lehmann 1955	Kühl *et al*. 2008
Vargula hilgendorfii (Müller 1890)	-----
Vestrogothia spinata Müller 1964	-----
Weinbergina opitzi Richter and Richter 1929	Moore *et al*. 2005
Worthenella cambrica Walcott 1911a	Legg 2013 (**Chapter 8**)
Xandarella spectaculum Hou *et al*. 1991	Hou and Bergström 1997
Xenusion auerwaldae Pompeckj 1927	Dzik and Krumbiegel 1989
Xylokorys chledophilia Siveter *et al*. 2007a	Siveter *et al*. 2007a, OUMNH (SP)
Yicaris dianensis Zhang *et al*. 2007	-----
Yohoia tenuis Walcott 1912	Whittington 1974, Haug *et al*. 2012c, ROM

Appendix 2. Phylogenetic character list

A2.1. Introduction

Below is a complete list of characters (*n* = 753), with descriptions, utilized in this study. Bold numbers in square brackets refer to previous data sets that have included the same characters; the first letter represents the first letter of the first author's surname, followed by the year of publication, and then the character number in the analysis. In the case of Legg *et al*. (2012b) and Legg *et al*. (2013), the first 580 characters are identical, therefore only a single reference **[L2012]** is used for these characters, and **[L2013]** is restricted to characters new to that study.

The following data sets have utilized characters employed in the current data set:

[B2002] Budd, G.E. 2002. A palaeontological solution to the arthropod head problem. *Nature*, **417**, 271-275.

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A2.2. Character list

Phylogenetic characters are divided into four distinct types for ease of reference: ***morphology*** (*n* = 702), ***development*** (*n* = 29), ***behaviour*** (*n* = 6), and, ***gene order and gene expression*** (*n* = 16). Descriptions are provided for selected characters introduced by Legg *et al*. (2012b, 2013), otherwise the reader is referred to the original character descriptions.

A2.2.1. Morphology

1. *Trunk annuli: (0) absent, (1) present*. **[R2011:18; L2012:1]**

2. *Tegumental annulations: (0) absent, (1) present*. **[R2011:19; L2012:2]**

3. *Segmented body: (0) absent, (1) present*. **[M2009:19; L2013:581]**

4. *Two long tagmata expressed in the appendages (anterior batch of appendages longer than posterior batch): (0) absent, (1) present*. **[M2009:27; L2013:582]**

5. *Isolated sclerites/nodes: (0) absent, (1) present*. **[M2009:28; L2013:583]**

6. *More than two plates or nodes on each trunk segment: (0) absent, (1) present*. **[L2011:32; L2013:584]**

7. *Spine-shaped sclerites: (0) absent, (1) present*. **[M2009:29; L2013:585]**

8. *Papillae/setae on trunk annuli: (0) absent, (1) present*. **[M2009:32; L2013:586]**

9. *Number of annuli per segment: (0) few (up to 6-7 per segment), long, continuous around trunk, (1) many (9-25), short, weak or absent laterally.* **[R1998:6; L2013:587]**

10. *Segments progressively shorten posteriorly: (0) absent, (1) present*. **[R1998:8; L2013:588]**

11. *Prominent, unsclerotised nodes on trunk segments: (0) absent, (1) present*. A number of lobopodians possess enlarged, unsclerotized nodes on their dorsum. These nodes are typically associated with a pair of appendages. Nodes may either be paired, as in *Xenusion*, or in a tightly packed row of four, as in *Hadranax*. **[L2013:589]**

12. *Sclerotization of cuticle into hard, articulated tergal exoskeleton: (0) absent, (1) present*. **[R2011:20; L2012:3]**

13. *Cuticle mineralization: (0) absent, (1) present, calcite, (2) present, calcium phosphate*. **[R2011:21; L2012:4]**

14. *Tendon cells with tonofilaments: (0) absent, (1) present*. **[R2011:23; L2012:5]**

15. *Dorsal longitudinal ecdysial suture with forking on head: (0) absent, (1) present*. **[R2011: 24; L2012:6]**

16. *Transverse and antennocellar sutures on head shield: (0) absent, (1) present*. **[R2011:25; L2012:7]**

17. *Resilin protein: (0) absent, (1) present*. **[R2011:26; L2012:8]**

18. *Moulting glands: (0) absent, (1) present*. **[R2011:27; L2012:9]**

19. *Distinct head: (0) absent, (1) present*. **[M2009:25; L2012:10]**

20. *Anterior margin of cephalon notched: (0) absent, (1) present*. **[O2013:28; L2012:11]**

21. *Anterior sclerite associated with ocular segment: (0) absent, (1) present*. **[D2009:14; L2012:12]**

22. *Frontal organs on prehypostomal sclerite: (0) absent, (1) present*. **[P2010:11; L2012:13]**

23. *Tergal covering of all head segments fused as cephalic shield: (0) absent, (1) present*. **[B2002:3; R2011:83; L2012:14]**

24. *Subtrapezoidal cephalic shield restricted to anterior-most head segments: (0) absent, (1) present*. **[L2012:15;** *cf*. **O2013:77]**

25. *Elevated marginal rim: (0) absent, (1) present*. **[O2013:33; L2012:16]**

26. *Anterior glossate process: (0) absent, (1) present*. An anterior 'tongue-shaped' process is present on the prosoma of some Carboniferous scorpions. **[L2012:17]**

27. *Anterior end of prosoma with medial marginal or submarginal pointed process: (0) absent, (1) present*. **[S2007:3; L2012:18]**

28. *Anterolateral spines: (0) absent, (1) present*. **[L2012:19; R2013:2]**

29. *Anterior cephalic spines elongate: (0) absent, (1) present.* This character is only applicable to taxa with anterolateral cephalic spines (**ch. 28**), i.e. marrellids. Elongate anterior cephalic spines are present in *Mimetaster* (Kühl and Rust 2010) and an undescribed marrellomorph from the Ordovician of Morocco (Van Roy 2006b, Van Roy *et al*. 2010). **[L2013:593]**

30. *Mediolateral spines: (0) absent, (1) present*. **[L2012:20; R2013:3]**

31. *Secondary spines on cephalic shield: (0) absent, (1) present*. **[L2012:21; R2013:5]**

32. *Free head shield: (0) absent, (1) present*. **[L2012:22; O2013:25]**

33. *Bivalved carapace: (0) absent, (1) present*. **[B2002:4; L2012:23]**

34. *Antero- and posterodorsal spines on carapace: (0) absent, (1) present*. This character refers to the elongate carapace spines of *Isoxys* (**Chapter 6**). **[L2013:590]**

35. *Carapace divided into five distinct plates: (0) absent, (1) present*. The carapace of *Balanus*, *Semibalanus* and adult specimens of the Silurian *Rhamphoverritor* is divided into five distinct plates. **[L2013:591]**

36. *Rostrum: (0) absent, (1) present*. **[R2001:10; L2013:592]**

37. *Head capsule: (0) absent, (1) present*. The cephalic shield of fuxianhuiids contains extensive ventro-lateral outgrowths that form a capsule (*sensu* Bergström *et al*. 2008) around the anterior trunk segments. **[L2012:24]**

38. *Cephalon composed of a small anterior plate and a posterior shield: (0) absent, (1) present*. The cephalon of euthycarcinoids is divided into two distinct plates, a small, circular anterior plate and a posteriorly expansive shield. The anterior plate encompasses the antennal (deutocerebral) somite and so is not considered the same as the anterior sclerite (*sensu* Budd 2008) (**ch. 21**). **[L2013:594]**

39. *Lateral cephalic furrow: (0) absent, (1) present*. The cephalon of branchiopods possesses a lateral furrow, giving the impression of possessing two distinct segments. **[L2013:595]**

40. C*ephalic doublure: (0) absent, (1) present*. **[L2012:25; O2013: 27]**

41. *Width of doublure: (0) narrow to moderately wide, (1) wide, (2) covers entire ventral side of cephalon.* Although described as state 2 in previous work (Bruton, 1981), coding for *Sidneyia* follows Stein (2012) in interpreting specimens that apparently have a long doublure as being preserved inclined

to bedding, such that the apparent margin of the doublure is actually the posterior margin of the head shield. **[L2012:26; O2013:78].**

42. *Marginal rim ornamented: (0) absent, (1) present.* **[O2013:34; L2013:596]**

43. *Notches on margin of cephalic shield, possibly indicative of original segmentation: (0) absent, (1) present*. The cephalon of mollisonids, particularly *Urokodia* and *Mollisonia symmetrica*, possesses distinct notches of spines along the lateral margins. **[L2013:597]**

44. *Cephalic tagmosis (number of limb-bearing segments): (0) two limb-bearing segments, (1) three limb-bearing segments, (2) four limb-bearing segments, (3) five limb-bearing segments, (4) cephalosoma with four post-pedipalpal locomotory limbs: (5) six limb-bearing segments: (6) seven limb-bearing segments.***[L2012:27;** *cf.* **R2011:84]**

45. *Vaulted cephalic shield: (0) absent, (1) present*. The cephalic shield of some aglaspidid arthropods is highly vaulted, i.e. anteroposteriorly short but dorsoventrally elongate (Van Roy 2006a). **[L2013:600]**

46. *Transverse furrows on prosomal carapace corresponding to margins of segmental tergites: (0) absent, (1) present*. **[R2011:86; L2012:28]**

47. *Cephalic shield with distinct propeltidium: (0) absent, (1) present*. **[S2007:6; L2012:29]**

48. *Mesopeltidium divided medially by a shallow sulcus: (0) absent, (1) present*. The mesopeltidium of scorpions is divided into two lateral lobes by a medial sulcus. **[L2012:30]**

49. *Sejugal furrow: (0) absent, (1) present*. **[S2007:7; L2012:31]**

50. *Cephalic furrows: (0) absent, (1) present*. **[O2013:38; L2013:599]**

51. *Cardiac lobe: (0) absent, (1) present*. **[R2011:87; L2012:32]**

52. *Glabellar furrows or lobes: (0) absent, (1) present*. **[L2012:33; O2013:35]**

53. *Cephalic kinesis: (0) absent, (1) present*. **[R2011:88; L2012:34]**

54. *Carapace adductor: (0) absent, (1) present*. **[R2011:89; L2012:35]**

55. *Carapace growth lines: (0) absent, (1) present*. **[R2011:90; L2012:36]**

56. *Flattened head capsule, with head bent posterior to the clypeus, accommodating antennae at anterior margin of head: (0) absent, (1) present*. **[R2011:91; L2012:37]**

57. *Clypeofrontal sulcus (epistomal suture): (0) absent, (1) present*. **[R2011:92; L2012:38]**

58. *Genal spines (posterior corners of head shield extended): (0) absent, (1) present, short (2) present (as long as trunk)*. **[L2012: 39;** *cf*. **R2011:93]**

59. *Complete postoccipital ridge on head: (0) absent, (1) present*. **[R2011:188; L2012:40]**

60. *Collum covering posterior part of head capsule and part of segment II: (0) absent, (1) present*. **[R2011:211; L2012:41]**

61. *Posterior cephalic band: (0) absent, (1) present*. **[O2013:37; L2013:598]**

62. *Cephalic articulation fused: (0) absent, (1) present*. **[L2012:42; O2013:46]**

63. *Fusion of prosoma and opisthosoma into a single functional unit: (0) absent, (1) present*. In mites the prosoma and opisthosoma are fused into a single unit with little or no evidence of original segmentation. **[L2013:602]**

64. *Cephalic shield overlapping anterior trunk tergite(s): (0) overlap similar to that between adjacent thoracic segments, (1) partial overlap on anterior trunk segment (2) cephalic shield covers multiple anterior tergites*. **[L2012:43]**

65. *Cephalic shield articulates with reduced trunk tergite: (0) absent, (1) present*. **[L2012:44; O2013:48]**

66. *Prosoma (cephalic shield)-opisthosoma (trunk) coupling mechanism: (0) absent, (1) present.* **[G2002:24; L2012:45]**

67. *Post-oral plate (sternum): (0) absent, (1) present*. Characters **68-71** refer to the post-oral sternum of euchelicerates, particularly scorpions, only. **[G2002:17; L2012:46]**

68. *Sternum: (0) divided, (1) undivided*. **[G2002:18; L2012:47]**

69. *Sternum shape: (0) triangular, (1) pentagonal, (2) small and circular, (3) ovoid*. **[L2012:48]**

70. *V-shaped medial sulcus on sternum: (0) absent, (1) present*. This character refers to the sternum of scorpions only. Extant scorpions lack a V-shaped sulcus, however, Carboniferous scorpions tend to have a pronounced sulcus. The sternum of Silurian scorpions, e.g. *Proscorpius*, is undivided, and hence this character is coded as absent in these taxa. **[L2012:49]**

71. *Posteromedial sulcus in sternum: (0) absent, (1) present*. This character is similar to character **70** as most taxa with a V-shaped sulcus also possess a poteromedial sulcus, however, it is also possible to find this character in isolation and therefore the two states were coded as separate characters. **[L2012:50]**

72. *Medial intercoxal region: (0) all pedal coxae separated medially, (1) anterior pedal abutting medially, posterior coxae separated, (1) anterior pedal coxae separated medially, (2) anterior pedal coxae separated medially, posterior coxae abutting, (3) all pedal coxae abutting medially, (4) epimera: coxae undifferentiated from ventral body wall*. **[S2007:17; L2012:51]**

73. *Number of thoracomeres involved in forming the cephalothorax: (0) no thoracomeres fused with the head, (1) one thoracomere fused with head and carapace (if present), (2) two thoracomeres fused with head and carapace: (3) three thoracomeres fused with head shield, (4) eight thoracomeres fused with head and carapace.* **[R2001:9; L2013:603]**

74. *Trunk narrows anteriorly relative to cephalic shield, widest posteriorly: (0) absent, (1) present*. **[L2012:52; O2013:49]**

75. *Trunk somites divided into distinct tergites and sternites: (0) absent, (1) present*. This character is coded for taxa which show evidence of demarcation between the dorsal tergites and ventral somites, such as *Nereocaris*, and is therefore distinct from character **132** which is restricted to taxa that have undergone fusion of the tergite, sternites and pleurites into a single unit. **[L2012:53]**

76. *Relative proportions of preabdominal tergites: (0) equal sized, (1) increase in area T1 to T4 (with T5 narrower), (2) increase in area T1 to T3 (with T4 and T5 progressively narrower), (3) tergites decrease in size posteriorly*. This character, and characters **77-79**, refers to the tergites of euthycarcinoids only. **[L2013:604]**

77. *Angle of anterolateral margin of preabdominal tergites (based on T2): (0) <100º, (1) >100º.* **[L2013:605]**

