the TIMETREE of LIFE

edited by **S. BLAIR HEDGES** and **SUDHIR KUMAR**

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Arthropods (Arthropoda)

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Abstract

Living arthropods comprise more than 1 million species and represent the majority of the Earth's animal diversity. This phylum of animals includes one extinct subphylum (Trilobita) and four living subphyla: Myriapoda (e.g., centipedes and millipedes), Chelicerata (e.g., spiders, mites, and horseshoe crabs), Hexapoda (e.g., insects), and Crustacea (e.g., shrimps and crabs). The relationships of the subphyla and classes remain uncertain, although some consensus is emerging for the relationships among hexapods and crustaceans. The current evidence suggests that arthropods originated before 630 million years ago (Ma), but that the divergences leading to the currently recognized subphyla occurred in the Ediacaran and the Cambrian (630–488 Ma).

With more than 1 million described species (*1*), arthropods are a marvelous evolutionary success. This phylum of animals includes one extinct subphylum (Trilobita, ~4000 described species) and four living subphyla: Myriapoda (e.g., centipedes and millipedes, ~11,500 species), Chelicerata (e.g., spiders, mites, and horseshoe crabs, ~70,000 species), Hexapoda (e.g., insects, ~948,000 species), and Crustacea (e.g., shrimps and crabs, ~68,000 species). The Phylum Arthropoda is characterized by species having an articulated chitinous exoskeleton divided into thick areas, corresponding to segments, joined by thin "rings" (*2*). Each segment typically carries a pair of articulated legs, and a number of anterior segments are fused into a cephalon. In most groups the cephalon carries eyes, and two or more pairs of limbs (*2*). Arthropods have been treated as a single animal group essentially since 1753, when Linnaeus called them Insecta in the first edition of the *Systema Naturae* (*3*). However, their monophyly has long been debated because of their morphological disparity (*4–6*). Molecular data eventually confirmed arthropod monophyly (*7*) and to date arthropods are classified into one extinct subphylum (the Trilobita) and four extant subphyla: Crustacea, Hexapoda, Myriapoda, and Chelicerata (Fig. 1). Each subphylum is further divided into classes (*8*). Here, I will review the relationships and divergence times among the arthropod classes and subphyla.

The higher-level relationships among arthropods are still uncertain. Traditionally, Hexapoda (insects and their allies) and Myriapoda (centipedes, millipedes, and their allies) were joined in the group Atelocerata. The Crustacea (crabs, shrimps, and their allies) were joined with Atelocerata in the group Mandibulata (*9*). Finally, Chelicerata (spiders, horseshoe crabs and their allies) were considered the closest relative of Mandibulata. Molecular phylogenetics revolutionized this scenario, supporting a derivation of Hexapoda from within a paraphyletic Crustacea (*7, 10–13*). The group composed of Hexapoda and Crustacea was named Pancrustacea

Fig. 1 A crab (*Metopaulias depressus*; Decapoda) from Jamaica (top); and a millipede (*Anadenobolus arboreus*; Diplopoda) from Puerto Rico (bottom). Credit: A. Sanchez.
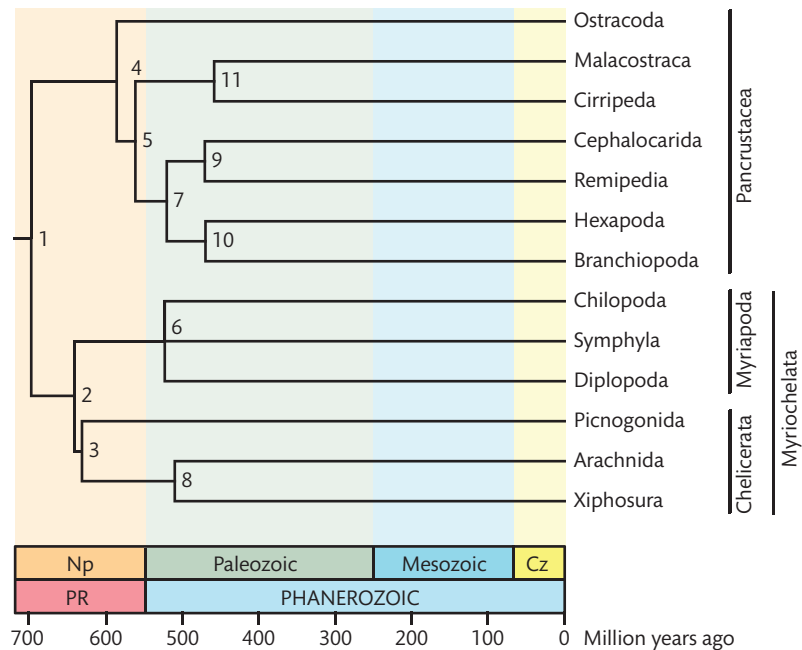
Fig. 2 A timetree of arthopods. The divergence times are from Table 1. This figure assumes the Myriochelata hypothesis, but see text for caveats. *Abbreviations*: Cz (Cenozoic), Np (Neoproterozoic), and PR (Proterozoic).

(*14*), and Mandibulata was redefined as the group joining Myriapoda and Pancrustacea. To date, Pancrustacea is arguably the best supported group of arthropod subphyla (*7, 10–13, 15–24*).

