

The Arthropoda: A Phylogenetic Framework

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2.1 Introduction

Arthropoda, the best-known member of the clade Ecdysozoa, is a phylum of protostome animals, its closest relatives being Onychophora (velvet worms) and Tardigrada (water bears). Arthropods are not only the largest living phylum in terms of species diversity, with 1,214,295 extant species, including 1,023,559 Hexapoda, 111,937 Chelicerata, 66,914 Crustacea and 11,885 Myriapoda (Zhang 2011), but they have probably been so since the Cambrian. The number of fossil arthropods is even harder to estimate; the EDNA fossil insect database lists ca. 25,000 species (<http://edna/palass-hosting.org/>); 1,952 valid species of fossil chelicerates were reported by Dunlop et al. (2008), and the decapod crustaceans include 2,979 fossil species (De Grave et al. 2009). Trilobites (19,606 species fide Adrain 2011) and ostracods (>50,000 species) are two of the best-represented arthropod groups in the fossil record.

Arthropods are also, together with Mollusca and Annelida, among the animal phyla with the greatest body plan disparity. This astonishing diversity and disparity of extant and extinct lineages have inspired hundreds of published research articles discussing different aspects of their phylogenetic framework, first focusing on anatomy and embryology, and later being strongly influenced by functional morphology. The advent of cladistic techniques in the mid-twentieth century and the widespread use of

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molecular data in the last 25 years—the first molecular approach to arthropod phylogeny was published in 1991 by Turbeville et al. (1991)—have revolutionized our understanding of the *Arthropod Tree of Life*. Given the amount of effort revisiting and reviewing arthropod phylogenetics, this chapter will touch upon some of the most fundamental questions: (a) the relationship of arthropods with other key protostome phyla and (b) the relationships between the major arthropod lineages (often referred to as classes, superclasses or subphyla: Pycnogonida, Euchelicerata, Myriapoda and Tetraconata—Tetraconata or Pancrustacea is widely accepted as a clade of arthropods that include the traditional classes Crustacea and Hexapoda, the former often found to be paraphyletic with respect to the latter). Finally, this chapter will provide a roadmap for future focus in arthropod phylogenetic and evolutionary research.

2.2 Arthropods in the Animal Tree of Life

Arthropods are protostome animals, and like other protostomes, they have an apical dorsal brain with a ventral longitudinal paired nerve cord and a mouth that typically originates from the embryonic blastopore. They have been traditionally considered to have a primary body cavity, or coelom, that has been restricted to the pericardium, gonoducts and nephridial structures (coxal glands, antennal/maxillary glands) (Brusca and Brusca 2003), but the true coelomic nature of arthropods has been recently called into question. The only putative coelomic cavities in *Artemia salina*, one of the species that underpinned former ideas about arthropods having a coelom, are the nephridial sacculus in the second antennal and second maxillary segments. However, these have been shown not to be remnants of any primarily large coelomic cavity (Bartolomaeus et al. 2009). Similarly, although many authors at one time considered arthropods to have a modified spiral cleavage (Anderson 1969)—as found in annelids, molluscs, nemerteans and platyhelminths

(Maslakova et al. 2004)—this idea is now rejected (Scholtz 1998).

The systematic position of arthropods has changed radically in the past two decades as a result of refinements in numerical phylogenetic analysis and even more so by the introduction of molecular data. Traditionally, arthropods, onychophorans and tardigrades—the three collectively known as Panarthropoda or Aiolopoda—were grouped with annelids in a clade named Articulata (Cuvier 1817), in reference to the segmental body plan in these phyla (Scholtz 2002). The competing Ecdysozoa hypothesis (Schmidt-Rhaesa et al. 1998; Giribet 2003) unites arthropods, onychophorans and tardigrades with a group of mostly pseudocoelomate animals with which they share a cuticle that is moulted at least once during the life cycle and lacks epidermal ciliation. Ecdysozoa was proposed originally on the basis of 18S rRNA sequence data (Aguinaldo et al. 1997; Giribet 1997; Giribet and Ribera 1998) but has subsequently been shown to have support from diverse kinds of molecular information (Edgecombe 2009) (see examples listed below). Concurrently, support has waned for the putative clade once thought to unite arthropods with annelids, despite various morphological phylogenies that retrieved Articulata (e.g. Nielsen et al. 1996; Sørensen et al. 2000; Nielsen 2001; Brusca and Brusca 2003). Contradictory support for Articulata was also found early based on morphological data analyses that explained the similarities of annelids to molluscs and other spiral-cleaving phyla without having to force arthropods to have “lost” spiral cleavage and a trochophore larva to salvage Articulata and recovered effectively Ecdysozoa (Eernisse et al. 1992), or has been shown to depend on the interpretation of certain morphological characters (Jenner and Scholtz 2005). In some cases, authors attempted to reconcile both hypotheses by making Ecdysozoa the sister group of Annelida, nested within Spiralia (Nielsen 2003), or by making Annelida paraphyletic to the inclusion of Ecdysozoa and Enterocoela (Almeida et al. 2003). Even before the molecular support for Ecdysozoa was proposed, some

visionary zoologists had already proposed a relationship of arthropods with the then known “aschelminth” phyla (Rauther 1909; Colosi 1967), and others had questioned the homology of segmentation in arthropods and annelids (Minelli and Bortoletto 1988). Kristensen (1991, p. 352), discussing the phylogenetic relationships of Loricifera, wrote

Annulation of the flexible buccal tube, telescopic mouth cone, and the three rows of placoids are found only in Tardigrada and Loricifera (Kristensen, 1987). Because tardigrades exhibit several arthropod characters (see Kristensen, 1976, 1978, 1981), this last finding supports a theory about a relationship between some aschelminth groups and arthropods (Higgins, 1961). That theory has recently gained support derived primarily from new ultrastructural data, e.g., the fine structure of the chitinous cuticular layer, molting cycle, sense organs, and muscle attachments.

Combined parsimony or Bayesian analyses of morphology and molecules have consistently retrieved Ecdysozoa rather than Articulata (Zrzavý et al. 1998b; Giribet et al. 2000; Peterson and Eernisse 2001; Zrzavý et al. 2001; Zrzavý 2003; Glenner et al. 2004). Likewise, molecular analyses of metazoan relationships have repeatedly recovered ecdysozoan monophyly, whether using just a few genes (e.g. Aguinaldo et al. 1997; Giribet and Ribera 1998; Giribet and Wheeler 1999; Giribet et al. 2000; Mallatt and Winchell 2002; Ruiz-Trillo et al. 2002; Mallatt et al. 2004; Telford et al. 2005; Mallatt and Giribet 2006; Bourlat et al. 2008; Paps et al. 2009a, b; Mallatt et al. 2010), or large collections of genes in phylogenomic analyses (e.g. Dunn et al. 2008; Hejnol et al. 2009; Holton and Pisani 2010; Philippe et al. 2011). When Ecdysozoa was rejected in molecular analyses, as happened in some early genome-scale analyses with depauperate taxonomic sampling, the rival group was Coelomata (nematodes falling outside a group that included arthropods and vertebrates) (Blair et al. 2002; Dopazo et al. 2004; Wolf et al. 2004; Philip et al. 2005), but Articulata was never tested because no annelid was represented in those analyses. Further analyses of these initial whole eukaryotic genomes, whether using intron conservation

patterns, rare genomic changes or standard sequence data, rejected Coelomata (Roy and Gilbert 2005; Irimia et al. 2007; Holton and Pisani 2010). Nowadays, even authors who once argued fervently for Articulata have accepted Ecdysozoa (e.g. Nielsen 2012).