78. *Preabdominal ornamentation: (0) absent, (1) present*. **[L2013:606]**

79. *Visible monosomite: (0) absent, (1) present*. **[L2013:607]**

80. *Reduced first tergite of trunk (microtergite): (0) absent, (1) present*. Both xiphosurans (Anderson and Selden 1997) and eurypterids (Dunlop and Webster 1999) possess a reduced first tergite, the anterior part of which is underneath the posterior margin of the prosoma. **[L2013:608]**

81. *Boundaries of anterior trunk segments reflexed anterolaterally: (0) absent, boundaries transverse or reflexed posterolaterally: (1) present.* **[L2012:54; O2013:50]**

82. *Lateral flaps (body extends laterally into imbricated, unsclerotised flaps): (0) absent, (1) present*. **[D2009:36; R2011:262; L2012:55]**

83. *Longitudinal ("gill-like") wrinkling on lateral part of flaps: (0) absent, (1) present*. **[D2009:38; R2011:263' L2012:56]**

84. *Strengthening rays on lateral flaps: (0) absent, (1) present*. **[D2009:37; L2013:619]**

85. *Free thoracic tergites: (0) absent, (1) present*. **[L2012:57; O2013:42]**

86. *Decoupling of thoracic tergites and segments: (0) absent, (1) present*. **[L2012:58; O2013:43]**

87. *Tergite articulations: (0) tergites non-overlapping, (1) extensive overlap of tergites, (2) edge-to-edge pleural articulations*. **[L2012:59; O2013:44]**

88. *Tergal scutes extend laterally into paratergal folds: (0) absent, (1) present*. **[R2011:264; L2012:60]**

89. *Trunk elongate (consisting of >25 somites): (0) absent, (1) present.* **[L2012:61]**

90. *Radial arrangement of tergal pleurae: (0) absent, (1) present*. **[L2012:62; O2013:53]**

91. *Trunk tergites with serrate lateral margin: (0) absent, (1) present*. **[E2011:17; L2012:63]**

92. *Paired tergal carinae: (0) absent, (1) present*. **[E2011:20; L2012:64]**

93. *Trunk effacement: (0) trunk with defined (separate or fused) tergite boundaries: (1) trunk tergite boundaries effaced laterally, (2) trunk tergite boundaries completely effaced*. **[L2012:65; O2013:45]**

94. *Trunk covered by fine tuberculation: (0) absent, (1) present.* A finely tuberculate cuticle is possessed by a number of aglaspidids. **[L2013:613]**

95. *Tuberculation on posterior margin of tergites: (0) absent, (1) present*. **[O2013:56; L2013:614]**

96. *Joints between posterior tergites functional, anterior ones variably fused: (0) absent, (1) present.* **[L2012:66; O2013:51]**

97. *Fusion of anterior trunk/opisthosomal tergites into a buckler: (0) absent, (1) present*. **[S2007:98; L2013:609]**

98. *Buckler completely fused: (0) absent (evidence of original segmentation), (1) present*. **[L2013:610]**

99. *Axial spines: (0) absent, (1) present*. **[O2013:57; L2013:615]**

100. *Posterior tergite bearing axial spine: (0) absent, (1) present*. **[L2012:67; O2013:52]**

101. *Anterior tergal processes: (0) absent, (1) present*. **[L2012:68; O2013:55]**

102. *Fusion of paratergal folds into a dorsal shield: (0) absent, (1) present*. **[L2012:69; R2013:1]**

103. *Spines on posterior margin of dorsal shield: (0) absent, (1) present*. **[L2013:625]**

104. *Dorsal marginal trunk rim: (0) absent, (1) present*. This character describes a distinct margin on the fused dorsal shield of vachonisiids and skaniids. This character is present in all skaniids and vachonisiids apart from *Skania fragilis*. **[L2013:611]**

105. *Trunk margins with dense setal fringe: (0) absent, (1) present*. A dense setal fringe is present on the trunk margin of the cheloniellid *Duslia* and an undescribed cheloniellid from the Ordovician of Morocco (Van Roy 2006b). **[L2013:612]**

106. *Thorax: (0) present, (1) absent*. This character is only applicable to taxa with a pygidium (**ch. 154**). A distinct thorax is absent in naraoids and *Phytophilaspis*. **[L2013:616]**

107. *Relative length of thorax: (0) longer than pygidium, (1) shorter than pygidium*. **[L2012:70; O2013:79]**

108. *Thoracic keel: (0) absent, (1) present*. The thorax of mollisonids possesses a distinct medial keel. **[L2013:617]**

109. *Elongate ventral spines on thoracic tergites: (0) absent, (1) present*. Both *Ecnomocaris* and *Thelxiopes* possess a row of elongate medial-ventral spines on their thoracic segments. **[L2013:618]**

110. *Reduced thorax: (0) absent, (1) present*. A reduced thorax, composed of five segments or fewer, is prevalent amongst nektaspids, particularly liwiids, *Panlongia* and *Campanamuta*. **[L2012:71]**

111. *Articulating half ring on thoracic segments: (0) absent, (1) present*. **[L2012:72; O2013:80]**

112. *Raised axial region: (0) absent, (1) present*. **[L2012:73]**

113. *Axial furrows: (0) absent, (1) present*. **[L2012:74; O2013:81]**

114. *Number of opisthosomal somites: (0) five, (1) eight, (2) nine, (3) 10, (4) 11, (5) 12, (6) 13.* **[S2007:95; L2012:75]**

115. *Fusion of tergites of postoral somites VIII and IX: (0) absent, (1) present*. **[S2007:100; L2012:76]**

116. *First mesosomal somite: (0) shorter than or equal in length to second mesosomal somite, (1) longer than second mesosomal somite*. This character is only applicable to scorpions. Extant scorpions typically possess an elongate second mesosomal tergite, however, in many Palaeozoic scorpions the first mesosomal tergite is typically shorter than the second. **[L2012:77]**

117. *Anterior transverse ridge on mesosomal tergites: (0) absent, (1) present*. A distinctive anterior ridge is present on the mesosomal tergites of some Carboniferous and extant scorpions. **[L2012:78]**

118. *Opisthosoma divided longitudinally: (0) absent, (1) present*. **[S2007:115; L2012:79]**

119. *Fusion of all (opisthosomal) tergites behind the opercular tergite into the thoracetron: (0) absent, (1) present*. **[R2011:240; L2012:80]**

120. *Opisthosoma greatly reduced, forming a slender tube emerging from behind the posteriormost legs, with a terminal anus: (0) absent, (1) present*. **[R2011:241; L2012:81]**

121. *Opisthosoma consisting of three somites or fewer: (0) absent, (1) present*. **[L2012:82]**

122. *Opisthosoma comprising a single somite, without a telson: (0) absent, (1) present*. **[L2012:83]**

123. *Demarcation of opisthosomal somites: (0) absent, (1) present*. In extant pycnogonids the opisthosoma is greatly reduced and has lost evidence of original segmentation. **[L2012:84]**

124. *Diplosegments: (0) absent, (1) present*. **[R2011:258; L2012:85]**

125. *Paramedian sutures: (0) absent, (1) present*. **[R2011:265; L2012:86]**

126. *Intercalary sclerites: (0) absent, (1) developed as small rings, (2) developed as pretergite and presternite*. **[R2011:266; L2012:87]**

127. *Trunk heterotergy: (0) absent, (1) present (alternating long and short tergites, with reversal of lengths between seventh and eighth walking leg-bearing segments)*. **[R2011:267; L2012:88]**

128. *Trunk sternites: (0) large sternum, (1) sternal area divided into two hemisternites by linea ventralis, (2) sternum mostly membranous, with pair of small sternites, (3) sternal plate bears Y-shaped ridge/apodeme, (4) sternites extended rearwards to form substernal laminae, (5) thoracic sternal areas*

reduced and partly invaginated along the median line, (6) sternal plate absent. **[R2011:268; L2012:89]**

129. *Pleural part of trunk segments: (0) pleurites absent, (1) supracoxal arches (catapleural and anapleural arches) on each segment, (2) pleural part of thoracic segments II and III consisting of a single sclerite with a large pleural process, (3) pleuron in each thoracic segment composed of a single sclerite divided into anterior and posterior parts by pleural suture, from which a pleural apophysis is invaginated, its internal end connected to the furcal arm*. **[R2011:270; L2012:90]**

130. *Procoxal and metacoxal pleurites surrounding coxa: (0) pleurites absent or incompletely surrounding coxa, (1) procoxa and metacoxa surround coxa*. **[R2011:271; L2012:91]**

131. *Pleuron filled with small pleurites: (0) absent, (1) present*. **[R2011:273; L2012:92]**

132. *Complete body rings: (0) absent (sternites and/or pleurites free), (1) present (sternites, pleurites and tergites fused)*. **[R2011:274; L2012:93]**

133. *Width of first opisthosomal segment: (0) broad, (1) narrow, developed as pedicel*. **[R2011:250; L2012:94]**

134. *Pleomere size: (0) first pleomere fully developed, of similar size and appearance of the more posterior pleomeres, (1) first pleomere reduced, smaller than the second pleomere, (2) more pleomeres reduced.* **[R2001:2; L2013:620]**

135. *Pleura of the second pleon segment: (0) pleura not overlapping other pleura, or pleura overlapping only those of the third pleomere, or pleura absent, (1) pleura of the second pleomere overlapping those of the first and third pleomere*. **[R2001:3; L2013:621]**

136. *Pereion tagmosis: (0) one locomotory tagma, (1) two locomotory tagmata*. **[R2011:253; L2012:95]**

137. *Thorax with three-limb bearing segments: (0) not differentiated, (1) three*. This character refers to the hexapod thorax only. **[R2011:254; L2012:96]**

138. *Abdomen differentiated as limb-free somites: (0) absent, (1) present*. In extant arthropods this tagma is posterior to the expression domains of *Ubx*, *abdA* and *abdB*. **[R2011:252; L2012:97;** *cf*. **O2013:59]**

139. *Abdomen as posterior differentiated segments (0) absent, (1) present*. **[L2012:98; O2013:60]**

140. *Length of abdomen: (0) 1 segment, (1) 2 segments, (2) 3 segments, (3) 5 segments*. **[L2012:99; O2013:59]**

141. *Spines on posterior margin of abdominal somites: (0) absent, (1) present*. The abdominal somites of *Canadaspis*, *Perspicaris* and *Loricicaris* (**Chapter 5**) possess rows of spines along their posterior margin. **[L2012:100]**

142. *Abdominal segmentation (in hexapods): (0) six segments, (1) ten segments, (2) eleven segments, (3) twelve segments*. **[R2011:316; L2012:101]**

143. *Segmentation of pleon: (0) seven segments, (1) six segments*. **[R2011:257; L2012:102]**

144. *Trunk bipartite with narrow posterior: (0) absent, (1) present*. The narrow posterior tagmata of the fuxianhuiids *Fuxianhuia* and *Guangweicaris* is differentiated from the anterior somites, which possess extensive lateral folds **[L2012:103]**

145. *Caudal metasoma: (0) absent, (1) present*. In scorpions, some chasmataspids, and some eurypterids the metasoma is caudal. **[L2012:104]**

146. *Number of metasomal somites: (0) zero, (1) two, (2) three, (3) five, (4) nine*. **[S2007:116; L2012:105]**

147. *Carinae on metasoma: (0) absent, (1) present*. **[L2012:106]**

148. *Elongate coxopleurites on ultimate legs: (0) absent, (1) present*. **[R2011:272; L2012:107]**

149. *Posterior tergites strongly curved in dorsal aspect compared to anterior tergites: (0) absent, (1) present*. **[L2012:108; O2013:61]**

150. *Long axis of postabdominal somites: (0) width greater than length, (1) length greater than width, (2) width to length ratio changes extensively posteriorly.* This character refers to the postabdomen of euthycarcinoids only. **[L2013:622]**

151. *Ornamented postabdominal surface: (0) absent, (1) present*. Some euthycarcinoids, e.g. *Kootixerxes*, possess a distinctive pattern of tuberculation on their postabdominal somites. **[L2013:623]**

152. *Extended posterior end (body axis projects posterior to ultimate pair of lobopods): (0) absent, (1) present*. **[M2009:23; L2013:624]**

153. *Post-appendicular area bulbous and flap-like: (0) absent, (1) present*. The lobopodian *Jianshanopodia*, the dinocaridid *Pambdelurion*, and possibly also the lobopodian *Siberion*, possess a post-appendicular bulbous flap, differentiated from the main body axis by a narrow demarcation. **[L2013:626]**

154. *Pygidium: (0) absent, (1) present*. **[C2004:47; E2011:21; L2012:109]**

155. *Pygidium with medial keel: (0) absent, (1) present*. **[L2012:110; O2013:64]**

156. *Pygidium small, rounded and bordered by curved tergal pleura: (0) present, (1) absent*. The pygidia of *Kiisortoqia* and *Siriocaris* consist of a small rounded plate surrounded by a tergal pleura. **[L2013:627]**

157. *Cephalon and pygidium isopygous and semi-circular: (0) absent, (1) present.* Both mollisonids, particularly *Mollisonia*, and liwiids possess a semi-circular, cephalon and pygidium of roughly equal size and shape. **[L2013:628]**

158. *Segmentation of pygidium: (0) absent, (1) present*. The pygidia of *Soomaspis* (Fortey and Theron 1994) and *Kangacaris* (Paterson *et al.* 2010) possess transverse furrows possibly indicative of original segmentation. **[L2013:629]**

159. *Broad marginal rim on pygidium: (0) absent, (1) present*. **[L2013:630]**

160. *Pygidium with broad-based medial spine: (0) absent, (1) present*. **[L2012:111; O2013:65]**

161. *Pygidium with lateral spines: (0) absent, (1) present*. **[L2012:112; O2013:66]**

162. *Nature and number of lateral pygidial spines: (0) none (absent), (1) serrated margin, (1) two, (2) four, (3) four plus one medial, (4) three plus one medially.* **[L2013:631]**

163. *Size of pygidium: (0) shorter to slightly longer than cephalon, (1) much longer than cephalon*. **[P2010:23; L2012:113]**

164. *Posterior tagmata with elongate lateral processes: (0) absent, (1) present*. This character is scored as present for both the lateral posterior processes of dinocaridids and bivalved stem-arthropods. The flap-like lateral processes of *Fortiforceps* and *Shankouia* are also coded as homologous. **[L2012:114]**

165. *Posterior tagmata composed of three paired tail flaps: (0) absent, (1) present*. **[R2011:317; L2012:115]**

166. *Lateral telson processes fused: (0) absent, (1) present*. The telsons of *Jugatacaris*, *Pectocaris* and *Odaraia* possess lateral processes which are fused together but show evidence of original segmentation (**Chapters 5-6**). **[L2012:116]**

167. *Posterior most tagma modified into a fluke: (0) absent, (1) present*. **[L2012:117]**