Molecular phylogenetics also questioned the validity of Mandibulata as many independent molecular studies recovered Myriapoda as the closest relative of Chelicerata. The group joining Myriapoda and Chelicerata was named Myriochelata by Pisani *et al.* (*21*) and Paradoxopoda by Mallat *et al.* (*18*). Support for the Myriochelata hypothesis has been found in mitochondrial genome analyses (*16, 19, 25, 26*), from the analysis of a concatenation of nine nuclear and 15 mitochondrial genes (*21*), and from the analysis of Hox genes (*17*). Analyses of *18S rRNA* and *28S rRNA* sequences have not provided conclusive support for this group (*24*). However, the largest sequence analysis thus far, including 40 Mb of expressed sequence tags and 21 animal phyla, supported Myriochelata (*36*). Putative derived characters of Myriochelata have been proposed (*25, 27*), but Mandibulata is generally favored in combined analyses of molecular and morphological data (*23*). Furthermore, concerns that Myriochelata may be a long-branch attraction artifact remain (*20*), and the Myriochelata vs. Mandibulata controversy cannot be considered settled.

Relationships within the subphyla of arthropods are also uncertain. Within Pancrustacea, the monophyly of the Class Hexapoda is well supported (*24*) and there is evidence that the closest relative of Hexapoda is most likely the Branchiopoda, the brine shrimps and their allies (*22, 24*). However, the relationships among the remaining classes of Pancrustacea remain uncertain. Similarly, the relationships among the myriapod classes are not yet resolved (*22*). The higher-level relationships within Chelicerata are better established, with Xiphosura (the horseshoe crabs) and the Arachnida (spiders, mites and their allies) forming a monophyletic group (*20*), closest to the Pycnogonida (sea spiders; *22*).

The arthropod fossil record is rich, but the tempo of early arthropod evolution is unclear. The earliest fossil arthropods are trilobites and date back to the Atdabanian stage (523–519 Ma) of the early Cambrian (*28*). However, the biogeographic distribution of the earliest trilobites suggests that diversification within Arthropoda must have predated the breakup of the late Neoproterozoic supercontinent Pannotia (~600–550 Ma; *29*). If this was true, the earliest arthropod history must be unrecorded in the fossil record (*30*).

Molecular clocks could be used to test the hypothesis that the earliest evolutionary history of Arthropoda was not recorded in the fossil record. However, only two

Table 1. Divergence times (Ma) and their credibility/confidence intervals (CI) among arthropods.

Timetree		Estimates					
		Ref. (*21*)		Ref. (*22*)		Ref. (*31*)	Ref. (*32*)
Node	Time	Time	CI	Time	CI	Time	CI
1	698.5	725.0	825–634	672.0	732–612	–	–
2	642.0	642.0	765–519	–	–	–	–
3	632.0	–	–	632.0	685–573	–	–
4	587.0	–	–	587.0	634–540	–	–
5	562.0	640.0	779–569	546.0	593–499	500.0	532–508
6	524.0	442.0	540–344	606.0	666–545	–	–
7	521.0	–	–	521.0	572–470	–	–
8	510.5	475.0	578–372	546.0	593–499	–	–
9	471.0	–	–	471.0	521–421	–	–
10	470.0	–	–	–	–	470.0	434–421
11	459.0	–	–	459.0	510–408	–	–

Note: Node times in the timetree represent the mean of time estimates from different studies.

studies investigated the earliest evolutionary history of this phylum using molecular clocks (*21, 22*), although some pertinent divergence time estimates are available from two other studies (*31, 32*) (Fig. 2, Table 1). Pisani *et al.* (*21*) used 61 genes to derive divergence times under a variety of global and relaxed molecular clock methods in a limited number of taxa (seven). In contrast, Regier *et al.* (*22*) used fewer genes (three) but included a larger number of taxa (17). Despite these differences, the two studies obtained similar results (*22*), which are also similar to those reported in Gaunt and Miles (*32*). However, estimates from Aris-Brosou and Yang (*31*) differ significantly from other studies. They used a variable number of mitochondrial and nuclear genes (1–14 depending on the clade) to estimate divergence times among several animal groups (including four of those in Fig. 2) in an approach where the rate variation among lineages was modeled as an Ornstein–Uhlenbeck process. Their results have been debated, primarily because they reported divergence times that were significantly younger than some corresponding fossil-based divergences (*33, 34*), and hence they cannot be correct. Only divergence times among arthropod groups inferred by Aris-Brosou and Yang (*31*) that did not postdate the corresponding fossil-based divergence time were included in Table 1.

The timetree of arthropod evolution (Fig. 2) indicates that Arthropoda originated in pre-Ediacaran times (~698 Ma), but that diversification of the major lineages occurred during the Ediacaran and the Cambrian (630–488 Ma). These results are mostly in agreement with the arthropod fossil record, and with what is known of the latest Neoproterozoic biogeography (*29*). Indeed, the only major incongruence between the fossil record and the molecular clock-based divergence times here reported is represented by the pre-Ediacaran (~698 Ma; see Table 1 and Fig. 2) divergence between Myriochelata and Pancrustacea. However, the results presented here reject the Cambrian explosion hypothesis, in which animal Phyla are assumed to originate in the lower Cambrian, or very close to Ediacaran–Cambrian (542 Ma) boundary (*35*). The great arthropod radiation was essentially completed by ~459 Ma, well before the end of the Ordovician.

Acknowledgments

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