Thus, an alliance between Panarthropoda and five moulting phyla with collar-shaped, circumoesophageal brains (i.e. Nematoda, Nematomorpha, Kinorhyncha, Priapulida and Loricifera) is the strongest available hypothesis. The latter five phyla are collectively named Cycloneuralia (some authors also include Gastrotricha in this group) or Introverta. The exact position of the three panarthropod phyla within this clade has remained unsettled, often because authors questioned the monophyly of Panarthropoda. The jointed appendages of arthropods have been homologized with the lobopods of onychophorans, a view strengthened by similar genetic patterning of the proximo-distal axes of both kinds of appendages (Janssen et al. 2010), as well as with the limbs of tardigrades. The homology of these paired ventrolateral segmental appendages, which also share segmentally arranged leg nerves, provides the most conspicuous apomorphy for Panarthropoda. Earlier, the appendages were also considered possible homologues of the annelid parapodia. Although some arguments from gene expression have been made in defence of this homology (Panganiban et al. 1997), they mostly pertain to general characters of lateral outgrowths of bodies, and even authors arguing in defence of Articulata have observed that the complexity of the similarities between panarthropod legs and parapodia is not great (Scholtz 2002). Their homology is not generally accepted now.

Under the Panarthropoda hypothesis, each of the three competing resolutions for the interrelationships between the three groups has been defended in recent studies, that is, either Onychophora, or Tardigrada, or a clade composed of them both is the candidate sister group of arthropods (reviewed by Edgecombe et al. 2011; Giribet and Edgecombe 2012). Phylogenomic data have repeatedly endorsed the first option, an onychophoran–arthropod clade (Giribet and

Edgecombe 2012), but the position of tardigrades has been less clear. Two placements for tardigrades recur in broadly sampled molecular analyses, being either sister group of Onychophora + Arthropoda or Nematoda, and in fact both of these alternatives are resolved for the same EST (expressed sequence tag) datasets (Roeding et al. 2007; Dunn et al. 2008; Hejnol et al. 2009; Meusemann et al. 2010; Campbell et al. 2011; Rehm et al. 2011) or mitogenomic data (Rota-Stabelli et al. 2010) under different analytical conditions. In the latter case, conditions intended to counter certain kinds of systematic error strengthen the support for tardigrades grouping with arthropods and onychophorans rather than with nematodes, and the same pattern has also been found for EST-based analyses (Campbell et al. 2011). Tardigrades, onychophorans and arthropods have also been united as a clade based on a uniquely shared micro-RNA (non-coding regulatory genes) (Campbell et al. 2011), with another micro-RNA grouping onychophorans and arthropods to the exclusion of tardigrades.

Thus, current evidence favours panarthropod monophyly with the subgroups (Tardigrada (Onychophora + Arthropoda)), but better sampling is required within Ecdysozoa before this issue is definitely resolved, as ESTs are absent for loriciferans and scarce for kinorhynchs, nematomorphs and priapulans. A rival clade that includes Tardigrada, Nematoda and Nematomorpha, and even Loricifera, has some morphological (Kristensen 1991) and limited molecular (Sørensen et al. 2008) support. In contrast, the alliance of tardigrades with onychophorans and arthropods, along with the fossil lobopodians and anomalocaridid-like taxa (“gilled lobopodians”), is consistent with a single origin of paired, segmental ventrolateral appendages in a unique common ancestor (Liu et al. 2011; Giribet and Edgecombe 2012).

Arthropod monophyly (Lankester 1904; Snodgrass 1938) is now nearly universally accepted based on morphological, developmental and molecular evidence, but this has not always been the case. The Manton School strongly advocated for arthropod polyphyly

(Tiegs and Manton 1958; Anderson 1973; Manton 1973, 1977; Willmer 1990), but this reasoning was based on differences between groups and conjectures about whether or not intermediate forms could be functionally viable; it did not provide characters that supported alternative sister group hypotheses with nonarthropod phyla. In the absence of explicit rival hypotheses, arthropod monophyly remains unchallenged and is supported by a suite of synapomorphies. These include a sclerotized exoskeleton, and legs that are composed of sclerotized podomeres separated by arthrodial membranes, two characters absent in onychophorans and tardigrades (some authors use the term Arthropoda to include Onychophora and Tardigrada, but we reject this nomenclature, as the members of those phyla have not undergone the arthropodization process). In all arthropods except pycnogonids, muscles attach at intersegmental tendons. Compound eyes across the Arthropoda share a similar developmental mode, with new eye elements being added in a peripheral proliferation zone of the eye field (Harzsch and Hafner 2006), and the presence of two optic neuropils in the inferred ancestor is apomorphic for arthropods as a whole (Harzsch 2006). Segmentation gene characters, such as a pair-rule function of the Pax protein (Angelini and Kaufman 2005; Gabriel and Goldstein 2007), and a conserved pattern of how neural precursors segregate (Eriksson and Stollewerk 2010a) map onto the tree as autapomorphies of Arthropoda compared with the states in Onychophora and Tardigrada. Under the criterion of monophyly, the parasitic Pentastomida are arthropods. This group had a long history of classification as “prot(o)arthropods” in its own phylum (Brusca and Brusca 1990), and an early divergence from the arthropod stem lineage is still endorsed by some morphologists (Castellani et al. 2011). The molecular arguments for a placement as ingroup crustaceans, grouped with branchiuran fish lice according to the Ichthyostraca hypothesis, are strong (Abele et al. 1989; Giribet et al. 2005; Møller et al. 2008; Regier et al. 2010; Sanders and Lee 2010), if in conflict with some morphological interpretations

(Waloszek et al. 2006), and are congruent with synapomorphies from sperm ultrastructure (reviewed by Giribet et al. 2005).

2.3 The Arthropod Tree of Life

The diversity of arthropods traditionally has included the classes (or comparatively higher-rank taxa) Chelicerata, Myriapoda, Hexapoda and Crustacea, with Pycnogonida sometimes considered part of Chelicerata (hence divided into Pycnogonida, Xiphosura and Arachnida), or their own class, due to their unique morphology and uncertain phylogenetic affinities. Recent developments have provided strong endorsement for paraphyly of Crustacea with respect to Hexapoda, and hence, we consider the extant arthropod phylogenetic conundrum as a four-taxon problem—Pycnogonida, Euchelicerata (=Xiphosura + Arachnida), Myriapoda and Tetraconata (=Pancrustacea)—with three alternative rootings (Fig. 2.1a–c).