168. *Medial telson process: (0) absent, (1) present*. *Nereocaris*, *Jugatacaris*, *Pectocaris* and *Odaraia* possess a dorso-medial telson process. In *Odaraia* this process is fused to the other telson elements. **[L2012:118]**

169. *Lateral telson processes spinose: (0) absent, (1) present*. **[L2012:119]**

170. *Lateral telson processes foliate: (0) absent, (1) present*. The lateral telson processes of *Perspicaris* and *Canadaspis* are 'leaf-shaped' with a crenulated or spinose margin. **[L2012:120]**

171. *Lateral telson processes recurved: (0) absent, (1) present*. In contrast to the straight processes of *Nereocaris* and dinocaridids, the lateral telson processes of *Odaraia* and *Protocaris* show noticeable curvature. **[L2012:121]**

172. *Lateral telson processes with lanceolate tips: (0) absent, (1) present*. **[L2012:122]**

173. *Telson processes flap-shaped: (0) absent, (1) present.* The lateral telson processes of *Fortiforceps* and the fuxianhuiids *Shankouia* and *Liangwangshania* are modified into paddle-shaped flaps. **[L2012:123]**

174. *Annulated caudal filament: (0) absent, (1) present*. **[R2011:318; L2012:124]**

175. *Abdominal segment XI modified as cerci: (0) absent, (1) present*. **[R2011:319; L2012:125]**

176. *Articulate furcal rami: (0) absent, (1) present*. **[R2011:320; L2012:126]**

177. *Uropods: (0) absent, (1) present*. **[R2011:321; L2012:127]**

178. *Paired flaps lateral to telson: (0) absent, (1) present*. The morphology of these flaps is covered by characters **179** and **192**. See Ortega-Hernández *et al*. (2013) for discussion. **[E2011:25; L2012:128; O2013:75]**

179. *Nature of lateral telson flaps: (0) "uropods", (1) furca*. **[L2012:129; O2013:76]**

180. *Pre-telson somite elongate and rigid: (0) absent, (1) present*. The pre-telson somite of *Pectocaris* and *Jugatacaris* are elongate, equivalent in length to three or more abdominal somites. **[L2012:130]**

181. *Telson: (0) absent, (1) present*. **[L2012:131]**

182. *Telson shape: (0) round, (1) laterally depressed, (2) dorso-ventrally depressed*. **[R2011:323; L2012:132]**

183. *Telson shape II: (0) styliform, (1) paddle-shaped, (2) cap-like, (3) lanceolate, (4) flagellate, (5) with at least two elongate lateral processes/spines.* **[L2012: 133;** *cf.* **O2013:68]**

184. *Anterior expansion of tail spine: (0) absent, (1) present*. **[O2013:69; L2013:632]**

185. *Tail spine with medial cleft: (0) absent, (1) present*. **[O2013:72; L2013:633]**

186. *Paddle with projections: (0) absent, (1) present*. **[O2013:73; L2013:634]**

187. *Telson curved dorsally: (0) absent, (1) present*. In some eurypterids, e.g. *Mixopterus*, the telson is dorsally curved. This character was also coded as present in scorpions which possess a bulbous aculeus with a dorsally curved tip. **[L2012:134]**

188. *Length of telson: (0) shorter than half the length of the trunk, (1) longer than half the length of the trunk*. **[L2012:135; O2013:70]**

189. *Segmentation of telson: (0) absent (unjointed), present*. **[P2010:28; L2012:136]**

190. *One pair of dorsal telsonal setae: (0) absent, (1) present*. **[R2011:324; L2012:137]**

191. *Telson fringed with setae: (0) absent, (1) present*. **[E2011:24; L2012:138]**

192. *Postventral plates: (0) absent, (1) present*. **[O2013:74; L2013:635]**

193. *Postventral plate medial attachment: (0) absent, (1) present*. **[O2013:82; L2013:636]**

194. *Lateral telson processes articulated: (0) absent, (1) present*. The lateral telson processes of *Nereocaris* show evidence of free movement, however, those of *Canadaspis* and *Perspicaris* appear to be fused to the telson. **[L2013:637]**

195. *Furcal length: (0) elongate (extend beyond posterior trunk margin), (1) short (does not extend beyond posterior trunk margin).* This character refers to the dorsal furcae of cheloniellids only. **[L2013:638]**

196. *Articulated cerci with elongate setae: (0) absent, (1) present*. **[L2013:639]**

197. *Paired terminal spinnerets: (0) absent, (1) present*. **[R2011:326; L2012:139]**

198. *Anal segment with a pair of large sense calicles, each with a long sensory seta: (0) absent, (1) present*. **[R2011:327; L2012:140]**

199. *Paired segmental ventrolateral appendages: (0) absent, (1) present*. **[L2012:141]**

200. *Segmental appendage musculature: (0) absent, (1) present*. **[L2012:142]**

201. *Differentiated uniramous frontal appendage: (0) absent, (1) present*. In onychophorans, dinocaridids, arthropods, and some onychophorans the anteriomost appendages differ in morphology from the trunk appendages and from other cephalic appendages. The homology of these appendages is uncertain (**Chapters 6-7**), but given the similarity in segmental organization

they likely share a common developmental pathway and so are coded as homologous herein. **[L2013:640]**

202. *Orientation of the anterior-most limbs: (0) lateral, (1) ventral*. The differentiated anterior appendages of lobopodians are typically laterally orientated, e.g. the 'grasping'-appendages of *Megadictyon*, and the antennae of *Aysheaia*, whereas arthropods typically possess ventrally orientated anterior appendages. **[L2012:143]**

203. *Anterior appendages differentiated from posterior trunk appendages: (0) absent, (1) present*. This character is distinct from character **201**, which refers to the anteriormost appendages only. **[L2012:144]**

204. *Grasping limbs: (0) absent, (1) present*. **[M2009:4; L2013:641]**

205. *Frontal appendage with row(s) of elongate spines along inner margin: (0) absent, (1) present*. **[R2011:146; L2012:145]**

206. *Spinose great appendage style: (0) unpaired annulated proboscis-like structure with branching tip, (1) around 15 segments with a double row of short spines, (2) single row of elongate ventral spines with fewer than 15 articles, (3) annulated lobopodous, (4) reduced number of subpentagonal podomeres*. **[L2013:642;** *cf.* **D2009:23]**

207. *Relative orientation of appendicular ("great-appendage") spines compared to appendage podomere: (0) perpendicular, (1) chelate or sub-chelate*. See **Chapter 6** for discussion. **[L2013:643]**

208. *Orientation of appendicular spines relative to the body: (0) ventral, (1) dorsal*. See **Chapter 6** for discussion. **[L2013:644]**

209. *Elongate basal spine on great-appendage: (0) absent, (1) present*. The 'great-appendage' of *Amplectobelua* possesses an elongate spine on its basal segments. **[L2013:645]**

210. *Frontal appendages attached or fused basally: (0) separated, (1) basally attached or fused*. **[M2009:6; R2011:147; L2012:146]**

211. *Lobopods with pads: (0) absent, (1) present*. **[R2011:276; L2012:147]**

212. *Strongly sclerotised, articulated limbs with pivot joints and intrinsic muscles: (0) absent, (1) present*. **[R2011:277; L2012:148]**

213. *Sclerotisation and arthropodisation of cephalic appendages: (0) absent, (1) present*. This character was coded as present in all arthropods, including radiodontans; the latter possess sclerotized cephalic appendages, but arthropodized trunk appendages are absent. **[L2012:149]**

214. *Sclerotisation and arthropodisation of trunk appendages: (0) absent, (1) present*. **[L2012:150]**

215. *Biramy in post-antennal limbs: (0) absent, (1) present*. **[R2011:278; L2012:151]**

216. *Post-antennal limb rami stemming from a protopodite that is rigid, antero-posteriorly flattened, bearing spines/setae along its inner edge: (0) absent (protopodite undifferentiated from limb stem), (1) present*. **[R2011:279; L2012:152]**

217. *Protopodite of post-mandibular limbs elongate, fleshy, extended as numerous soft, setiferous endites: (0) absent, (1) present*. **[R2011:280; L2012:153]**

218. *Coxopodite articulation: (0) arthrodial membrane only, (1) pleural condyle, (2) sternal condyle, (3) sternal and pleural condyle, (4) internal plate*. **[R2011:288; L2012:154]**

219. *Endopods multiannulated with elongate setae: (0) absent, (1) present*. This character refers to the setiferous endopods of euthycarcinoids. **[L2013:648]**

220. *Cephalic exopods longer than endopods: (0) absent, (1) present*. Numerous putative stem-mandibulates, including marrellomorphs and 'Orsten' crustaceomorphs, possess exopods which may be over twice as long as their accompanying endopods. This character was coded as present in *Marrella*, which possesses an elongate, setiferous 'swimming-paddle' considered homologous to the exopods (Rak *et al*. in press), but no corresponding endopod. **[L2013:649]**

221. *Preabdominal appendage length: (0) equal, (1) shortening posteriorly, (2) lengthening posteriorly.* **[L2013:650]**

222. *Elongate exopod tipped with setal "brush": (0) absent, (1) present.* The elongate exopods of some marrellomorph arthropods, particularly skaniids and vachonisiids, are tipped with a concentration of filamentous setae, often attached to a broad semi-lunate base, reminiscent of a sweeping brush. **[L2013:651]**

223. *Exopods of second antennal and mandibular (where exopod present) segments multi-annular with inwardly directed spines, including larval/juvenile stages: (0) absent, (1) present*. **[R2011:283; L2012:155]**

224. *Exopods fringed by strong setae: (0) setae absent, (1) strong, cylindrical or flattened setae present*. **[R2011:284; L2012:156]**

225. *Bilobate exopod shaft (proximal lobe hinged along length of basipodite, bearing imbricated lamellar setae; distal lobe fringe of short setae): (0) absent (exopod is an undivided flap), (1) present*. **[R2011:285; L2012:157]**

226. *Proximal section of exopod: (0) lobe, (1) shaft*. **[C2004:14; P2010:33; L2012:158]**

227. *Distal lobe of exopod: (0) small to moderate sized flap, (1) large, tear-drop shaped lobe with long attachment.* **[L2012:159; O2013:12]**

228. *Divided exopod with septum: (0) absent, (1) present*. **[L2012:160; O2013:13]**

229. *Imbricated exopod lamellae: (0) absent, (1) present*. **[L2012:161; O2013:14]**

230. *Exopod lamellae: (0) thick, flat, (1) delicate, comb-like*. **[L2012:162; O2013:15]**

231. *Shape of "simple" exopods: (0) rounded, (1) subtriangular, (2) with lamellae, (3) triangular, fin-shaped.* This character is only applicable to taxa possessing 'simple' exopods, i.e. an exopod composed of a single, flap-like segment. **[L2012:163]**

232. *Differentiation of setae along exopod: (0) uniform or gradationally variable setae along length of exopod, (1) lamellar setae confined to proximal lobe, with distal lobe bearing slender setae*. **[E2011:30; L2012:164]**

233. *Exopod shaft consisting of numerous segments each bearing a single seta/filament: (0) absent, (1) present*. **[L2012:165]**

234. *Pre-„great-appendage" appendages: (0) absent, (1) present*. This character is only applicable to taxa bearing a 'great-appendage' or 'specialized post-antennal appendage', many of which possess a pair of antennae anterior to these appendages (**Chapter 7**). **[L2012:166]**

235. *Frontal filaments: (0) absent, (1) present*. **[R2011:148; L2012:167]**

236. *Appendage of second (deutocerebral) head segment: (0) locomotory leg 1, (1) antenna (antennula in crustaceans), (2) chelicerae / chelifore with few podomeres, terminal podomeres bearing spines on outer side of distal margins, with terminal pincer, (3) jaw*. **[R2011:149; L2012:168]**

237. *Antennal rami: (0) uniramous, (1) polyramous, (2) one ramus + scale*. **[R2011:150; L2012:169]**

238. *Antennule lobate, divided along most of its length into sensilla-bearing lobes: (0) absent (non-lobate antenna/first antenna), (1) present*. **[R2011:151; L2012:170]**

239. *Antennular sensilla: (0) sensilla present on non-terminal part of antennule (antenna in myriapods and hexapods), (1) confined to tip*. **[R2011:152; L2012:171]**

240. *Antennal apical cone sensilla: (0) absent, (1) present*. **[R2011:153; L2012:172]**

241. *Two lateral areas bearing club-like sensilla on terminal antennal article: (0) absent, (1) present*. **[R2011:154; L2012:173]**

242. *Intrinsic muscles of antennae: (0) absent, (1) present*. **[R2011:155; L2012:174]**

243. *Scape and pedicel differentiated, with Johnson"s organ: (0) absent, (1) present*. **[R2011:156; L2012:175]**

244. *Antennal circulatory vessels: (0) joined, (1) separate, (2) absent*. **[R2011:157; L2012:176]**

245. *Ampullo-ampullary dilator and ampullo-aortic dilator: (0) absent, (1) present*. **[R2011:158; L2012:177]**

246. *Stratocyst in basal segment of first antenna: (0) absent, (1) present*. **[R2011:159; L2012:178]**

247. *Cheliceral segmentation: (0) three segments or more, (1) two segments.* **[L2012:179;** *cf.* **R2011:160]**

248. *Number of spine-bearing articles on chelate appendage: (0) three+moveable finger, (1) two+moveable finger, (2) one+moveable finger; (3) moveable finger only*. **[E2011:5; L2012:180]**

249. *Great-appendage geniculate: (0) absent, (1) present*. This character was included to accommodate the observations of Haug *et al*. (2012c), who recognised a distinctive flexure in the frontal appendages of arthropods with chelate/sub-chelate anterior limbs. This character is coded as inapplicable for taxa without chelate/sub-chelate anterior appendages and was coded as present in *Odaraia*, *Perspicaris* and *Canadaspis* (following Legg *et al*. in review, **Chapter 7**) but absent in *Branchiocaris* and *Loricicaris*, which possess chelate anterior appendages that lack a corresponding geniculation (**Chapter 5**). **[L2013:646]**

250. *Number of segments in "short-great-appendage": (0) two proximal elements plus four spinose distal elements, (1) two plus three, (2) two plus two, (3) two plus one, (4) five or more with an undifferentiated peduncle*. See Haug *et al*. (2012c) for discussion. **[L2013:647]**

251. *Long spinose projections on distal part of terminal three podomeres of chelate appendage bearing flagellum: (0) absent, (1) present.* **[E2011:6; L2012:181]**

252. *Length of flagellate great-appendage: (0) flagellae terminate at midlength of trunk, (1) flagellae extending to end of body*. **[E2011:7; L2012:182]**

253. *Plagula ventralis: (0) absent, (1) present*. **[R2011:161; L2012:183]**

254. *Chelicerocarapacal articulation: (0) absent, (1) present*. **[S2007:20; L2012:184]**

