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Review Article

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

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A B S T R A C T

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

1. Introduction

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

For the purpose of this review, major competing hypotheses for the fundamental groupings in the Arthropoda are introduced by their proper names. I see little point in presenting "the" morphological perspective and (or versus) "the" molecular perspective because morphologists have advocated hypotheses as different from each other as any of them are to any molecular result (morphologists have supported either Tetraconata or Atelocerata, Mandibulata or Schizoramia, etc.). Likewise there is no singular molecular tree for arthropods because different genes or different analyses have differed in the clades that they resolve. That said, certain recurring patterns can be recognised with different classes of evidence, e.g., molecular phylogenies are split between myriapods being most closely allied to chelicerates (Paradoxopoda/Myriochelata) or to hexapods and crustaceans (Mandibulata), but irrespective of what markers are employed, a hexapod–crustacean clade (Tetraconata) is emphatically favoured rather than a myriapod–hexapod clade (Atelocerata).

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

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

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

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

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

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

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

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

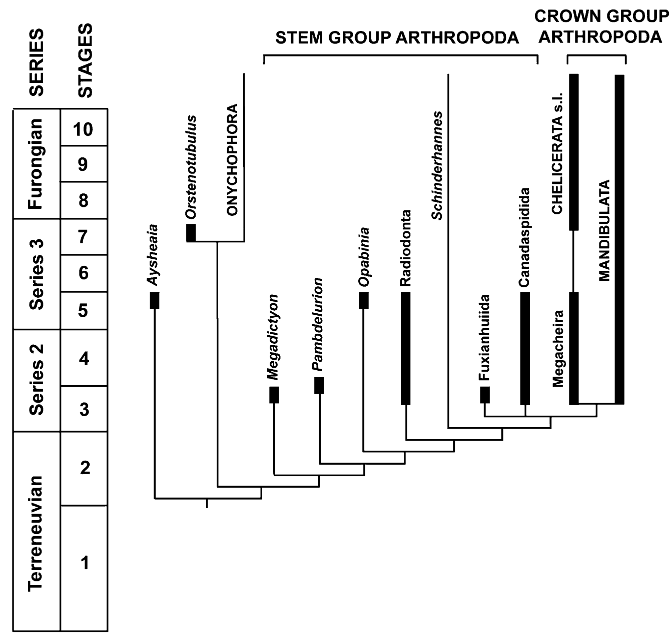

Fig. 1. Relationships of stem group arthropods (after Daley et al., 2009) plotted against Cambrian time scale. Assignment of Lagerstätten to stages follows Zhu et al. (2006). Stages 1 and 6–8 have been formalised as the Fortunian, Druman, Guzhangian and Paibian, respectively. In the arthropod crown group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

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

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

3. Arthropod monophyly: no longer a controversy

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