Relationships between these groups have been debated for decades. Through much of the twentieth century, the only nearly universally accepted result was the monophyly of Atelocerata (also known as Tracheata)—a clade composed of hexapods and myriapods (e.g. Snodgrass 1938; Wheeler et al. 1993) (Fig. 2.1d). However, the addition of molecular and novel anatomical and developmental data has helped to reinterpret arthropod relationships, with the result that Atelocerata has been overturned. In most contemporary studies, hexapods are associated with crustaceans instead of with myriapods (e.g. Friedrich and Tautz 1995; Giribet et al. 1996, 2001, 2005; Regier and Shultz 1997; Giribet and Ribera 1998, 2000; Zrzavý et al. 1998a; Hwang et al. 2001; Regier et al. 2005a, 2008, 2010; Mallatt and Giribet 2006; Meusemann et al. 2010; von Reumont and Burmester 2010; Campbell et al. 2011; Regier and Zwick 2011; Rota-Stabelli et al. 2011; von Reumont et al. 2012) in a clade named Tetraconata in reference to the shared presence of four crystalline cone cells in the compound eye ommatidia in both groups (Richter 2002). A few

groups of morphologists still argue in support of Atelocerata (Bitsch and Bitsch 2004; Bäcker et al. 2008), though this follows as a consequence of either examining a single character system (e.g. pleurites around the leg base in the case of Bäcker et al. 2008) or not including the rival characters for Tetraconata in the analysis. Morphologists who recognize Tetraconata have reinterpreted the putative apomorphies of Atelocerata as likely being convergences due to terrestrial habits (Harzsch 2006), and numerical cladistic analyses that incorporate the neuro-anatomical evidence for Tetraconata retrieve that group in favour of Atelocerata (Giribet et al. 2005; Rota-Stabelli et al. 2011). Perhaps, the only novel argument in support of Atelocerata in modern times is a similar expression pattern of the *Drosophila collier* gene (*col*) in the limbless intercalary segment of the head in a few studied myriapods and insects (Janssen et al. 2011). This conserved function of *col* in insects and myriapods as a putative synapomorphy is overwhelmed by a much larger body of neuro-anatomical and molecular data that speak in favour of a crustacean–hexapod clade. Thus, the *col* function could have been lost in early head development in crustaceans or may indeed have evolved convergently in insects and myriapods.

A perfectly resolved *Arthropod Tree of Life* is still elusive, but the notion that arthropod phylogeny can be depicted as “chaos” (Bäcker et al. 2008) is obsolete. Several patterns, including a basic unrooted topology, are congruent among nearly all new sources of data, and today, most authors interpret the arthropod phylogeny problem as a rooting problem (Giribet et al. 2005; Caravas and Friedrich 2010; Giribet and Edgecombe 2012) and not as alternative conflicting topologies. These three alternative rootings result in (a) Pycnogonida as sister to all other arthropods (=Cormogonida) (Zrzavý et al. 1998a; Giribet et al. 2001); (b) Chelicerata monophyletic and sister group to Mandibulata (Regier et al. 2008, 2010; Rota-Stabelli and Telford 2008; Regier and Zwick 2011; Rota-Stabelli et al. 2011), or those arthropods with true mandibles (Edgecombe et al. 2003), as opposed to cheliceres or chelifores; and (c) a

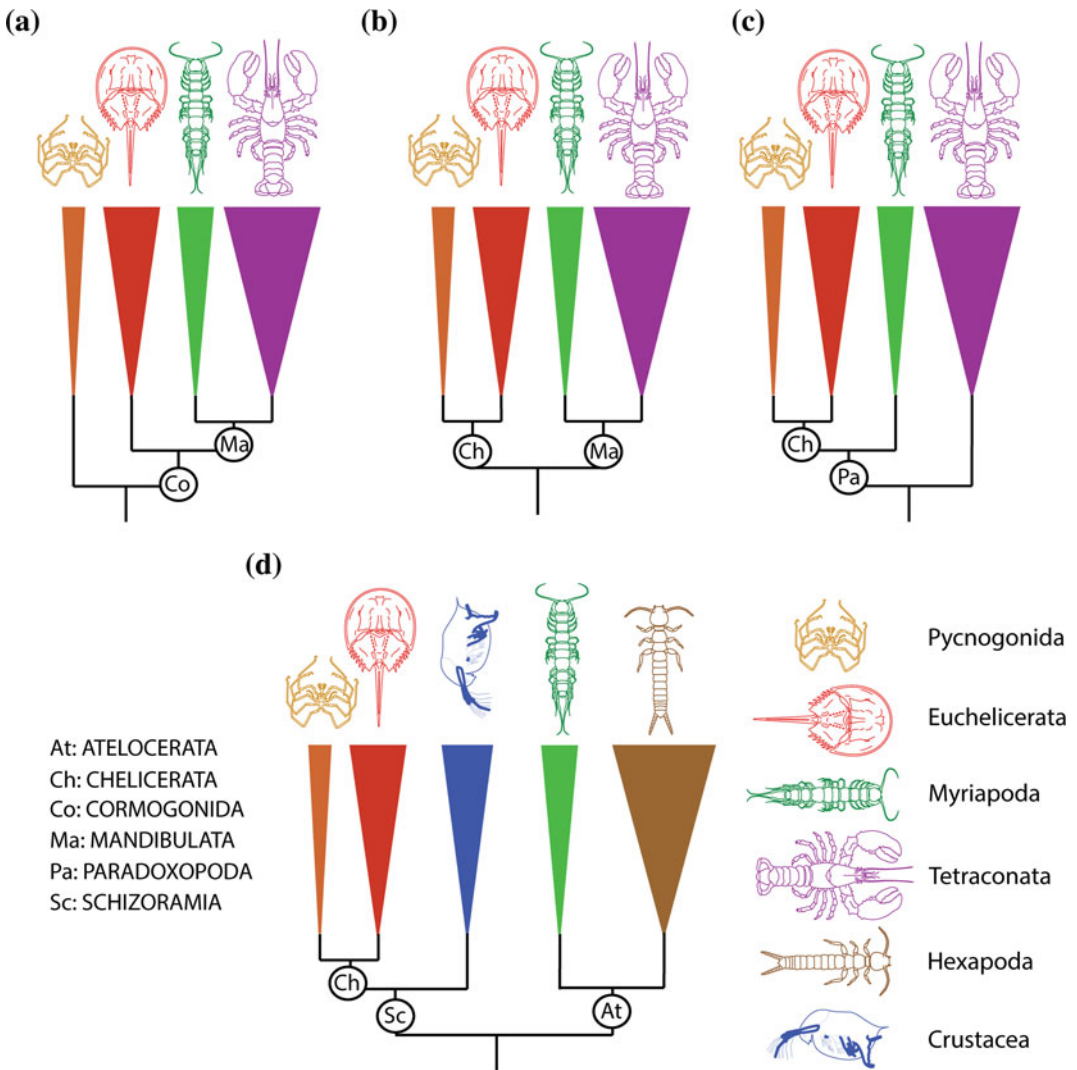


Fig. 2.1 Alternative hypotheses of arthropod relationships, including the three currently recognized rooting options. **a** Cormogonida. **b** Chelicerata versus Mandibulata.

c Paradoxopoda/Myriochelata. **d** A traditional view of arthropod relationships with the putative clades Schizoramia and Atelocerata/Tracheata

clade named Paradoxopoda (=Myriochelata) that joins myriapods with the chelicerate groups (Friedrich and Tautz 1995; Hwang et al. 2001; Mallatt et al. 2004; Pisani et al. 2004; Mallatt and Giribet 2006; Dunn et al. 2008; von Reumont et al. 2009; Rehm et al. 2011) (Fig. 2.1a–c). Whereas the choice between these hypotheses involves the placement of the root, a few traditional morphological hypotheses present more fundamental topological conflict. Among the conflicting hypotheses are

Atelocerata and Schizoramia (Fig. 2.1d), the latter uniting Crustaceomorpha and Arachnomorpha (Bergström 1979; Hessler 1992).