255. *Cheliceral tergo-deuteromerite muscle: (0) absent, (1) present*. **[R2011:162; L2012:185]**

256. *Naked cheliceral fang: (0) absent, (1) present*. The chelicerae of most chelicerates are covered in a layer of setae, however, in spiders (Araneae) these setae are lacking. **[L2012:186]**

257. *Cheliceral venom gland: (0) absent, (1) present*. **[S2007:27; L2012:187]**

258. *Appendage on third (tritocerebral) head segment: (0) unspecialised locomotory limb, (1) second antenna, (2) absent (intercalary segment), (3) pedipalp, (4) oral papilla with slime glands and adhesive glands, (5) subchelate appendage, (6) "swimming paddle"*. **[R2011:163; L2012:188]**

259. *Nature of second (first post-antennal/raptorial) cephalic appendages: (0) biramous walking leg or antennae, (1) uniramous walking legs.* **[L2013:652; O2013:6]**

260. *First post-antennal limbs with proximal endite in early larvae: (0) absent, (1) present*. **[H2010:6; L2013:653]**

261. *First post-antennal limbs with proximal endite in later developmental stages: (0) absent, (1) present*. **[H2010:7; L2013:654]**

262. *Proximal endite enlarged to form coxa in first post-antennal limb: (0) absent, (1) present*. **[H2010:8; L2013:655]**

263. *First post-antennal exopod with 3-2 setation pattern: (0) absent, (1) present*. **[H2010:10; L2013:656]**

264. *Antennal exopod morphology: (0) up to six annuli each bearing a seta, (1) two podomeres, (2) one plus two podomeres, (3) with a scale bearing setae, (4) spinneret seta.* **[L2013:664]**

265. *Single segmented antennal scale: (0) absent, (1) present*. **[R2011:164; L2012:189]**

266. *Antennal naupliar protopod: (0) short, (1) long*. **[R2011:165; L2012:190]**

267. *Palpal coxae fused ventromedially: (0) absent, (1) present*. **[S2007:30; L2012:191]**

268. *Rostrosoma: (0) absent, (1) present*. **[S2007:33; L2012:192]**

269. *Pedipalp (or equivalent) limb morphology: (0) pediform, (1) raptorial, (2) chelate (non-scorpion-type), (3) chelate (scorpion-type)*. **[L2012:193;** *cf.* **R2011:166]**

270. *Pedipalp patella: (0) shorter than, or equal in length to manus, (1) longer than manus.* This character is applicable to scorpions only. **[L2012:194]**

271. *Prominent carina on pedipalp patella: (0) absent, (1) present*. This character is applicable to scorpions only. **[L2012:195]**

272. *Palpal apotele: (0) absent, (1) present*. **[S2007:47; L2012:196]**

273. *Ratio between the tarsus and the tibia of the opilionid palp: (0) subequal, (1) tarsus shorter than tibia, (2) tarsus longer than tibia*. **[G2002:61; L2013:665]**

274. *Raptorial second (tritocerebral) appendages: (0) absent, (1) present*. A raptorial second appendage is present in uropygids. **[L2012:197]**

275. *Exopod on tritocerebral segment much longer than endopod: (0) absent, (1) present*. This character refers to exopods that are more than twice the length of the endopod and is thus distinct from character **220** which is also coded as present for taxa in which the exopod is only marginally longer than the endopod. **[L2012:198]**

276. *Nature of third (second post-antennal/raptorial) cephalic appendages: (0) biramous walking legs, (1) uniramous walking legs.* **[O2013:7; L2013:657]**

277. *Second post-antennal limb with proximal endite in early larvae: (0) absent, (1) present*. **[H2010:13; L2013:658]**

278. *Third post-antennal limb with proximal endite in early larvae: (0) absent, (1) present*. **[H2010:20; L2013:659]**

279. *Third post-antennal limb with proximal endite in later developmental stage: (0) absent, (1) present*. **[H2010:21; L2013:660]**

280. *Third post-antennal limb with setiferous multi-annulated exopod: (0) absent, (1) present*. **[H2010:22; L2013:661]**

281. *Fourth post-antennal limb with proximal endite in early larvae: (0) absent, (1) present*. **[H2010:26; L2013:662]**

282. *Modified cephalic appendages with micro-hooks for host attachment: (0) absent, (1) present*. This character is coded as present in the tongue worm *Railietiella* and the fish louse *Argulus*. **[L2013:663]**

283. *Oviger: (0) absent, (1) present*. **[R2011:189; L2012:199]**

284. *Largest podomere of oviger: (0) first, (1) second, (3) sixth*. **[L2012:200]**

285. *Walking leg I antenniform: (0) absent, (1) present*. **[L2012:201]**

286. *Walking leg III and IV with femur shorter than patella and with principle site of flexion/extension at patella-tibia joint: (0) absent, (1) present*. **[S2007:48; L2012:202]**

287. *Walking leg II longer than adjacent leg and modified as feeler: (0) absent, (1) present*. **[R2011:190; L2012:203]**

288. *Distal ends of walking legs flattened: (0) absent, (1) present*. **[L2012:204]**

289. *Coxal swing: (0) absent, (1) present*. **[R2011:287; L2012:205]**

290. *Musculi lateralis: (0) absent, (1) present*. **[R2011:292; L2012:206]**

291. *Coxotrochanteral joint: (0) simple, (1) complex*. **[R2011:293; L2012:207]**

292. *Trochanterofemoral joint of walking legs: (0) transverse bicondylar, (1) vertical bicondylar*. **[R2011:296; L2012:208]**

293. *Patellotibial joint of walking legs: (0) dorsal monocondylar, (1) simple bicondylar, (2) vertical bicondylar, dorsal hinge*. **[R2011:300; L2012:209]**

294. *Walking leg femur: (0) shorter than, or equal in length to patella, (1) longer than patella*. **[L2012:210]**

295. *Femoropatellar joint: (0) transverse dorsal hinge, (1) bicondylar articulation, (2) hinge*. **[S2007:69; R2011:301; L2012:211]**

296. *Origin of posterior transpatellar muscle: (0) arises on distodorsal surface of femur, transverses femoropatellar joint ventral to axis of rotation, receives fibres from wall of patella, (1) arises on distal process of femur, transverses femoropatellar joint dorsal to axis of rotation, does not receive fibres from patella*. **[R2011:302; L2012:212]**

297. *Tibiotarsus: (0) separate tibia and tarsus, (1) unjointed tibiotarsus*. **[R2011:303; L2012:213]**

298. *Elastic arthrodial sclerites spanning the tibia-tarsus joints: (0) absent, (1) present*. **[R2011:304; L2012:214]**

299. *Divided tarsus (basitarsus and telotarsus): (0) absent, (1) present*. **[S2007:82; L2012:215]**

300. *Telotarsus in adults with two or more tarsomeres: (0) absent, (1) present*. **[S2007:84; L2012:216]**

301. *Three telotarsomeres on appendages of postoral somites IV-VI: (0) absent, (1) present*. **[S2007:85; L2012:217]**

302. *Tarsal organ: (0) absent, (1) present*. **[R2011:306; L2012:218]**

303. *Pretarsal depressor muscle origin: (0) on tarsus, (1) on tibia or patella*. **[R2011:307; L2012:219]**

304. *Apotele of walking leg I: (0) absent, (1) present*. **[S2007:90; L2012:220]**

305. *Pulvillus: (0) absent, (1) present*. **[S2007:92; L2012:221]**

306. *Exopod of post-mandibular limb multisegmented with inward pointing setae: (0) absent, (1) present*. **[R2012:15; L2012:222]**

307. *Mandible (gnathobasic appendage of third limb-bearing metamere is main feeding limb of adult head): (0) absent, (1) basipodite with elaboration of proximal endite, (2) mandible a coxal endite embedded between the labrum and hypopharynx to form a chewing chamber*. **[R2011:168; L2012:224]**

308. *Mandible with row of teeth along inner edge: (0) absent, (1) present*. **[O2009:15; L2013:666]**

309. *Segmentation of endopod on mandible: (0) six segments, (1) five segments*. **[L2013:667]**

310. *Lacinia mobilis on larval (embryonic) mandible: (0) absent, (1) present*. **[R2001:15; L2013:668]**

311. *Toothed endite on mandible: (0) absent, (1) present* **[L2013:669]**.

312. *Mandibular base plate forming side of head: (0) absent, (1) present*. **[R2011:169; L2012:225]**

313. *Telognathic mandible with musculated gnathal lobe, flexor arising dorsally on cranium: (0) absent, (1) present*. **[R2011:170; L2012:226]**

314. *Pectinate lamellae on mandible: (0) absent, (1) present*. **[R2011:171; L2012:227]**

315. *Mandibular gnathal edge: (0) consisting of molar and incisor process, (1) only ellipsoid molar present, (2) number of teeth arranged in a row, (3) shovel with terminal teeth, (4) group of paired teeth and hair pad*. **[R2011:172l L2012:228]**

316. *Second (anterior) mandibular cranial articulation: (0) absent, (1) present*. **[R2011:173; L2012:229]**

317. *Ball-and-socket mandibular articulation: (0) absent, (1) present, formed between clypeal condyle and mandibular ridges*. **[R2011:174; L2012:230]**

318. *Mandibular scutes: (0) absent, (1) present*. **[R2011:175; L2012:231]**

319. *Mandibular palp: (0) present, (1) absent*. **[R2011:176; L2012:232]**

320. *Hand-shaped „movable appendage" between* pars incisiva *and* par molaris *of mandible: (0) absent, (1) present*. **[R2011:177; L2012:233]**

321. *Posterior tentorial apodeme: (0) absent, (1) present as metatentorium, (2) paired separate rods*. **[R2011:178; L2012:234]**

322. *Pre- and metatentorium fused: (0) absent, (1) present*. **[R2011:179; L2012:235]**

323. *Anterior tentorial arms: (0) absent, (1) cuticular tentorium developed as ectodermal invagination, (2) cuticular fulcro-tentorium*. **[R2011:180; L2012:236]**

324. *Posterior suspension of anterior apodemes to cranial wall: (0) absent, (1) present*. **[R2011:181; L2012:237]**

325. *Anterior tentorium: (0) separate, rod-like anterior tentorial apodemes, (1) anterior part of tentorial apodeme forms arched, hollow plate that approach each other mesially but remain separate, (2) anterior tentorium an unpaired roof*. **[R2011:182; L2012:238]**

326. *Swinging tentorium, mandible abducts by tentorial movements: (0) absent, (1) present*. **[R2011:183; L2012:239]**

327. *Mandibular articulation with tentorium: (0) gnathal lobe articulates with epipharyngeal bar, (1) mandible articulates with hypopharyngeal bar*. **[R2011:184; L2012:240]**

328. *Suspensory bar from mandible: (0) absent, (1) present*. **[R2011:185; L2012:241]**

329. *Intergnathal connective lamina: (0) absent, (1) present*. **[R2011:186; L2012:242]**

330. *Mandibulo-hyopharyngeal muscle: (0) absent, (1) present*. **[R2011:187; L2012:243]**

331. *Maxilla 1: (0) absent (locomotory limb on fourth metamere), (1) present*. **[R2011:193; L2012:244]**

332. *First maxillary precoxa: (0) absent, (1) present*. **[R2011:194; L2012:245]**

333. *Number of medially directed lobate endites on first maxilla: (0) two endites, (1) one endite*. **[R2011:195; L2012:246]**

334. *First maxillary palps: (0) present (including telopodite of positionally equivalent limb in chelicerates), (1) absent*. **[R2011:196; L2012:247]**

335. *First maxillary palp hypertrophied: (0) absent, (1) present*. **[R2011:197; L2012:248]**

336. *First maxillary palp an elongate cleaning organ: (0) absent, (1) present*. **[R2011:198; L2012:249]**

337. *First maxilla divided into cardo, stipes, lacinia, and galea, with similar musculature and function: (0) absent, (1) present*. **[R2011:199; L2012:250]**

338. *Interlocking of galea and superlingua: (0) absent, (1) present*. **[R2011:200; L2012:251]**

339. *First maxilla coalesced with sternal intermaxillary plate: (0) absent, (1) present, (2) mental elements of gnathochilarium consolidated*. **[R2011:201; L2012:252]**

340. *Second maxillae on fifth metamere: (0) appendage developed as trunk limb, (1) well developed maxilla differentiated as a mouthpart, (2) vestigial appendage, (3) appendage lacking, (4) well developed, not a mouth part, (5) long antenniform appendage.* **[R2011:202; L2012:253]**

341. *Maxillula with 1+3 endites: (0) absent, (1) present* **[L2013:670]**.

342. *Second maxilla exopod: (0) present, forming a broad plate, (1) modified to scaphognathite, (2) absent*. **[R2001:18; L2013:671]**

343. *Second maxilla palp: (0) present, (1) vestigial or absent*. **[R2001:19; L2013:672]**

344. *Egg tooth on second maxilla: (0) absent (no embryonic egg tooth on cuticle of fifth limb-bearing metamere), (1) present*. **[R2011:203; L2012:254]**

345. *Maxillary plate: (0) absent, (1) present*. **[R2011:204; L2012:255]**

346. *Coxae of second maxillae medially fused: (0) absent (coxae of appendages of fifth metamere not fused), (1) present*. **[R2011:205; L2012:256]**

347. *Symphylan-type labium: (0) absent, (1) present*. **[R2011:206; L2012:257]**

348. *Linea ventralis: (0) absent, (1) present*. **[R2011:207; L2012:258]**

349. *Divided glossae and paraglossae: (0) undivided pair of glossae and paraglossae, (1) glossae and paraglossae bilobed*. **[R2011:208; L2012:259]**

350. *Rotation of labial* Anlagen*: (0) absent, (1) present*. **[R2011:209; L2012:260]**

351. *Widened apical segment of labial palp: (0) absent, (1) present*. **[R2011:210; L2012:261]**

352. *Direct articulation between first and fourth articles of telopodite and maxillipede: (0) absent (first and fourth articles of telopodite of sixth metamere lack a common hinge), (1) present*. **[R2011:212; L2012:262]**

353. *Coxosternite of maxilliped sclerotised in midline: (0) coxae separated medially, with sternite present in adult, (1) coxosternal plates meeting, with flexible hinge, (2) coxosternal plate meeting medially, hinge sclerotised and non-functional*. **[R2011:213; L2012:263]**

354. *Maxilliped coxosternite deeply embedded into cuticle above second trunk segment: (0) not embedded, (1) embedded*. **[R2011:214; L2012:264]**

355. *Maxilliped segment with pleurite forming a girdle around coxosternite: (0) small lateral pleurite, (1) large girdling pleurite*. **[R2011:215; L2012:265]**

356. *Sternal muscles truncated in maxilliped segment, not extending into head: (0) sternal muscles extended into head, (1) sternal muscles truncated*. **[R2011:216; L2012:266]**

357. *Maxillary exite: (0) segmented, (1) brachial plate, (2) single segment*. **[L2013:673]**

358. *Exopod on maxilliped: (0) absent, (1) present*. **[L2013:674]**

359. *Maxilliped tooth plate (anteriorly-projected, serrate coxal endite): (0) absent, (1) present*. **[R2011:217; L2012:267]**

360. *Maxilliped poison gland: (0) absent, (1) present*. **[R2011:218; L2012:268]**

361. *Maxilliped distal segments fused as a tarsungulum: (0) separate tarsus and pretarsus, (1) tarsus and pretarsus fused as tarsungulum*. **[R2011:219; L2012:269]**

362. *First thoracopod: (0) unmodified appendage, (1) transformed into a maxilliped*. **[R2001:21; L2013:675]**

363. *Additional thoracopods transformed into maxillipeds: (0) absent, (1) second (and third) thoracopod modified into maxillipeds, (2) five „maxillipeds".* **[R2001:22; L2013:676]**

364. *Reduced sixth appendage: (0) absent, (1) present*. This character is present in ostracods. **[L2013:682]**

365. *Epipodite on sixth appendage: (0) absent, (1) present*. **[L2013:683]**

366. *Phyllopodous appendages: (0) absent, (1) present*. **[L2013:684]**

367. *Number of pleon appendages: (0) six, (1) three (third to fifth pleopods missing)*. **[R2001:4; L2013:685]**

368. *First thoracopod exopod: (0) present, (1) absent*. **[R2001:23; L2013:686]**

369. *First thoracopod epipodite: (0) epipodite respiratory and does not differ in general from the epipodites of more posterior thoracopods, (1) epipodite produces a respiratory current, it is respiratory itself or non-respiratory, (2) epipodite present, but not producing a respiratory current and non-respiratory, (3) epipodite absent*. **[R2001:24; L2013:687]**

370. *Thoracopods 2-8, number of epipodites (without oostegites) on at least some thoracopods: (0) one, (1) two (often two branches, developing from one Anlage) present, (2) more than two epipodites, typically an arthrobranchiae and pleurobrachiae, (3) none.* **[R2001:25; L2013:688]**

371. *Thoracopods 2-8, position of epipodites: (0) lateral, (1) at least one branch carried under the thorax.* **[R2001:26; L2013:689]**

372. *Exopod on thoracopods 2-8: (0) present, at least on some thoracopods, flagellate or vestigial, (1) completely absent from all thoracopods.* **[R2001:30; L2013:690]**

373. *Thorax-coxa articulation: (0) allows promotion/remotion, (1) allows abduction/adduction*. **[R2001:31; L2013:691]**

374. *Coxa-basis articulation: (0) dicondylic, allows abduction/adduction, (1) monocondylic, motion in different direction is possible*. **[R2001:32; L2013:692]**

375. *Intreabasal articulation: (0) absent, (1) present*. **[R2001:33; L2013:693]**

376. *Coxal plates on thoracopods: (0) absent, (1) present*. **[R2001:34; L2013:694]**

377. *Thoracopods 4-5 chelate: (0) absent, (1) present*. **[R2001:35; L2013:695]**

378. *Thoracopod 6 chelate: (0) absent, (1) present*. **[R2001:36; L2013:696]**

379. *Pleopods: (0) biramous, (1) uniramous*. **[R2001:37; L2013:697]**

380. *Appendicules internae on the endopods: (0) absent, (1) present*. **[R2001:38; L2013:698]**

381. *Vermiform cleaning thoracopod: (0) absent, (1) present*. This character is present in the ostracods *Vagula*, *Nasunaris*, *Nymphatelina* and *Colymboarthon*. **[L2013:699]**

382. *Claspers as modified anterior thoracopods (applicable for taxa with phyllopodous limbs only): (0) absent, (1) one pair of claspers (at least movable finger), (2) two pairs of claspers*. **[R2011:251; L2012:270]**

383. *Moveable endite on walking leg coxae: (0) absent, (1) present*. **[S2007:53; L2012:271]**

384. *Length of podomeres VI-4 and VI-5: (0) VI-5 > VI-4, (1) VI-5 = VI-4, (2) VI-4 >VI-5*. **[T2007:17; L2012:272]**

385. *Walking legs II-IV spinose: (0) absent, (1) present*. **[L2012:273]**

386. *Walking legs V spinose: (0) absent, (1) present*. This character is applicable to eurypterids only. **[L2012:274]**

387. *Leg VI modified into a "pusher": (0) absent, (1) present*. The posteriormost walking legs of xiphosurans possess spatulate tarsal processes, referred to as a 'pusher'. **[L2012:275]**

388. *Leg VI modified into a swimming paddle: (0) absent, (1) present*. The distal podomere of the posterior cephalic appendages of eurypterids and chasmataspidids is paddle shaped. Although this feature has been considered absent from some chasmataspidids, e,g, *Chasmataspis* (Dunlop *et al*. 2004), the preservation of these taxa is not adequate to determine if this a genuine absence. **[L2012:276]**

389. *Podomere 9 on appendage VI: (0) absent, (1) present*. In some eurypterids a small podomere is present on the tip of the swimming paddle. **[L2012:277]**

390. *Podomere 7a: (0) absent, (1) present*. A small accessory podomere is present on the sixth walking legs and swimming paddles of eurypterids and chasmataspidids. **[L2012:278]**

391. *Walking legs chelate: (0) absent, (1) present*. This character is coded as applicable to chelicerates only. **[L2012:279]**

392. *Locomotory limbs with spinules/papillae: (0) absent, (1) present*. **[M2009:9; L2013:677]**

393. *Terminal claws on appendages: (0) absent, (1) present*. **[M2009:10; L2013:678]**

394. *More than two claws per limb: (0) absent, (1) present*. **[M2009:11; L2013:679]**

395. *One pair of limbs behind the last pair/set of sclerites: (0) absent, (1) present*. **[M2009:30; L2013:680]**

396. *Trunk limbs with appendiculae or branches: (0) absent, (1) present*. **[L2011:18; L2013:681]**

397. *Endopod segmentation in locomotory limbs: (0) ca. 20 segments, without terminal claw, (1) eight segments (excluding protopodite) and terminal claw,*

(2) at most five or six segments and terminal (pretarsal) claw. **[R2011:282; L2012:280]**

398. *Appendage of first thoracic somite underneath the cephalo-thoracic articulation: (0) absent, (1) present*. **[L2012:281; O2013:8]**

399. *Trunk endopods: (0) absent, (1) present*. **[L2012:282; O2013:9]**

400. *Appendage on first opisthosomal segment: (0) appendage present in post-embryonic stage, (1) appendage absent.* **[R2011:247; L2012:283]**

401. *Appendage of seventh metamere incorporated into cephalic tagmata: (0) absent, (1) present*. The anterior trunk appendages of xiphosurans are incorporated into the cephalon and are functionally part of the head. **[L2012:284]**

402. *Appendage VII greatly reduced and plate-like: (0) absent, (1) present*. In xiphosurans the VII appendage lacks a distinctive endopod and is reduced into a plate-like operculum. **[L2012:285]**

403. *Limb VII as chilaria: (0) absent, (1) present*. **[R2011:248; L2012:286]**

404. *Pectines: (0) absent, (1) present*. **[R2011:249; L2012:287]**

405. *Plate-like opisthosomal appendages: (0) absent, (1) present*. In euchelicerates the mesosomal appendages typically lack endopods and are modified into plate-like operculae. **[L2012:288]**

406. *Opisthosomal silk glands and spiggots: (0) absent, (1) present*. **[L2012:289]**

407. *Opisthosomal spinnerets: (0) absent, (1) present*. **[L2012:290]**

408. *Location of opisthosomal spinneret: (0) near middle of opisthosoma, (1) near posterior of opisthosoma*. **[S2007:113; L2012:291]**

409. *Anterior medial „spinnerets": (0) absent, (1) present*. **[S2007:114; L2012:292]**

410. *Transverse sutures on ventral plate: (0) absent, (1) present*. The mesosomal opercula are fused into a single unit in some eurypterids and arachnids. In chasmataspidids and some eurypterids lateral operculae are separated by a transverse suture. **[L2012:293]**

411. *Anterior opercula plate: (0) absent, (1) present*. **[L2012:294]**

412. *Meso- and metathorax in mature stage bearing wings: (0) absent, (1) present*. **[R2011:255; L2012:295]**

413. *Wing flexion: (0) absent, (1) present*. **[R2011:256; L2012:296]**

414. *Furcula: (0) absent, (1) present*. **[R2011:291; L2012:297]**

415. *Coxal vesicles: (0) absent, (1) present, (2) eversible*. **[R2011:289; L2012:298]**

416. *Styli: (0) absent, (1) present*. **[R2011:290; L2012:299]**

417. *Trunk limbs with lobate endites formed by folds in limb bud: (0) absent, (1) present*. **[R2011:281; L2012:300]**

418. *Trunk endopod endites: (0) spiniferous, (1) rounded.* **[R2012:13; L2012:301]**

419. *Spiniferous endites differentiated into primary (small) and secondary (long) sets: (0) absent, (1) present*. **[L2012:302]**

420. *Trochanteronotal muscle: (0) absent, (1) present*. **[R2011:294; L2012:303]**

421. *Trochanter distal joint: (0) mobile, (1) short, ring-like trochanter lacking mobility at joint with prefemur*. **[R2011:295; L2012:304]**

422. *Unique trochanteral femur-twisting muscle: (0) absent, (1) present*. **[R2011:297; L2012:305]**

423. *Unique femur-tibia pivot joint: (0) absent, (1) present*. **[R2011:298; L2012:306]**

424. *Patella/tibia joint: (0) free, (1) fused*. **[R2011:299; L2012:307]**

425. *Tarsus segmentation (in hexapods): (0) not subsegmented, (1) subsegmented*. **[R2011:305; L2012:308]**

426. *Pretarsal levator muscle: (0) present, (1) absent (depressor is sole pretarsal muscle)*. **[R2011:308; L2012:309]**

427. *Pretarsal claws: (0) paired, (1) unpaired*. **[R2011:309; L2012:310]**

428. *Pretarsal claw articulation: (0) on pretarsal base, (1) on distal tarsomere*. **[R2011:310; L2012:311]**

429. *Plantulae: (0) absent, (1) present*. **[R2011:311; L2012:312]**

430. *Trunk exopod setae: (0) short, fine setae, (1) long, flattened, tapering distally, with slight separation, (2) lamellate setae, (3) widely space filamentous setae*. **[L2012:313;** *cf.* **R2011:242;** *cf*. **E2011:29]**

431. *Paddle-like epipods: (0) absent, (1) present*. **[R2011:286; L2012:314]**

432. *Cilia: (0) present in several organ systems, including photoreceptor, nephridia, and genital tracts, (1) present in (at most) sperm*. **[R2011:22; L2012:315]**

433. *Bismuth staining of Golgi complex beads: (0) absent, (1) present*. **[R2011:28; L2012:316]**

434. *Circumoesophageal brain: (0) absent, (1) present*. In cycloneuralians the oesophagus passes through a circular neural mass. This character is absent in all panarthropods. **[L2012:317]**

435. *Immigration of cells during neurogenesis: (0) segregation and immigration of single cells, (1) immigrating clusters of post-mitotic cells*. **[R2011:47; L2012:318]**

436. *Segmental invaginations of neuroectoderm giving rise to ventral organs: (0) absent, (1) present*. **[R2011:48; L2012:319]**

437. *Neuronal stem cells with asymmetrical division: (0) absent, (1) present*. **[R2011:49; L2012:320]**

438. *Cellular derivatives of neuroectoderm: (0) neuroectoderm generates epidermal and neural cells, (1) central area of neuroectoderm generates neural cells only*. **[R2011:50; L2012:321]**

439. *Early differentiating neurons aCC, pCC, RP2, U-CQ, EL and AUN: (0) absent, (1) present*. **[R2011:51; L2012:322]**

440. *EC neurons: (0) Eca and Ecp only,(1) Eca, Ecp and Ecl*. **[R2011:52; L2012:323]**

441. *Anterior pair of serotonergic neurons with neurites that cross to contralateral side: (0) absent, (1) present*. **[R2011:53, L2012:324]**

442. *Posterior pair of serotonergic neurons with neurites that cross to contralateral side: (0) absent, (1) present*. **[R2011:54; L2012:325]**

443. *Serotonergic somata clustered: (0) unclustered, (1) clusters of about 10 cells*. **[R2011:55; L2012:326]**

444. *Serotonergic cell group „b" of* Harzsch (2004)*: (0) absent, (1) present*. **[R2011:56; L2012:327]**

445. *Single median serotonergic neurons „c" and „d" of* Harzsch (2004)*: (0) absent, (1) present*. **[R2011:57; L2012:328]**

446. *Globuli cells: (0) confined mainly to brain, in massive clusters, (1) making up majority of neuropil and ventral layer of ventral nerve cord*. **[R2011:58; L2012:329]**

447. *Corpora allata: (0) absent, (1) present*. **[R2011:59; L2012:330]**

448. *Intrinsic secretory cells in protocerebral neurohemal organ: (0) absent, (1) present*. **[R2011:60; L2012:331]**

449. *Enlarged epipharyngeal ganglia: (0) absent, (1) present*. **[R2011:61; L2012:332]**

450. *Innervation of mouth area by anterior stomogastric nervous system: (0) absent, (1) present*. **[R2011:62; L2012:333]**

451. *Ganglia of pre-oesophageal brain: (0) protocerebrum, (1) protocerebrum and deutocerebrum, (2) proto-, deuto- and tritocerebra*. **[R2011:63; L2012:334]**

452. *Ganglia of post-oral appendages fused into single nerve mass: (0) absent, (1) present*. **[R2011:64; L2012:335]**

453. *Bilateral neuropils: (0) absent, (1) present*. **[R2011:65; L2012:336]**

454. *Fan-shaped body in brain: (0) absent, (1) present*. **[R2011:66; L2012:337]**

455. *Midline neuropil (m11): (0) absent, (1) present*. **[R2011:67; L2012:338]**

456. *Midline neuropil 2: (0) absent, (1) present*. **[R2011:68; L2012:339]**

457. *Position of midline neuropil: (0) superficial to protocerebrum, (1) embedded within protocerebral matrix*. **[R2011:69; L2012:340]**

458. *Looped axons provide local tangential connections to midline neuropil: (0) absent, (1) present*. **[R2011:70; L2012:341]**

459. *Neurons defining modules to midline neuropil: (0) heterolateral neurons, the cells bodies of which are remote from neuropil, (1) perpendicular local neurons*. **[R2011:71; L2012:342]**

460. *Size variation in somata supplying midline neuropil: (0) uniform, (1) variable*. **[R2011:72; L2012:343]**