In this chapter, we focus on developments in two key areas, comparative anatomy and novel molecular approaches, each of which has advanced greatly since the publication of the first arthropod phylogenies combining morphology and multiple molecular markers (Wheeler et al. 1993; Zrzavý et al. 1998a; Giribet et al. 2001). Since then, the quantity of

molecular data devoted to this problem has increased exponentially with recent genomic approaches. The techniques used to analyse developmental and anatomical data have also improved considerably as a result of new technological advances. For example, a classical technique for studying internal anatomy, histological sectioning, is now aided by computer reconstruction (e.g. Stegner and Richter 2011 for cephalocarids). Non-invasive, non-destructive techniques for anatomical imaging are continually being refined. Among these are confocal laser microscopy, micro-computed tomography and magnetic resonance imaging (Hörschmeyer et al. 2002; Friedrich and Beutel 2010). Other new techniques have been developed to focus on particular organ systems, for example, studies on the circulatory system that apply micro-CT techniques and 3D reconstruction with corrosion casting are a source of new characters for several arthropod groups (Wirkner and Richter 2004; Wirkner and Prendini 2007; Huckstorf and Wirkner 2011). While these techniques have had an impact, they have still been applied to a limited (yet valuable) number of taxa, both fossil and extant.

2.3.1 Neural Cladistics

Comparative anatomy was the traditional source of data for inferring arthropod phylogeny, coupled with evidence from embryonic and post-embryonic development (Anderson 1973). Among anatomical systems that are currently receiving intensive study for their phylogenetic signal, the nervous system is perhaps prevalent, an approach that has come to be called neurophylogeny (Richter et al. 2010) or neural cladistics (Strausfeld and Andrew 2011). Nervous system characters had already played an important role in arthropod phylogenetics in the early twentieth century (Strausfeld 2012). Indeed, one of the major insights of this early neuroanatomical research was the ancestry of hexapods from crustaceans rather than from myriapods, a hypothesis that drew its support from characters that have returned to the

forefront of debate, such as eye ultrastructure and configurations of the optic neuropils (Hanström 1926). A crustacean ancestry of hexapods laid dormant through the decades in which myriapods were upheld as the closest relatives of hexapods, until the mid-1990s. Since then, neuroanatomists have provided compelling corroboration for crustacean paraphyly as well as many other key nodes in the arthropod tree by applying new staining/immunoreactivity and imaging techniques, coupled with analysis of the data by cladistic methods.

Character matrices based on the nervous system (Harzsch 2006; Strausfeld 2009; Strausfeld and Andrew 2011) consistently resolve Malacostraca and Hexapoda as more closely related to each other than either is to Branchiopoda or is to Maxillopoda, as upheld earlier by Hanström. Character support for a malacostracan–hexapod clade to the exclusion of branchiopods is provided by such shared features as optic neuropils that have a nesting of the lamina, medulla, lobula and lobula plate and their connections by crossed axons (chiasmata). To explain the distribution of character states on a tree in which cephalocarids and remipedes are positioned stemward of branchiopods within Tetraconata, branchiopod brains have been interpreted as secondarily simplified from an ancestor that shared traits seen in the brains of malacostracans and remipedes (Strausfeld and Andrew 2011). Character polarities are, however, very much dependent upon the exact pattern of relationships between these crustacean groups and Hexapoda, an area that is subject to instability between different analyses (notably for the relationship between remipedes and cephalocarids).

The mode of development of neural tissue has played a major role in recent discussion about where the root should be placed between the main extant arthropod groups, which corresponds to the controversy over Mandibulata versus Paradoxopoda. Detailed similarities in chelicerate and myriapod neurogenesis have been recognized for nearly a decade (Dove and Stollewerk 2003; Kadner and Stollewerk 2004; Mayer and Whittington 2009) and present a

contrast with the stem cell–like division of neural precursors in insects and crustaceans (Ungerer et al. 2011). The question becomes one of polarity—whether the chelicerate–myriapod characters are symplesiomorphies, inherited from the ancestor of all arthropods, or are potential synapomorphies that provide anatomical support for Paradoxopoda. To resolve this matter, neurogenesis in the arthropod sister group, Onychophora, has been examined using immunohistochemistry and confocal laser microscopy (Mayer and Whittington 2009; Whittington and Mayer 2011), supplemented by new data from gene expression of *Delta*, *Notch* and *ASH* (Eriksson and Stollewerk 2010a, b). The results remain open to interpretation, the onychophorans being argued to share characters with insects and crustaceans, being thus a plesiomorphic state, which would make the condition in myriapods and chelicerates apomorphic, providing positive support for Paradoxopoda (Mayer and Whittington 2009; Whittington and Mayer 2011). Other authors instead suggest that onychophorans possess unique and divergent character states that cannot be homologized with those of insects and crustaceans and that myriapods have characters of neural precursor cells that are consistent with Mandibulata rather than with Paradoxopoda (Eriksson and Stollewerk 2010a). Knowledge on the neurogenesis of pycnogonids at this level is entirely lacking, but would constitute an obvious starting point to look into in order to possibly settle this debate.

The most recent neural cladistic analysis (Strausfeld and Andrew 2011) has retrieved Mandibulata as a monophyletic group, but it has also exposed the ongoing problem of correctly rooting Arthropoda, for example, Onychophora unite with Chelicerata as a putative clade for the same data. The latter grouping is contradicted by many other kinds of data and signals an incorrect root position, possibly resulting from a distant outgroup (annelids were used as an outgroup rather than as tardigrades and/or cycloneurians). Though Mandibulata is depicted as the “state of play” in some recent studies (as in Regier et al. 2010; Rota-Stabelli et al. 2011), it need be cautioned that anatomical and gene

expression data supporting Paradoxopoda continue to emerge. As an example, we note expression patterns along the proximo-distal axis of the limb, specifically the expression domains of homothorax (*hth*) and extradenticle (*exd*). These are comparable with chelicerates (spiders and harvestmen) and millipedes (Abzhanov and Kaufman 2000; Prpic et al. 2003; Prpic and Damen 2004; Pechmann and Prpic 2009; Sharma et al. 2012). *hth* is expressed broadly in much of the developing appendage, whereas *exd* is restricted to the proximal podomeres. Taken together with the inverse spatial relationship between *hth* and *exd* in onychophorans and pancrustaceans (Prpic et al. 2003; Prpic and Telford 2008; Janssen et al. 2010), the expression data are consistent with a sister group relationship between chelicerates and myriapods.

2.3.2 Novel Molecular Approaches

Understanding of arthropod relationships has been transformed by molecular data, with vast refinements in both sampling and techniques since an initial wave of analyses was conducted in the early 1990s (Abele et al. 1989; Wheeler 1989; Kim and Abele 1990; Turbeville et al. 1991; Carmean et al. 1992; Spears et al. 1992; Pashley et al. 1993; Wheeler et al. 1993). Until the past few years, molecular phylogenies relied on direct sequencing of a few selected genes that were amplified with specific primers—an approach now called a “target-gene approach”. Arthropod phylogenies were often inferred from nuclear ribosomal genes (Friedrich and Tautz 1995; Giribet et al. 1996; Giribet and Ribera 2000; Mallatt and Giribet 2006; von Reumont et al. 2009), nuclear protein-encoding genes (Regier and Shultz 1997; Shultz and Regier 2000; Regier and Shultz 2001; Regier et al. 2004, 2005a), or a combination of these with mitochondrial genes (Giribet et al. 2001, 2005; Giribet and Edgecombe 2006). These studies typically used just a few genes to build trees. Other analyses instead focused on mitogenomics (Boore et al. 1995; Hwang et al. 2001; Lavrov et al. 2002; Masta and Boore 2008; Rota-Stabelli

et al. 2010), the analysis of complete mitochondrial genomes. Although the early analyses of mitochondrial genes from the 1990s sometimes yielded contradictory and/or morphologically anomalous results (Ballard et al. 1992), many of these problems have now been identified as resulting from a deficient taxon sampling, too few molecular data, systematic error or combinations of these defects.