461. *Olfactory lobes linked to a lateral component of protocerebrum by olfactory globular tract: (0) absent, (1) present*. **[R2011:73; L2012:344]**

462. *Segmental association of glomeruli: (0) linked to specific appendages / ganglia, (1) supplied by all legs / ganglia*. **[R2011:74; L2012:345]**

463. *Arcuate body in brain: (0) absent, (1) present*. **[R2011:75; L2012:346]**

464. *Ellipsoid body in brain: (0) absent, (1) present*. **[R2011:76; L2012:347]**

465. *Nobuli in brain: (0) absent, (1) present*. **[R2011:77; L2012:348]**

466. *Protocerebral bridge: (0) absent, (1) present*. **[R2011:78; L2012:349]**

467. *Mushroom body calyces: (0) absent, (1) present*. **[R2011:79; L2012:350]**

468. *Deutocerebral olfactory lobe with glomeruli: (0) absent, (1) present*. **[R2011:80; L2012:351]**

469. *Number of globuli cell clusters in the deutocerebrum associated with the offactory lobe: (0) one, (1) two.* **[R2001:44; L2013:702]**

470. *Deutocerebral olfactory-globular tract: (0) absent, (1) uncrossed, (2) with chiasma*. **[R2011:81; L2012:352]**

471. *Deutocerebrum with bipartite antennular neuropils: (0) absent, (1) present*. **[R2011:82; L2012:353]**

472. *Multi-faceted eyes: (0) absent, (1) present*. This character is not the same of character **473** which refers to compound eyes only but also refers to the clusters of ocelli observed in some lobopodian taxa (Ma *et al*. 2012a). **[L2013:700]**

473. *Rhabdomeric lateral eyes with new elements formed at a proliferation zone at side of developing eye field: (0) absent, (1) present*. **[R2011:94; L2012:354]**

474. *Form of lateral eyes: (0) facetted, (1) simple lens with cup-shaped retina, (2) stemmata*. **[R2011:95; L2012:355]**

475. *Proliferation zone of lateral eye field: (0) row-by-row addition, (1) intermediate (*Scutigera*) type, (1) morphogenetic front*. **[R2011:96; L2012:356]**

476. *Compound eyes medial margins: (0) separate, (1) medially contiguous, (2) fused*. **[R2011:97; L2012:357]**

477. *Single enlarged lateral eye: (0) absent, (1) present*. A single enlarged lateral eye is present in cambropachycopids. **[L2013:701]**

478. *Compound eye stalked, basally articulated: (0) absent (eye sessile), (1) present*. **[D2009:12; R2011:98; L2012:358]**

479. *Position of lateral facetted eyes: (0) ventral, (1) dorsal*. **[P2010:3; L2012:359]**

480. *Eyes located close to medial margin of cephalic shield: (0) absent, (1) present.* The lateral eyes of the aglaspidids *Chlupacaris* and *Flobertia* are located on a central node on the cephalic shield. This is in contrast to other aglaspidids which typically have lateral eyes located towards the anterolateral margins of the cephalic shield. **[L2013:601]**

481. *Four or five ventral eyes arranged in a subtransverse band across head shield: (0) absent, (1) present*. **[E2011:9; L2012:360]**

482. *Visual surface with calcified lenses bounded by circumocular suture: (0) absent, (1) present*. **[C2004:21; P2010:4; L2012:361]**

483. *Dorsal bulge in exoskeleton accommodating drop-shaped ventral eyes: (0) absent, (1) present*. **[L2012:362; O2013:22]**

484. *Eye slits: (0) absent, (1) present*. **[L2012:363; O2013:23]**

485. *Compound eyes internalised early in ontogeny, shifted dorsally into a cuticular pocket: (0) absent, (1) present*. **[R2011:99; L2012:364]**

486. *Ophthalmic ridges (0) absent, (1) present*. **[R2011:100; L2012:365]**

487. *Number of corneagenous cells: (0) many, (1) two*. **[R2011:101; L2012:366]**

488. *Corneagenous cells containing pigment grains: (0) corneagenous cells lacking pigment grains, (1) corneagenous cells are primary pigment cells*. **[R2011:102; L2012:367]**

489. *Bipartite distal pigment cells with an inner pigment-free portion, and an outer pigment-bearing portion separated by an extracellular space: (0) distal pigment cells not bipartite, (1) distal pigment cells bipartite*. **[R2011:103; L2012:368]**

490. *Interommatidial pigment cells attached to cornea and basement membrane: (0) absent, (1) present*. **[R2011:104; L2012:369]**

491. *External pigment cells covering whole ocellar corpus: (0) absent, (1) present*. **[R2011:105; L2012:370]**

492. *Ultrastructure of ommatidia: (0) bipartite cone completely round in transverse sections, cone without any extensions, (1) cone with two lateral extensions (in transverse section button-like), formed by one cone cell each.* **[R2001:49; L2013:704]**

493. *Ommatidium with crystalline cone: (0) cone absent, (1) cone present*. **[R2011:106; L2012:371]**

494. *Crystalline cone cells: (0) tetrapartite crystalline cone, lacking accessory cells, (1) cone bipartite, with two accessory cells, (2) pentapartite cone, (3) tripartite cone*. **[R2011:107; L2012:372]**

495. *Reduction of processes of crystalline cone-producing cells: (0) all cells have processes that pass through clear zone and rhabdom, (1) only accessory cells have processes*. **[R2011:108; L2012:373]**

496. *Distally displaced nuclei of accessory crystalline cone cells: (0) absent, (1) present*. **[R2011:109; L2012:374]**

497. *Clear zone between dioptric apparatus and retina: (0) absent (apposition eye), (1) present (superposition eye)*. **[R2011:110; L2012:375]**

498. *Circumretinular sheath cells: (0) absent, (1) present*. **[R2011:111; L2012:376]**

499. *Optic chiasma between lamina and medulla: (0) absent, (1) present*. **[R2011:112; L2012:377]**

500. *Medulla divided into two layers by Cuccati bundle: (0) undivided, (1) divided*. **[R2011:113; L2012:378]**

501. *Lobula or protolobula receiving crossed axons from medulla: (0) absent, (1) present*. **[R2011:114; L2012:379]**

502. *Number of optic neuropils: (0) two, (1) three*. **[R2001:47; L2013:703]**

503. *Third optic neuropil (lobula) separated from protocerebrum: (0) absent, (1) present*. **[R2011:115; L2012:380]**

504. *Fourth optic neuropil (lobula plate), receiving uncrossed axons from medulla: (0) absent, (1) present*. **[R2011:116; L2012:381]**

505. *Lateral eye rhabdomes with quadratic network: (0) absent, (1) present*. **[R2011:117; L2012:382]**

506. *Number of median eyes: (0) none, (1) two, (2) three, (3) four, (4) one (embryonic), (5) one (potential fused) associated with lateral eyes*. **[R2011:118; L2012:383]**

507. *Inverted median eye: (0) absent, (1) present*. **[R2011:119; L2012:384]**

508. *Median eyes fused to naupliar eyes: (0) absent, (1) present*. **[R2011:120; L2012:385]**

509. *Type of naupliar eye: (0) inverse, (1) everse*. **[R2011:121; L2012:386]**

510. *Nauplius eye* sensu stricto*: (0) absent, (1) present*. **[R2001:53; L2013:705]**

511. *Naupliar eye shape: (0) globular, (1) triangular*. **[R2011:122; L2012:387]**

512. *Tapetal cells in cups of naupliar eye: (0) absent, (1) present*. **[R2011:123; L2012:388]**

513. *Bellonci organ: (0) absent, (1) present*. **[L2013:706]**

514. *Dorsal frontal organ (malacostracan type): (0) absent, (1) present*. **[R2011:124; L2012:389]**

515. *Ventral frontal organ: (0) absent, (1) present*. **[L2013:707]**

516. *Ocular tubercle: (0) absent, (1) present*. **[R2011:125; L2012:390]**

517. *Position of ocular tubercle: (0) central, (1) anterior*. This character is coded as applicable only to pycnogonids. **[L2012:391]**

518. *Slit sensilla: (0) absent, (1) present*. **[R2011:46; L2012:392]**

519. *Trichobothria innervated by several sensory cells, with dendrites having only indirect contact with the hair base: (0) absent, (1) present*. **[R2011:126; L2012:393]**

520. *Basal bulb in trichobothria: (0) absent, (1) present*. **[R2011:127; L2012:394]**

521. *Appendage III (arachnid leg 1) with coxapophyses forming preoral chamber: (0) absent, (1) present.* **[S2007:50; L2012:395]**

522. *Shape of coxapophyses 1: (0) triangular, (1) spatulate, (2) lacrimiform*. Scorpions possess elongate coxapophyses on their anterior walking leg coxae (**ch. 521**). Extant taxa tend to possess spatulate or lacrimiform coxapophyses, whereas Palaeozoic taxa tend to have more triangular coxapophyses. **[L2012:396]**

523. *Appendage IV (arachnid leg 2) with coxapophyses forming preoral chamber: (0) absent, (1) present*. **[S2007:51; L2012:397]**

524. *Post-cephalic filter feeding apparatus with sternitic food grooves: (0) absent, (1) present*. **[R2011:145; L2012:398]**

525. *Antennal gland: (0) present, (1) absent.* **[R2001:57; L2013:708]**

526. *Maxillary gland: (0) present, (1) absent*. **[R2001:58; L2013:709]**

527. *Salivary gland position: (0) ectodermal, on second maxilla, (1) mesodermal segmental organs on first maxilla*. **[R2011:191; L2012:399]**

528. *Maxillary salivary gland opening: (0) pair of opening at base of second maxilla, (1) median opening at midventral groove of labium, (2) median opening on salivarium, between labium and hypopharynx*. **[R2011:192; L2012:400]**

529. *Mouth position: (0) terminal, (1) ventral*. **[R2011:128; L2012:401]**

530. *Head / mouth orientation: (0) prognathous, mouth directed anteroventrally, (1) hypognathous, mouth directed ventrally, (2) mouth directed posteriorly, (1) mouth directed ventrally (non-hypognathous)*. **[R2011:129; L2012:402]**

531. *Proboscis: (0) absent, (1) present.* **[L2012:403]**.

532. *Radially arranged circumoral structures (papillae, plates or lamellae): (0) absent (bilaterally symmetrical mouthparts), (1) present*. **[R2011:130; L2012:404]**

533. *Circumoral structures as a circlet of overlapping plates with teeth on their inner margins ("peytoia apparatus"): (0) absent, (1) present*. **[R2011:131; L2012:405]**

534. *Oral papillae: (0) absent, (1) present*. **[L2011:2; L2013:710]**

535. *Oral cone: (0) absent, (1) present*. The circumoral mouth parts of dinocaridids is sclerotized into an oral cone with a varied morphology (**ch. 536**) **[L2013:711]**

536. *Structure of mouth part apparatus (ch. 405): (0) variable number of undifferentiated plates, (1) 32 plates with differentiation of four enlarged plates in a cross arrangement.* **[D2009:8; L2013:712]**

537. *Epistome-labrum / clypeolabrum: (0) absent, (1) present*. **[R2011:132; L2012:406]**

538. *Sclerotization of epistome-labrum / clypeolabrum (hypostome): (0) absent, (1) present*. **[L2012:407]**

539. *Hypostome attachment: (0) wide attachment, with or without suture, (1) natant, (2) narrow overlap with pre-hypostome, (3) narrow attachment at hypostomal suture*. **[P2010:12; L2012:408]**

540. *Hypostome divided into anterior and posterior parts by transverse suture: (0) absent, (1) present*. **[P2010:13; L2012:409]**

541. *Specialised copepodoid cephalo-thoracic feeding apparatus: (0) absent, (1) present*. Copepods, mystacocarids and the Cambrian 'Orsten' taxon *Skara* possess a similar feeding system, described in detail by Haug *et al*. (2011b). **[L2013:713]**

542. *Fleshy labrum: (0) absent, (1) present*. **[R2011:133; L2012:410]**

543. *Labral posterior tooth: (0) absent, (1) present*. **[R2001:16; L2013:714]**

544. *Entognathy (overgrowth of mandibles and maxillae by cranial folds): (0) absent, (1) present*. **[R2011:134; L2012:411]**

545. *Admentum differentiated latero-ventrally on each side of head capsule, developed from posterior part of mouth fold: (0) absent, (1) present*. **[R2011:135; L2012:412]**

546. *Sclerotic sternum formed by antennal to maxillulary sternites, including paragnaths on mandibular sternum: (0) absent, (1) present*. **[R2011:136; L2012:413]**

547. *Intercheliceral epipharygeal sclerite: (0) absent, (1) present*. **[S2007:191; L2012:414]**

548. *Gnathosoma: (0) absent, (1) present*. **[S2007:32; L2013:715]**

549. *Tritosternum: (0) absent, (1) present*. **[R2011:137; L2012:415]**

550. *Postcerebral pharynx: (0) absent, (1) present*. **[S2007:199; L2012:416]**

551. *Hypopharynx: (0) absent or only median lingua, (1) complete hypopharynx of lingua and paired superlinguae*. **[R2011:138; L2012:417]**

552. *Fulturae: (0) absent or limited to a hypopharyngeal suspensor, (1) present, in a groove between arthrodial membrane of maxilla and labium*. **[R2011:139; L2012:418]**

553. *Posterior process of tentorium fused anteriorly with hypopharyngeal bar and transverse bar: (0) absent, (1) present*. **[R2011:140; L2012:419]**

554. *Triradiate pharyngeal lumen: (0) absent, (1) present*. **[R2011:141; L2012:420]**

555. *Flexible buccal tube and stylet apparatus: (0) absent, (1) present*. **[R2011:142; L2012:421]**

556. *Three-branched epistomal skeleton supporting the pharyngeal dilator muscles: (0) absent, (1) present*. **[R2011:143; L2012:422]**

557. *U-shaped anterior gut diverticulae: (0) absent, (1) present*. A U-shaped anterior gut diverticula is present in fuxianhuiids, e.g. *Chengjiangocaris* (Budd 2008) and *Perspicaris*. **[L2012:423]**

558. *Proventriculus (in the foregut): (0) absent, (1) present*. **[R2011:228; L2012:424]**

559. *Lateralia and inferolateralia anteriores in the cardiac chamber: (0) absent, (1) present*. **[R2011:229; L2012:425]**

560. *Unpaired superomedianum at transition from cardia to pyloric chamber: (0) absent, (1) present*. **[R2011:230; L2012:426]**

561. *Inferomedianum anterius (midventral cardiac ridge): (0) absent, (1) present*. **[R2011:231; L2012:427]**

562. *Inferomedianum posterius (midventral pyloric ridge): (0) absent, (1) present*. **[R2011:232; L2012:428]**