The target-gene approach still forms the basis for some modern work on arthropod phylogenetics. The number of markers has substantially increased, drawing on as many as 62 nuclear protein-encoding genes (Regier et al. 2008; Regier and Zwick 2011), as has the taxon sampling, up to 75 taxa (Regier et al. 2010). The use of large numbers of markers obtained through standard PCR approaches has been an important advance, and in the case of the arthropod dataset, it permits a clear choice of Mandibulata over Paradoxopoda and injects new hypotheses for crustacean interrelationships (though some of these have been questioned because they do not account for serine codon usage bias and are contradicted under alternative analytical conditions: Rota-Stabelli et al. 2013). The downsides of this method are that it is time-consuming, it is difficult to consistently amplify large numbers of genes for many taxa, and many of the selected genes may present problems of paralogy that are difficult to detect by PCR approaches alone (Clouse et al. submitted).

Developments in sequencing technology and shotgun approaches following the sequencing of the first complete eukaryotic genomes of *Caenorhabditis elegans*, *Drosophila melanogaster* and *Homo sapiens* ushered in a new era in the production of DNA sequence data. “Next-generation sequencing” uses random sequencing strategies and automated processes to collect hundreds or thousands of genes from cDNA libraries obtained from mRNA, for a fraction of the effort required to amplify multiple markers. The genes are processed automatically in phylogenetic analyses (Dunn et al. 2008; Edgecombe et al. 2011) that have come to be known as “phylogenomic”—based on a sizeable fraction of a transcriptome or a genome (Morozova

et al. 2009). The random sequencing of clones from a cDNA library generates large numbers of ESTs, and soon, studies combined the data from full genomes with novel ESTs generated for a diverse sampling of protostomes (Dunn et al. 2008; Hejnal et al. 2009) or arthropods in particular (Roeding et al. 2009; Meusemann et al. 2010; Campbell et al. 2011; Rehm et al. 2011; Rota-Stabelli et al. 2011; von Reumont et al. 2012).

With respect to the basal split in Arthropoda, EST-based studies to date have come down in favour of either Paradoxopoda (Fig. 2.1b) or Mandibulata (Fig. 2.1c), generally observing the choice between the two to be sensitive to taxon sampling, but also to gene sampling. The first EST analyses supported the Paradoxopoda hypothesis (Dunn et al. 2008; Hejnal et al. 2009; Roeding et al. 2009; Meusemann et al. 2010), whereas others support a split between Chelicerata and Mandibulata (Campbell et al. 2011; Rota-Stabelli et al. 2011). The most densely sampled analysis, which added some crustacean lineages missing from earlier studies (von Reumont et al. 2012), retrieved Mandibulata when their entire taxon/character sample was used, but support shifted to Paradoxopoda when the matrix was reduced according to criteria that the authors believed would lessen “noise”. The two hypotheses were likewise found to be variably supported for different taxonomic samples in EST analyses by Andrew (2011).

Most EST libraries until 2010 were obtained using standard Sanger capillary sequencers. High-throughput sequencing with next-generation sequence technologies such as Roche 454 (Margulies et al. 2005) and more recently Solexa *Illumina* (Illumina_Inc 2007) can produce up to hundreds of thousands or millions of sequences per sample, at a fraction of the cost of the earlier Sanger technology sequencing. These technological developments will radically increase the amount of data available for analysis, especially for non-model organisms (Riesgo et al. 2012).

Molecular data have also made an important contribution towards producing reliable chronograms of arthropod cladogenesis and diversification (Muriene et al. 2010; Sanders and Lee

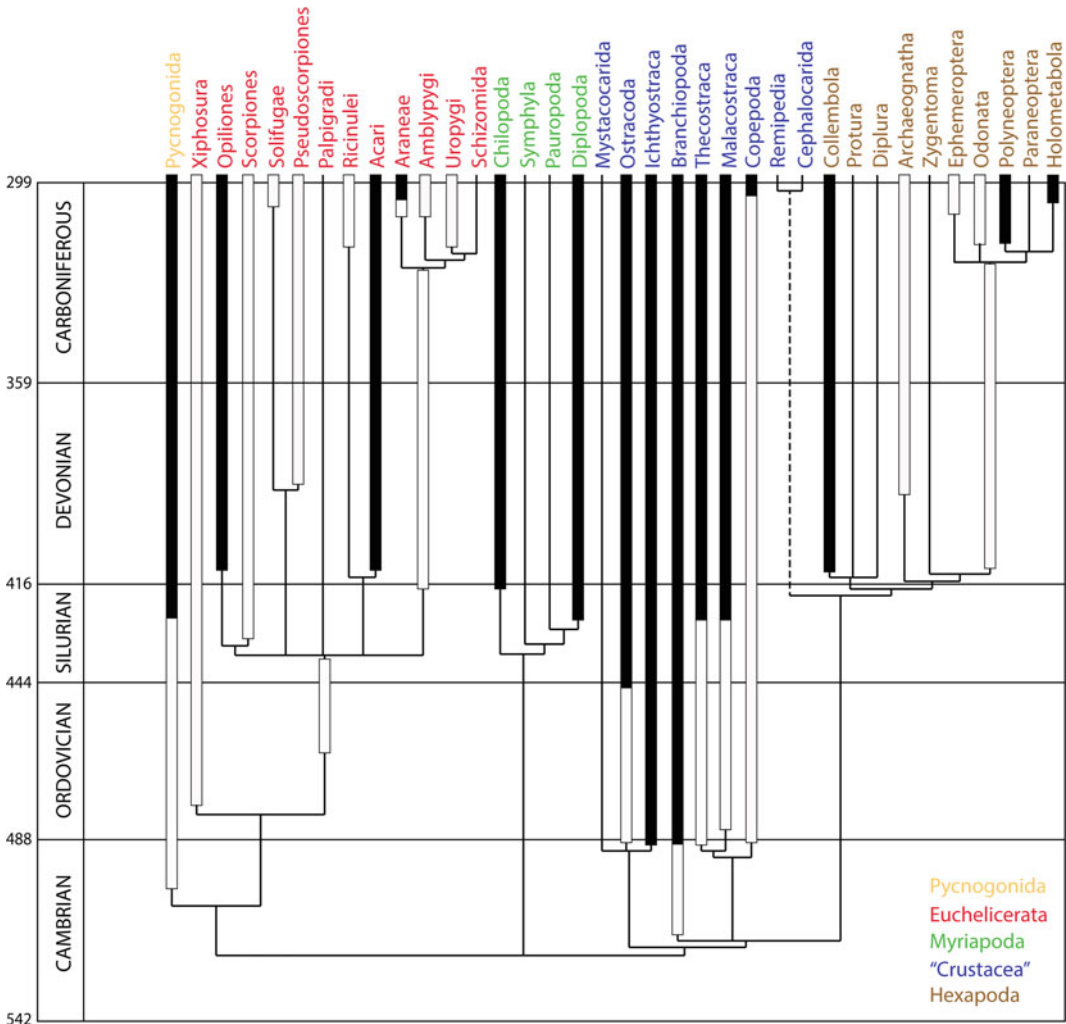


Fig. 2.2 Relationships between living arthropod lineages with palaeontological calibration. *Solid bars* indicate the presence of unambiguous fossils assigned to the crown group, and empty bars indicate the presence of fossils assigned to the stem group. Fossil data obtained from original sources and reviews, including Dunlop

(2010; Rehm et al. 2011). Palaeontology continues contributing most of the data to the age of lineages because minimum ages from fossils (Fig. 2.2) calibrate the molecular estimates for divergences. Modern molecular estimates of the splits between the deep arthropod clades such as Chelicerata versus Mandibulata (or the rival split of Paradoxopoda versus Tetraconata) date these events to the Ediacaran Period (635–542 My) (Pisani 2009; Erwin et al. 2011; Rehm et al. 2011). This is more consistent with the fossil

record than were earlier analyses that used more immature clock models, which retrieved divergences between onychophorans and arthropods and basal splits in Arthropoda dating to the Cryogenian (reviewed by Pisani 2009). Even so, the Ediacaran has not yet yielded credible body or trace fossils of arthropods, and an Ediacaran “fuse” of some tens of millions of years separates the latest molecular divergence of arthropods from the first appearance of arthropod trackways in the early Cambrian.

(2010) for Chelicerata, Edgecombe (2010) and Rehm et al. (2011). Relationships within Tetraconata mostly based on Regier et al. (2010). As a convention, divergences are depicted as shallow as warranted by fossils; deeper divergences are inferred from molecular dating; see Sanders and Lee (2010) and Rehm et al. (2011)

2.4 Advancing Arthropod Phylogenetics

While many of the new developments discussed above have contributed to stabilize the arthropod tree (Fig. 2.2), there are several areas in need of refinement. In this section, we navigate the main arthropod clades and suggest possible areas of inquiry.

The persistent controversy over whether the root of the arthropod tree identifies Mandibulata or Paradoxopoda as clades would best be tested by additional genomic data on Pycnogonida, the currently unsampled orders of Arachnida, and Myriapoda. Taxon sampling in those groups is sparse (e.g. only one myriapod was used in the currently best-sampled EST analyses; von Reumont et al. 2012), and the EST libraries available to date for these groups are shallow when compared to those of other arthropod groups, for which whole genomes or extensive genetic resources are at hand (Clark et al. 2007). The recent sequencing of several pancrustacean genomes, as well as the first myriapod genome for the centipede *Strigamia maritima* and the genome of the horseshoe crab *Limulus polyphemus*, should be key in resolving some of the most fundamental questions about deep arthropod phylogeny. Fossil data are also important for establishing an accurate position of the root (Edgecombe 2010), but the methodological difficulties in combining morphology with genomic-level data remain largely unexplored (Giribet 2010). New kinds of molecular characters should also be more broadly sampled to include arthropod lineages that have thus far been unexplored. For example, the hypothesis that myriapods share two novel micro-RNAs with crustaceans and hexapods that are not shared with chelicerates (Campbell et al. 2011; Rota-Stabelli et al. 2011) has been tabled as a new argument in favour of a monophyletic Mandibulata. The presence of these micro-RNAs should be determined in more myriapods (e.g. symphylans and pauropods), crustaceans and arachnids.

2.4.1 Chelicerata

Euchelicerata is nearly always identified as monophyletic, apart from in some mitogenomic analyses (e.g. Masta et al. 2009), which have repeatedly placed pycnogonids within Arachnida, often attracted to Acari, and in some trees that were not based on explicit data analysis (Simonetta 2004). Beyond the relatively straightforward question of euchelicerate monophyly, though, molecular datasets to date (Wheeler and Hayashi 1998; Giribet et al. 2002; Masta et al. 2009; Pepato et al. 2010; Regier et al. 2010) have mostly conflicted with morphology (Shultz 1990; Wheeler and Hayashi 1998; Giribet et al. 2002; Shultz 2007), apart from identifying the clade Tetrapulmonata (and in some cases recovering its internal phylogeny congruently with morphology; Regier et al. 2010). In many analyses, the molecules have not even recovered the basal dichotomy between Xiphosura (horseshoe crabs) and Arachnida. Possible causes for the difficulty in recovering these relationships are the old history of the group, the extinction of key lineages (arachnids include several high-ranking extinct groups such as the orders Trigonotarbida, Haptopoda and Phalangiotarbida, as well as stem-group arachnid taxa such as Eurypterida and Chasmataspida; Dunlop 2010) or intrinsic problems of the molecular data. The monophyly and phylogenetic affinities of Acari (Dunlop and Alberti 2008; Pepato et al. 2010) and the precise position of Palpigradi and Ricinulei remain as some of the most puzzling issues. Likewise, challenging are the relationships between a set of arachnid orders that have been regarded as solidly placed from the perspective of morphology—Scorpiones, Opiliones, Pseudoscorpiones and Solifugae. The currently favoured morphological hypothesis in which scorpions and harvestmen form the clade Stomothecata (Shultz 2007) conflicts with the largest available molecular datasets for arachnids (Regier et al. 2010). The latter unite scorpions with the tetrapulmonates, but that group (Pulmonata in Regier

et al. 2010) is not strongly supported. A similar situation pertains to pseudoscorpions and solifuges. Their grouping as a clade, Haplocnemata, is widely endorsed by arachnologists because of numerous shared derived morphological characters (Weygoldt and Paulus 1979; Shultz 2007). Alternative sister groups based on nuclear genes (Solifugae + Ricinulei; Pseudoscorpiones + parasitiform Acari) have weak support (Regier et al. 2010). Figure 2.2 depicts the relationships between these groups as resolved by morphology.

A sister group relationship between Pycnogonida and Euchelicerata has a long tradition among morphologists, though few strong synapomorphies have been identified (Dunlop and Arango 2005). The main alternative placement for Pycnogonida, as sister group to all other arthropods according to the Cormogonida hypothesis (Fig. 2.1a), has been based on absences of certain morphological characters shared by other arthropods, such as intersegmental tendons and a labrum or labral anlagen, being interpreted as primitively absent. Recent electron microscopic study of pycnogonid embryos in search of potential labral homologues has failed to identify a plausibly homologous structure (Machner and Scholtz 2010), which is consistent with a position of Pycnogonida outside Euchelicerata + Mandibulata. Additional characters that have been tabled as potentially plesiomorphic in pycnogonids refer to the presence of a terminal mouth at the end of a proboscis and a Y-shaped pharynx (Miyazaki 2002), both characters widely found in the introvertan ecdysozoans and in some tardigrades (Schmidt-Rhaesa et al. 1998; Giribet 2003). The choice between Chelicerata (i.e. Pycnogonida + Euchelicerata) and Cormogonida is not decisively settled with current molecular datasets, although the former seems to be preferred. The sister group relationship between pycnogonids and euchelicerates was retrieved by Regier et al. (2010) in their analyses of nuclear coding genes, though they observed a “more basal placement of Pycnogonida” (i.e. Cormogonida) to provide only a marginally poorer fit to the data.