563. *Atrium between inferomediana connecting cardiac primary filter grooves with pyloric filter grooves: (0) absent, (1) present*. **[R2011:233; L2012:429]**

564. *Formation of the midgut: (0) by entoderm, (1) at the border between stomodaeum and proctodaeum*. **[R2001:73; L2013:716]**

565. *Gut caecae: (0) absent, (1) present along the midgut, (2) restricted to the anterior part of the midgut*. **[R2011:234; L2012:430]**

566. *Serially repeating midgut glands: (0) absent, (1) reniform, metameric midgut glands with submillimetric lamellae, (2) radiating tubular diverticula.* **[D2009:16; R2011:235; L2012:431]**

567. *Proctodeal dilation: (0) posterior section of hindgut simple, lacking a dilation, (1) proctodeum having a rectal ampulla with differentiated papillae*. **[R2011:236; L2012:432]**

568. *Pyloric region with ring of flattened cells with thick intima: (0) absent, (1) present*. **[R2011:237; L2012:433]**

569. *Peritrophic membrane: (0) absent, (1) present*. **[R2011:238; L2012:434]**

570. *Tubular, radiating diverticula with intracellular digestion: (0) absent, (1) present*. **[R2011:239; L2012:435]**

571. *Metanephridia with sacculus with podocytes: (0) absent, (1) present*. **[R2011:29; L2012:436]**

572. *Distribution of segmental glands: (0) on many segments, (1) in at most last four segments and first two post-cephalic segments, (2) on second antennal and maxillary segments only*. **[R2011:30; L2012:437]**

573. *Maxillary nephridia: (0) absent in postembryonic stadia, (1) paired, (2) fused nephridia of both maxillary segments*. **[R2011:31; L2012:438]**

574. *Coxal gland orifice, leg I: (0) absent, (1) present*. **[R2011:32; L2012:439]**

575. *Tömösváry organ ("temporal organs" at side of head behind insertion of antennules): (0) absent, (1) present*. **[R2011:33; L2012:440]**

576. *Salivary gland reservoir: (0) absent, (1) present*. **[R2011:34; L2012:441]**

577. *Malpighian tubules formed as endodermal extensions of the midgut: (0) absent, (1) present*. **[R2011:35; L2012:442]**

578. *Malpighian tubules formed as ectodermal extensions of the hindgut: (0) absent, (1) single pair of juncture of midgut and hindgut, (2) multiple pairs at anterior end of hindgut*. **[R2011:36; L2012:443]**

579. *Form of ectodermal Malpighian tubules: (0) elongate, (1) papillate*. **[R2011:37; L2012:444]**

580. *Neck organ: (0) absent, (1) present*. **[R2011:38; L2012:445]**

581. *Coxal organs on last pair of legs: (0) absent, (1) present*. **[R2011:378; L2012:446]**

582. *Pair of repugnatorial glands in the carapace: (0) absent, (1) present*. **[R2011:380; L2012:447]**

583. *Position of repugnatorial glands: (0) on the side of the cephalic shield, visible from above, (1) below the side of the cephalic shield, not visible from above*. **[G2002:13; L2013:728]**

584. *Pleural defense glands with benzoquinones: (0) absent, (1) present*. **[R2011:381; L2012:448]**

585. *Aculeus with sting / opisthosomal venom gland: (0) absent, (1) present*. **[R2011:382; L2012:449]**

586. *Shape of aculeus: (0) rounded, (1) lacrimiform*. The basal portion of the aculeus is lacrimiform in Carboniferous and extant scorpions, but rounded and bulbous in Silurian scorpions. **[L2012:450]**

587. *Posterior oblique muscles of Box-Truss Axial Muscle System (BTAMS): (0) absent, (1) present*. **[S2007:127; L2012:451]**

588. *Endosternum (ventral tendons fused into prosomal endosternum): (0) absent, (1) present*. **[R2011:259; L2012:452]**

589. *Endosternum fenestrate: (0) absent, (1) present*. **[S2007:130; L2012:453]**

590. *Suboral suspensor: (0) absent, (1) present*. **[S2007:131; L2012:454]**

591. *Ventral endosternal suspensor attached on coxa of anterior adjacent somite: (0) absent, (1) present*. **[S2007:133; L2012:455]**

592. *Dorsal endosternal suspensor of fourth postoral segment with anterolateral carapacal insertion: (0) absent, (1) present*. **[R2011:260; L2012:456]**

593. *Trunk endoskeleton in each segment: (0) pair of lateral connective plates, (1) pair of sternocoxal rods (ventral apodemes), (2) complex connective endosternite, (3) mainly cuticular, composed of two intrasegmental furcal arms and intersegmental spinal process*. **[R2011:269; L2012:457]**

594. *Oblique muscle layer in body wall: (0) no oblique layers, (1) oblique layers*. **[R2011:220; L2012:458]**

595. *Longitudinal muscles attach to intersegmental tendons: (0) absent, (1) present*. **[R2011:275; L2012:459]**

596. *Longitudinal muscles: (0) united sternal and lateral longitudinal muscles, (1) separate sternal and longitudinal muscles, with separate segmental tendons*. **[R2011:221; L2012:460]**

597. *Superficial pleural muscles: (0) absent, (1) present*. **[R2011:222; L2012:461]**

598. *Crossed, oblique dorsoventral muscles: (0) absent, (1) present*. **[R2011:223; L2012:462]**

599. *Deep dorsoventral muscles in the trunk: (0) absent, (1) present*. **[R2011:224; L2012:463]**

600. *Circular body muscle: (0) present, (1) present*. **[R2011:225; L2012:464]**

601. *Discrete segmental cross-striated muscles attached to cuticular apodemes: (0) absent, (1) present*. **[R2011:226; L2012:465]**

602. *Trunk muscles: (0) straight, (1) twisted*. **[R2011:227; L2012:466]**

603. *Pleon musculature: (0) simple, (1) precaridoid, (2) cardioid*. **[R2001:59; L2013:717]**

604. *Haemoglobin: (0) absent, (1) present*. **[R2011:39; L2012:467]**

605. *Subcutaneous hemal channels in body wall: (0) absent, (1) present*. **[R2011:40; L2012:468]**

606. *Dorsal heart with segmental ostia and pericardial sinus: (0) absent, (1) present*. **[R2011:41; L2012:469]**

607. *Number of pairs of ostia: (0) more than five, (1) five, (2) three, (3) two, (4) one, (5) none*. **[R2001:61; L2013:718]**

608. *Extension of heart: (0) in whole thorax (head in part) and pleon, (1) thorax, (2) only posterior part of thorax and pleon*. **[R2001:62; L2013:719]**

609. *General form of heart: (0) long, extended, (1) bulbous, (2) simple, short.* **[R2001:63; L2013:720]**

610. *Arteria subneuralis/supraneuralis: (0) absent, (1) present*. **[R2001:64; L2013:721]**

611. *Aorta descendens: (0) undivided sternal artery passes through the nervous system, (1) sternal artery branches off into three branches dorsal of the ventral nervous system, all branches pass separately through the nerve cord*. **[R2001:66; L2013:722]**

612. *Atrium between the inferomediana connecting the cardac primary filter grooves with the pyloric filter grooves: (0) absent, (1) present*. **[R2001:71; L2013:723]**

613. *Number of secondary filter grooves in the inferomedianum posterius: (0) numerous, (1) eight to six, (2) three, (3) two, (4) one.* **[R2001:72; L2013:724]**

614. *Internal valves formed by lips of ostiae projecting deeply into heart lumen (to prevent haemolymph backflow within the heart): (0) absent, (1) present.* **[R2011:42; L2012:470]**

615. *Circumesophageal circulatory loop with ventral trumpet-shaped opening toward head: (0) absent, (1) present*. **[R2011:43; L2012:471]**

616. *Aorta descendens connects heart and ventral vessel: (0) absent, (1) present*. **[R2011:44; L2012:472]**

617. *Myoarterial formation with aortic dilations associated with oesophageal dilator muscles: (0) absent, (1) present*. **[R2011:45; L2012:473]**

618. *Respiratory exites: (0) absent, (1) present*. This character is coded as present in arthropods, including dinocaridids which possess lateral, possibly repiratory, extensions of the body. **[L2012:474]**

619. *Dorsal bands of blade-like gills: (0) absent, (1) present*. **[D2009:41; R2011:261; L2012:475]**

620. *Lamellate respiratory organ derived from posterior wall of opisthosomal limb buds: (0) absent, (1) present*. **[R2011:243; L2012:476]**

621. *Spines on lamellar margins: (0) absent, (1) present*. See Scholtz and Kamenz (2006) for a discussion of characters **621-623**. **[L2012:477]**

622. *Shape of pillars of haemolymph space inside gill/lung lamellae: (0) at least two perikarya meeting midway in the haemolymph space, (1) pillars, including a strong axis of microtubules*. [**L2012:478]**

623. *Lamellar orientation: (0) horizontal, (1) vertical*. **[L2012:479]**

624. *Respiratory lamellae on opisthosomal somite 2: (0) absent, (1) present*. **[S2007:121; L2012:480]**

625. *Respiratory lamellae on opisthosomal somite 3: (0) absent, (1) present*. **[S2007:122; L2012:481]**

626. *Respiratory lamellae on opisthosomal somites 4-6: (0) absent, (1) present*. **[S2007:123; L2012:482]**

627. *Respiratory lamellae on opisthosomal somites 7: (0) absent, (1) present*. **[S2007:124; L2012:483]**

628. *Tracheae / spiracles: (0) absent, (1) pleural spiracles, (2) spiracles at bases of walking legs, opening into tracheal pouches, (3) single pair of spiracles on head, (4) dorsal spiracle opening to tracheal lungs, (5) open-ended tracheae with spiracle on second opisthosomal segment, (6) many spiracles scattered on body, (7) pair of spiracles in the collar region, (8) four pairs of opisthosomal stigmata with irregular unprotected openings, (9) opening on opisthosomal somites 3 and 4*. **[R2011:312; L2012:484]**

629. *Longitudinal and transverse connections between segmental tracheal branches: (0) tracheae not connected, (1) tracheae connected*. **[R2011:313; L2012:485]**

630. *Pericardial tracheal system with chiasmata: (0) dendritic tracheae, (1) long, regular pipe-like tracheae with specialised moulting rings*. **[R2011:314; L2012:486]**

631. *Abdominal spiracles: (0) present (pleural spiracles on posterior part of trunk), (1) absent on first abdominal segment, (2) absent on all abdominal segment*. **[R2011:315; L2012:487]**

632. *Intrasternite stigmata: (0) absent (opening to book-lungs at margin of sternite), (1) present*. **[R2011:246; L2012:488]**

633. *Carapace: (0) non-respiratory, (1) with respiratory function*. **[R2001:7; L2013:725]**

634. *Respiratory function in pleopods: (0) absent, (1) present*. **[R2001:41; L2013:726]**

635. *Cylindroleberidid-type gills: (0) absent, (1) present*. **[L2013:727]**

636. *Crural glands: (0) absent, (1) present*. **[R2011:379; L2012:489]**

637. *Female abdomen with ovipositor formed by gonapophyses of segments VIII and IX: (0) absent, (1) present*. **[R2011:331; L2012:490]**

638. *Gonangulum sclerite fully developed as ovipositor base, articulating with tergum IX and attached to 1st valvula / valvifer: (0) absent, (1) present*. **[R2011:332; L2012:491]**

639. *Gonads: (0) primarily prosomal, (1) primarily opisthosomal*. **[S2007:151; L2012:492]**

640. *Ladder-like opisthosomal glands: (0) absent, (1) present*. **[S2007:152; L2012:493]**

641. *Male gonads on two distinct parts, one producing sperm and another producing a holocrine secretion similar to degenerate sperm: (0) absent, (1) present*. **[S2007:153; L2012:494]**

642. *Genital opening appearing to open in prosomal region: (0) absent, (1) present*. **[S2007:155; L2012:495]**

643. *Ovipositor: (0) absent, (1) present*. **[R2011:333; L2012:496]**

644. *Ovipositor morphology: (0) segmented (jointed type), (1) unsegmented (unjointed type)*. **[G2002:173; L2013:740]**

645. *Spermatophore: (0) absent, (1) present*. **[R2001:80; L2013:739]**

646. *Spermatophore sclerotized: (0) absent, (1) present*. See Kamenz *et al*. (2011) for a discussion of characters **646** and **647**. **[L2012:497]**

647. *Stalked spermatophore attached to substratum: (0) absent, (1) present*. **[L2012:498]**

648. *Legs of seventh trunk segment transformed into gonopods: (0) absent, (1) present*. **[R2011:334; L2012:499]**

649. *Dignathan-type penes: (0) absent, (1) present*. **[R2011:335; L2012:500]**

650. *Penis (spermatopositor) opening on anteroventral part of opisthosoma: (0) absent, (1) present*. **[R2011:336; L2012:501]**

651. *Penis form: (0) short, membranous, undivided, (1) long, chitinous, divided into shaft and glans*. **[R2011:337; L2012:502]**

652. *Genital appendage: (0) absent, (1) present*. A genital appendage is present in eurypterids and chasmataspidids. **[L2012:503]**

653. *Male parameres: (0) undifferentiated, (1) pair of lateral plates on segment XI, (2) pair of parameres on segment IX, (3) incorporated into phallic apparatus as sclerite*. **[R2011:338; L2012:504]**

654. *Penis on abdominal segment IX: (0) absent, (1) present*. **[R2011:339; L2012:505]**

655. *Female gonopore position: (0) on same somite as male, (1) two segments anterior to male, (2) six segments anterior to male, (3) seven segments anterior to male*. **[R2011:340; L2012:506]**

656. *Female gonopore parity: (0) paired, (1) medium, unpaired*. **[R2011:341; L2012:507]**

657. *Genital operculum divided, incorporated into pedicel: (0) absent, (1) present*. **[R2011:342; L2012:508]**

658. *Lacrimiform genital operculae: (0) absent, (1) present*. The genital operculae of *Compsoscorpius* and extant scorpions are lacrimiform. **[L2012:509]**

659. *Genital operculum overlapping third opisthosomal sternite: (0) absent, (1) present*. **[R2011:343; L2012:510]**

660. *Postgenital appendages: (0) opercular and/or lamellar, (1) poorly sclerotized or eversible, (2) absent*. **[R2011:344; L2012:511]**

661. *Embryonic gonoduct origin: (0) gonoduct arising as a mesodermal coelomoduct, (1) gonoduct arising as a secondary ectodermal ingrowth, (2)*

gonoduct arising in association with splanchnic mesoderm. **[R2011:345; L2012:512]**

662. *Lateral testicular vesicles linked by central, posteriorly-extended deferens duct: (0) absent, (1) present*. **[R2011:346; L2012:513]**

663. *Testicular follicles with pectinate arrangement: (0) absent (elongate testicular sac or sacs), (1) several pectinate follicles present*. **[R2011:347; L2012:514]**

664. *Spermatophore web produced by „Spingriffel" structure: (0) absent, (1) present*. **[R2011:348; L2012:515]**

665 *Sperm dimorphism (microsperm and macrosperm): (0) absent, (1) present*. **[R2011:350; L2012:516]**

666. *Acrosomal complex in sperm: (0) bilayered (filamentous actin perforatorium present), (1) monolayered (perforatorium absent), (2) acrosome absent*. **[R2011:351; L2012:517]**

667. *Pseudoacrosome with dorsal ribbon, granulosome, apical membrane and pseudoacrosomal granular material: (0) absent, (1) present*. **[R2011:352; L2012:518]**

668. *Perforatorium bypasses nucleus: (0) absent (perforatorium penetrates nucleus), (1) present*. **[R2011:353; L2012:519]**

669. *Periacrosomal material: (0) absent, (1) present*. **[R2011:354; L2012:520]**

670. *Striated core in subacrosomal space: (0) absent, (1) present*. **[R2011:355; L2012:521]**

671. *Sperm nuclear membrane: (0) present, (1) absent, chromatine diffuse.* **[R2001:77; L2013:736]**

672. *Sperm microtubular arms or spikes: (0) absent, (1) present*. **[R2001:78; L2013:737]**

673. *Cross striated perforatorium (possible centriolar root homologous): (0) absent, (1) present*. **[R2001:79; L2013:738]**

674. *Centrioles in sperm: (0) proximal and distal centrioles present, perpendicular to each other, (1) coaxial centrioles, (2) single centriole, (3) centrioles absent, (4) doublet centrioles with radial „foot"*. **[R2011:356; L2012:522]**

675. *Centriole adjunct: (0) absent, (1) present*. **[R2011:357; L2012:523]**

676. *Sperm „accessory bodies" developed from the centriole: (0) absent, (1) present*. **[R2011:358; L2012:524]**

677. *Cristate, non-crystalline mitochondrial derivatives in sperm: (0) absent, (1) present*. **[R2011:359; L2012:525]**

678. *Three filamentous mitochondria symmetrically derivatives in sperm: (0) absent, (1) present*. **[R2011:360; L2012:526]**

679. *Connecting bands between axoneme and mitochondria: (0) absent, (1) present*. **[R2011:361; L2012:527]**

680. *Axoneme parallels entire length of nucleus: (0) absent, (1) present*. **[R2011:362; L2012:528]**

681. *Supernumary axonemal tubules (peripheral singlets): (0) absent, (1) present, formed from the manchette, (2) present, formed from axonemal doublets*. **[R2011:363; L2012:529]**

682. *Number of protofilaments in wall of accessory tubules: (0) 13, (1) 16*. **[R2011:364; L2012:530]**

683. *Mediodorsal peripheral doublet (doublet 1) connected to dorsal ribbon by an obliquely orientated membrane: (0) absent, (1) present*. **[R2011:365; L2012:531]**

684. *Axonemal endpiece „plume": (0) endpiece not extended, (1) endpiece extended, plume-like*. **[R2011:366; L2012:532]**

685. *Sperm motility: (0) present, (1) absent*. **[R2011:367; L2012:533]**

686. *Nucleus of sperm forms spiral ridge: (0) absent, (1) present*. **[R2011:368; L2012:534]**

687. *Sperm nucleus with manchette of microtubules: (0) absent, (1) present*. **[R2011:369; L2012:535]**

688. *Coiling of spermatozoa flagellum: (0) absent (filiform), (1) present*. **[R2011:370; L2012:536]**

689. *Medial microtubules in spermatozoan axoneme: (0) 9+2, (1) 9+3, (2) 9+0, (3) 12+0, (4) 9+1*. **[R2011:371; L2012:537]**

690. *Sperm conjugation: (0) absent, (1) present*. **[R2011:372; L2012:538]**

691. *Female spermathecae formed by paired lateral pockets in mouth cavity: (0) absent, (1) present*. **[R2011:373; L2012:539]**

692. *Ovary shape: (0) sac- or tube shaped, entire, (1) divided into ovarioles, (2) ovarian network*. **[R2011:374; L2012:540]**

693. *Location of ovary germarium: (0) germarium forms elongate zone in the ventral or lateral ovarian wall, (1) germarium in the terminal part of each egg*

tube, (2) single, median mound-shaped germarium on the ovarian floor, (3) paired germ zones on ovarian wall, (4) median zone on ovarian roof. **[R2011:375; L2012:541]**

694. *Subdivision of ovary into a well-defined anterior germarium and an elongate vitellarium: (0) absent, (1) present.* See Kubrakiewicz *et al*. (2012) for a discussion of characters **694-696**. **[L2013:729]**

695. *Localization of the germaria within the trunk and/or head region of the body: (0) absent, (1) present*. **[L2013:730]**

696. *Unpolarized somatic cells accommodating germline cells: (0) absent, (1) present*. **[L2013:731]**

697. *Site of oocyte growth: (0) in ovarian lumen, (1) on outer surface of ovary, in haemocoel, connected by egg stalk*. **[R2011:376; L2012:542]**

698. *Ventral marsupium formed by oostegites: (0) absent, (1) present*. **[R2011:377; L2012:543]**

699. *Oostegite position: (0) on thoracopods 2-8, (1) on thoracopods 2-6, (2) on thoracopods 3-6.* **[R2001:28; L2013:733]**

700. *Reduction of the oostegites after every brood: (0) absent, (1) present*. **[R2001:29; L2013:734]**

701. *First and/or second pleopods modified for sperm transfer in males: (0) absent, (1) somatopod petasma, including modification of the exopods of the second pleopod, (2) endopod of the first pleopod completely modified for sperm transfer, modification different in the second endopod*. **[R2001:39; L2013:735]**

702. *Ventral brood pouch: (0) absent, (1) present*. **[O2009:56; L2013:732]**

A2.2.2. Development

703. *Non-migratory gastrulation (extremely limited movement of small-celled presumptive areas: (0) absent, (1) present.* **[R2011:1; L2012:544]**

704. *Early cleavage: (0) total cleavage with radially oriented position of cleavage products, (1) intralecithal cleavage (nuclei undergo several divisions within the yolk mass without concurrent cytokinesis)*. **[R2011:2; L2012:545]**

705. *Role of serosa (= cuticle secreting membrane) in definitive dorsal closure (formation of dorsal body wall): (0) serosa and embryo contribute to definitive dorsal closure, (1) provisional dorsal closure (serosa degenerates without contributing to definitive dorsal closure)*. **[R2011:3; L2012:546]**

706. *Differentiation of amnion as provisional dorsal closure of embryo: (0) absent, (1) present*. **[R2011:4; L2012:547]**

707. *Blastokinesis: (0) absent, (1) open amnionic cavity, (2) closed amnionic cavity, amnioserosal fold fuses beneath the embryo*. **[R2011:5; L2012:548]**

708. *Blastodermal cuticle (cuticular egg envelope): (0) absent, (1) present*. **[R2011:6; L2012:549]**

709. *Ectoteloblasts (forming part of metanaupliar/egg-naupliar region of germ band): (0) absent, (1) present at anterior border of blastopore*. **[R2011:7; L2012:550]**

710. *Number of ectoteloblasts: (0) 19, (1) variable, (2) none*. **[R2001:86; L2013:744]**

711. *Arrangement of ectoblasts: (0) forming a ring around the caudal papilla (giving rise to embryonic ventral and dorsal material), (1) forming a transverse row (only the ventral side of the embryo is formed by ectoteloblasts and the dorsal side is closed much later in development)*. **[R2001:87; L2013:745]**

712. *Caudal papilla: (0) absent, (1) present, anteroventrally folded, derived from preanal growth zone*. **[R2011:8; L2012:551]**

713. *Origin of fat body: (0) fat body cells developed from vitellophages in yolk, (1) fat body cells developed from walls of mesodermal somites*. **[R2011:9; L2012:552]**

714. *Yolk distribution in the embryo: (0) posterior part of the embryo contains no yolk, (1) posterior part of the embryo contains yolk*. **[R2001:89; L2013:747]**

715. *Midgut developed into yolk: (0) midgut cells enclose the yolk, (1) lumen of embryonic midgut lacking yolk globules*. **[R2011:10; L2012:553]**

716. *Fate map ordering of embryonic tissues: (0) presumptive mesoderm posterior to presumptive midgut, (1) presumptive mesoderm anterior to midgut, (2) mesoderm midventral, cells sink and proliferate, midgut internalises during cleavage, (3) mesoderm diffuse through ectoderm, (4) midgut develops from anterior/posterior rudiments at each end of midventral mesoderm band*. **[R2011:11; L2012:554]**

717. *Fate of embryonic growth zone (in chelicerates): (0) with a growth zone rising to both the prosoma and opisthosoma, (1) with a growth zone giving rise to the opisthosoma*. **[R2011:12; L2012:555]**

718. *Direct development: (0) absent, (1) present*. **[R2001:82; L2013:741]**

719. *Epimorphic development: (0) absent, (1) present*. **[R2011:13; L2012:556]**

720. *Nauplius larva (orthonauplius) or egg-nauplius: (0) absent, (1) present*. **[R2011:14; L2012:557]**

721. *Free-living nauplius larva: (0) present, (1) absent*. **[R2001:83; L2013:742]**

722. *Folding of early embryo: (0) ventrally folded, (1) dorsally folded*. **[R2001:88; L2013:746]**

723. *Pupoid stage (motionless stage after hatching, pupoid remains encased in embryonic cuticle): (0) absent, (1) present*. **[R2011:15; L2012:558]**

724. *Imaginal (pre-adult) moult: (0) present, (1) absent*. **[R2011:16; L2012:559]**

725. *Cyclic parthenogenesis as part of the life cycle: (0) absent, (1) present*. **[R2011:17; L2012:560]**

726. *Development of appendages: (0) advanced development of anterior head appendages, (1) continuous anteroposterior decrease in the degree of appendage formation*. **[R2001:84; L2013:744]**

727. *Number of thoracic appendages in hatchling: (0) eight, (1) seven, (2) six*. **[R2001:90; L2013:748]**

728. *Embryonic dorsal organ: (0) present, (1) absent*. **[R2001:91; L2013:749]**

729. *Form of embryonic dorsal organ: (0) simple layer, (1) cup-shaped*. **[R2001:92; L2013:750]**

730. *Transient paired dorsal organs: (0) absent, (1) present*. **[R2001:93; L2013:751]**

731. *Cyprid larva: (0) absent, (1) present*. A non-feeding, pre-attachment, larval stage is present in *Balanus*, *Semibalanus* and *Rhamphoverritor*. **[L2013:752]**

A2.2.3. Behaviour

732. *Tail fan escape reaction: (0) absent, (1) present*. **[R2011:322; L2012:561]**

733. *Egg cluster guarded until hatching, female coiling around egg cluster: (0) absent, (1) female coils ventrally around cluster, (2) female coils dorsally around egg cluster*. **[R2011:328; L2012:562]**

734. *Peripatoid and foetoid stages protected by mother: (0) absent, (1) present*. **[R2011:329; L2012:563]**

735. *Female gonopod used to manipulate single egg: (0) absent, (1) present*. **[R2011:330; L2012:564]**

736. *"By-passing" foreplay, spermatophore transfer on web, "waiting" ritual by females: (0) absent, (1) present*. **[R2011:349; L2012:365]**

737. *Brood care: (0) absent, (1) brood care with thoracopods without feeding by the mother, (2) brood care attaching the eggs to the pleopods, (3) brood care using a dorsal brood pouch, (4) brood care using a marsupium formed by oostegites, (5) brood care using elongated first pleopod.* **[R2001:81; L2013:753]**

A2.2.4. Gene order and gene expression

738. Distal-less *expression in mandible (or positionally equivalent limb): (0) present (including transient expression in embryo and in palp), (1) absent*. **[R2011:167; L2012:223]**

739. Labial *expression domain: (0) expressed over multiple segments, (1) expression confined to second antenna/intercalary segment*. **[R2011:383; L2012:566]**

740. Proboscipedia *expression domain: (0) collinear with labial and deformed domains, (1) anterior boundary of main expression domain of* proboscipedia *behind anterior boundary of* Deformed. **[R2011:384; L2012:567]**

741. Deformed *expression domain: (0) expressed over three or more segments, (1) expression confined to mandibular and first maxillary segment*. **[R2011:385; L2012:568]**

742. Antennipedia *expression domain: (0) strong throughout trunk, (1) restricted from the posterior of the embryo*. **[R2011:386; L2012:569]**

743. *Antisense* Ubx *expression: (0) absent, (1) present.* Antisense *Ultrbithorax* expression is present in myriapods but absent in all other extant arthropods and onychophorans (Janssen and Budd 2010). **[L2012:570]**

744. *Relative position of COI and COII: (0) COI/COII, (1) COI/L2/COII*. **[R2011:387; L2012:571]**

745. *Relative position of tRNA-L: (0) 1su rRNA/L1/L2/NADH 1, (1) 1su rRNA/L1/NADH 1, (2) NADH 1/H"/1su rRNA/L1, (3) 1su rRNA/NADH 1, (4) 1su rRNA/L1/L2/Cytb*. **[R2011:388; L2012:572]**

746. *Relative postion of tRNA-R and tRNA-N: (0) R/N, (1) R/K/N, (2) N/E/R, (3) N/A/S1/R, (4) R/S1*. **[R2011:389; L2012:573]**

747. *Relative position of tRNA-C and tRNA-Y: (0) Y/C, (1) Y/Q/C, (2) C/Q, (3) Q/Y/C, (4) Q/Y/F, (5) Q/I/C*. **[R2011:390; L2012:574]**

748. *Relative position of tRNA-P and tRNA-T: (0) T/-P, (1) –P/T, (2) T between W and cytb, (3) P between nad4L and nad1, (4) T between S2 and nad1*. **[R2011:391; L2012:575]**

749. Distal-less *expression domain in limbs: (0) expression throughout entire medial and distal part of appendage, (1) „ring and sock" pattern (gap in expression between tibia and femur)*. **[R2011:392; L2012:576]**

750. Dachshund *expression domain in limbs: (0) expression proximally (in trochanter and femur), (1) expression distally in a narrow band*. **[R2011:393; L2012:577]**

751. Extradenticle *expression domain in limbs: (0) expression present in distal part of leg, (1) expression confined to proximal part of leg*. **[R2011:394; L2012:578]**

752. Homothorax *expression domain in limbs: (0) expression lacking in distal part of leg, (1) expression along length of leg*. **[R2011:395; L2012:579]**

753. Collier *expression in the intercalary segment: (0) absent, (1) present*. The *Drosophila collier* ortholog is expressed in the intercalary segment of myriapods and hexapods (Janssen *et al*. 2011). **[L2012:580]**