2.4.2 Myriapoda

The rediscovery of myriapod monophyly has been identified as one of the successes of arthropod molecular phylogenetics (Regier et al. 2008). A long tradition of postulating that Myriapoda was non-monophyletic resulted from the Atelocerata hypothesis. In that framework, myriapods were identified as a grade from which hexapods evolved (Dohle 1980; Kraus and Kraus 1994, 1996). From the mid-1960s through the mid-1990s, myriapod paraphyly often took the form of Progoneata (symphylans, pauropods and diplopods) being sister group of Hexapoda in a putative clade called Labiophora, with Chilopoda being sister group to that assemblage. Intriguingly, key proponents of arthropod polyphyly through that era were strong defenders of the monophyly of Myriapoda (e.g. Anderson 1973). Sidnie Manton (1964) perceptively observed that myriapods share a unique structure of the tentorial endoskeleton which has come to be known as the “swinging tentorium”. Throughout Myriapoda, the posterior process of the tentorium is fused to a transverse bar that extends to the lateral cranial wall (Koch 2003a); downward and outward movements of these tentorial apodemes provide the abductor force that opens the mandibles. This character system remains an autapomorphy of Myriapoda.

The rediscovery of Myriapoda is linked to the demise of Atelocerata. The unambiguous molecular and very strong neuroanatomical support for a hexapod–crustacean clade that excludes Myriapoda effectively solves the question of myriapod paraphyly; if the shared characters of Myriapoda no longer have to be seen as atelocerate symplesiomorphies, then the only parsimonious solution is to identify them as myriapod autapomorphies (Shear and Edgecombe 2010). Recent analyses that used a broad sampling of genes and taxa (Regier et al. 2010; Regier and Zwick 2011) have resolved Myriapoda as monophyletic, with strong support, corroborating previous molecular phylogenetic analyses.

A challenge to myriapod monophyly had been raised in neural cladistic analyses, specifically a possibility that Diplopoda could be basally positioned in Arthropoda, falling outside a group that united other myriapods with Tetracnata and that “partial Mandibulata” clade with Chelicerata (Loesel et al. 2002; Strausfeld et al. 2006). This hypothesis is derived from the absence of a specific midline neuropil in the brain in spirostreptid millipedes that is shared by other arthropods (as well as onychophorans). Expanded character and taxonomic sampling in neural cladistic datasets have corrected this anomalous placement of millipedes: Diplopoda and Chilopoda are sister groups in current cladograms (Strausfeld and Andrew 2011). The addition of comparable data for Symphyla and Pauropoda is an obvious target for future work.

Shifting attention from myriapod monophyly to the basal split within the group, the 75-taxon, 62-gene dataset (Regier et al. 2010; Regier and Zwick 2011) yielded a division that corresponds to the standard morphological tree, that is, Chilopoda as sister group to Progoneata. Within Progoneata, however, conflict with morphology emerges, and this presents the most pressing issue in Myriapoda as a whole. The union of diplopods and pauropods as a clade named Dignatha has not been seriously challenged from the perspectives of morphology and development (Dohle 1980; Shear and Edgecombe 2010). These putative sister groups share many detailed characters, including a limbless post-maxillary segment, the vas deferens opening on conical penes on the same trunk segment, spiracles at the bases of the walking legs that open to tracheal pouches, a motionless post-hatching (“pupoid”) stage and three leg pairs in the first free-living stage. Because of the strength of support for Dignatha from these similarities, it was unexpected when sequence-based analyses instead retrieved a grouping of Pauropoda with Symphyla rather than with Diplopoda (Regier et al. 2005b; Gai et al. 2008; Regier et al. 2010; Dong et al. 2012). However, pauropods and symphylans have been seen to attract in anomalous positions (sometimes even falling outside Arthropoda) in analyses of nuclear ribosomal

genes (Giribet and Ribera 2000; von Reumont et al. 2009). Their grouping with nuclear coding genes thus needs to be critically evaluated as a possible artefact of systematic error.

2.4.3 Tetracnata

Monophyly of Tetracnata has long been recognized from diverse molecular datasets (see citations above) and indeed has never been challenged by Atelocerata in any sequence-based analysis. Tetracnata is in no sense a “molecular grouping”, though, as explained above, it reflects a hypothesis put forward by neurobiologists in the early twentieth century, and in its contemporary form, it is reinforced by important morphological characters of eye ultrastructure (Richter 2002), brain and optic lobe anatomy (Harzsch and Hafner 2006; Strausfeld 2009; Strausfeld and Andrew 2011), serotonin reactivity in the nerve cord (Harzsch 2004) and similarities in neurogenesis (Ungerer and Scholtz 2008).

Whether crustaceans are monophyletic or paraphyletic with respect to hexapods (Schram and Koenemann 2004; Giribet et al. 2005; Richter et al. 2009) and if the latter, precisely which crustacean lineage constitutes the sister group of hexapods, remain labile (Grimaldi 2010). The case for crustacean paraphyly has mostly come from molecular datasets, but morphologists have been far from universal in endorsing the traditional hypothesis of a monophyletic Crustacea. Schram and Koenemann (2004) and Richter et al. (2009) evaluated most of the traditionally diagnostic or putatively autapomorphic characters of Crustacea and found that they are often ambiguous or likely symplesiomorphic. Cladistic analyses of neural characters, either manually computed (Harzsch 2006) or analysed using parsimony programs (Strausfeld et al. 2006; Strausfeld and Andrew 2011), resolve Crustacea as paraphyletic with respect to Hexapoda.

The alternative sister group hypotheses for each major crustacean clade have been summarized (Jenner 2010), so we focus on developments in the latest molecular analyses using

large numbers of genes. Among these are some new hypotheses not anticipated based on other data sources. For example, an analysis of 62 markers suggests that a putative clade composed of Cephalocarida + Remipedia (named as Xenocarida) is sister to Hexapoda, while Branchiopoda forms a clade with Malacostraca, Thecostraca and Copepoda (Regier et al. 2010). The latter grouping, named Multicrustacea by Regier et al. (2010), has also been retrieved using different kinds of molecular data, notably the EST analyses of Meusemann et al. (2010) and Andrew (2011) and compilations of molecular and morphological data by Oakley et al. (2013). The branchiopod–malacostracan–hexapod three-taxon statement lies at the heart of current conflict between various datasets and analyses. Rather than grouping branchiopods and malacostracans together (as in Regier et al. 2010), neural cladistics instead identifies Malacostraca as the likely sister group of hexapods (Strausfeld 2009; Strausfeld and Andrew 2011). In contrast to both of these resolutions, larger gene samples in EST analyses repeatedly resolve Branchiopoda as sister group to Hexapoda (Roeding et al. 2009; Meusemann et al. 2010; Campbell et al. 2011; Rota-Stabelli et al. 2011), although Cephalocarida and Remipedia were not sampled in those studies. The first ESTs of remipedes suggest that they are indeed the sister group of Hexapoda (von Reumont et al. 2012), but an alliance with Cephalocarida has not yet been tested, and these data reflect the signal of earlier EST analyses in resolving branchiopods as more closely related to remipedes and hexapods than are malacostracans. A comparable clade composed of branchiopods + cephalocarids and remipedes + hexapods was named Alotriocarida by Oakley et al. (2013). Denser taxon sampling of key crustacean lineages (e.g. Mystacocarida) is still needed in phylogenomic analyses before a definitive solution can be proposed. In particular, the attraction of remipedes and cephalocarids warrants close scrutiny because this relationship has not been anticipated from the perspective of morphology, though it has been detected for some time in

molecular datasets (Giribet et al. 2001; Regier et al. 2005a). Reanalysis of the Regier et al. (2010) 62-gene dataset by Rota-Stabelli et al. (2013) found the remipede–cephalocarid grouping to be model dependent and sensitive to the analysis of either nucleotides or amino acids. Irrespective of the eventual placement of Cephalocarida, the congruent signal from large samples of nuclear coding genes (Regier et al. 2010) and ESTs (von Reumont et al. 2012), together with the discovery of hexapod-type haemocyanins in remipedes (Ertas et al. 2009), makes a strong case for Remipedia being closely allied to hexapods.

The issue of hexapod monophyly was for a few years disputed in some mitogenomic analyses (Carapelli et al. 2007), but has since been resolved in favour of a single origin using larger molecular datasets (Timmermans et al. 2008; Meusemann et al. 2010; Regier et al. 2010; von Reumont et al. 2012; Oakley et al. 2013). At the base of Hexapoda, the status of Entognatha as a clade or a grade remains sensitive to taxon sampling and methods of molecular data analysis (Giribet et al. 2004). Morphologists had, over the past 20 years, largely abandoned Entognatha, arguing that entognathy in collembolans and proturans did not have a common origin with that in diplurans (Koch 1997, 2000), and the latter instead shared derived characters with Ectognatha, that is, “Entognatha” was a paraphyletic group (Bitsch and Bitsch 2004; Giribet et al. 2005, among others, from numerical cladistic analyses; Machida 2006 from embryological data; Dallai et al. 2011 from sperm ultrastructure). The resurrection of Entognatha as a possible clade is a recurring theme in molecular analyses, which also produced a novel hypothesis within that group—Nonocolata. The Nonocolata hypothesis advocates a sister group relationship between Protura and Diplura to the exclusion of Collembola. It was originally proposed based on nuclear ribosomal genes (Giribet et al. 2004; Luan et al. 2005; Gao et al. 2008; von Reumont et al. 2009), but has found further support in some phylogenomic analyses (Meusemann et al. 2010). Nonocolata was a novel

solution because it conflicted with the standard morphological hypothesis of a sister group relationship between Protura and Collembola, a group named Ellipura. Morphologists have, however, observed that Nonoculata is able to accommodate some anatomical features shared by proturans and diplurans but not collembolans (Koch 2009). The situation remains contentious because denser taxon sampling in EST analyses yields trees that unite Protura and Collembola as Ellipura, rather than giving support for Nonoculata (von Reumont et al. 2012).

A few phylogenetic problems remain unresolved at the base of the insect tree. Among them is the position of the relictual silverfish *Tricholepidion* relative to remaining Zygentoma (Wygodzinsky 1961). In some analyses, *Tricholepidion* appears as sister group to Dicondylia (Zygentoma + Pterygota) (Beutel and Gorb 2001; Giribet et al. 2004), whereas other data speak in favour of it being sister group to other Zygentoma or within that group (Koch 2003b; Dallai et al. 2004).

Monophyly of the winged insects (Pterygota) has been recognized since the earliest studies of insect phylogeny, but the resolution of the basal-most lineages of winged insects, Odonata and Ephemeroptera, remains contentious to this date. Current datasets support either their grouping as a clade named Palaeoptera or that they comprise a grade leading to Neoptera in either of the two possible arrangements, which represent the Metapterygota and Chiasmomyaria hypotheses (Hovmöller et al. 2002; Ogden and Whiting 2003; Whitfield and Kjer 2008; Simon et al. 2009; Trautwein et al. 2012). This conundrum has been called “the Palaeoptera problem” and qualified as presently “intractable” (Trautwein et al. 2012), although recent morphological work based on head structure adds support to Palaeoptera (Blanke et al. 2012). Neopteran monophyly is widely accepted, but two of the three putative lineages nested within it, Polyneoptera and Paraneoptera (= Acercaria), lack robust support, and the cladistic structure of the tree remains poorly understood (Trautwein et al. 2012). Exciting developments within Polyneoptera are the discovery and systematic placement

of the order Mantophasmatodea (Klass et al. 2002; Terry and Whiting 2005; Cameron et al. 2006; Eberhard et al. 2011), the inclusion of Isoptera as a family of Blattodea (Terry and Whiting 2005; Inward et al. 2007) and the possible resolution of Zoraptera as the sister group to the dictyopteran orders (Ishiwata et al. 2011).

Resolution within Holometabola is now comparatively stable, including the acceptance that fleas are members of the scorpionfly order Mecoptera (Whiting 2002; Wiegmann et al. 2009; Friedrich and Beutel 2010). Recent analyses have resolved “the Strepsiptera problem” (Whiting et al. 1997) towards the Coleoptera side, placing them as the sister group of beetles (Niehuis et al. 2012). The early divergence of Hymenoptera, which comprises the sister group to all other Holometabola, has found recent support in analyses of both single-copy nuclear genes (Wiegmann et al. 2009) and morphology (Friedrich and Beutel 2010).

2.5 Final Remarks

New approaches to studying anatomy and molecular analyses that are increasingly becoming phylogenomic in scope have converged on many of the main issues in arthropod phylogeny. Monophyly of Ecdysozoa, Panarthropoda and an Onychophora + Arthropoda clade provides a context for evaluating the internal phylogeny of Arthropoda, which is itself unambiguously monophyletic. Pycnogonida and Euchelicerata probably form a clade, Chelicerata, and its most likely sister group is Mandibulata, though various lines of evidence still signal an alternative alliance between chelicerates and myriapods, or Paradoxopoda. Myriapoda is monophyletic and in the context of Mandibulata constitutes the sister group to Tetraconata, composed of a paraphyletic Crustacea from which a monophyletic Hexapoda arose, most probably from a shared ancestor with Remipedia (and doubtfully Cephalocarida). Key outstanding issues are the interrelationships between arachnid orders and crustacean classes, notably whether cephalocarids group with

remipedes and whether branchiopods or malacostracans are more closely related to remipedes and hexapods or to each other. The dating of arthropod diversification needs to be refined by improved clock methods and careful integration of fossil constraints. Geologically, Chelicerata (at least Pycnogonida) have a Cambrian origin, while Arachnida started diversifying by the Early Silurian, probably concurrently with Myriapoda. The deepest splits within Tetracnata demonstrably date to no younger than the Cambrian, as shown by spectacularly preserved Late Cambrian fossils that can be identified as branchiopods, copepods and ostracods (Harvey et al. 2012), and early Cambrian maxillopodan-type metanauplius larvae (Zhang et al. 2010; see Chap. 15). Though molecular dating and palaeontologically inferred ghost lineages date the origins of Hexapoda to the Cambrian, the clade's diversification is probably Silurian–Devonian and has been correlated with the origin of vascular plants (Kenrick et al. 2012). We expect that with the current availability and facilities for generating genomic data of a diverse selection of arthropods, a broad consensus will be found for the most diverse group of animals, a group with more than 500 million years of evolutionary history.

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