

Origin and Terrestrialization of Arthropods

Subjects: Evolutionary Biology

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Arthropods, the most diverse form of macroscopic life in the history of the Earth, originated in the sea. Since the early Cambrian, at least ~518 million years ago, these animals have dominated the oceans of the world. By the Silurian–Devonian, the fossil record attests to arthropods becoming the first animals to colonize land. However, a growing body of molecular dating and palaeontological evidence suggests that the three major terrestrial arthropod groups (myriapods, hexapods, and arachnids), as well as vascular plants, may have invaded land as early as the Cambrian–Ordovician. These dates precede the oldest fossil evidence of those groups and suggest an unrecorded continental “Cambrian explosion” a hundred million years prior to the formation of early complex terrestrial ecosystems in the Silurian–Devonian.

Keywords: terrestrialization ; arthropods ; Cambrian explosion ; molecular clocks ; arachnids

1. Arthropod Origins

It is difficult to precisely estimate terrestrial arthropod biodiversity in deep time due to the caveats of the fossil record; terrestrial arthropod fossils are usually limited to sites of exceptional preservation known as *Konservat-Lagerstätten*, and therefore their stratigraphic and environmental distribution is discontinuous. However, it can be supposed that, as in the modern biosphere, arthropods were probably the largest component of the diversity and abundance of Palaeozoic land animals, given the lack of initial competition and the phylogenetic diversity of those that are present in the terrestrial Palaeozoic fossil record. Indeed, arthropods are likely to have been the dominant animal group in terms of biodiversity in perpetuity for the past 520 million years ^[1]. Arthropods are characterised by presenting internal and external body segmentation with regional specialisations (tagmosis: in the case of insects, for example, they possess a thorax where legs and wings are inserted while there are no extremities in the abdomen); an external skeleton composed of articulated sclerotized parts; body segments that originally had associated articulated limbs; growth through successive moults (ecdysis); and an open circulatory system with a dorsal heart with lateral valves ^[2]. This set of unique characteristics suggests that they are a monophyletic group (descendants of a common ancestor who possessed the diagnostic characteristics of the lineage). Arthropods are represented by chelicerates (with arachnids such as spiders and scorpions, and marine groups such as pycnogonids and horseshoe crabs); myriapods (such as millipedes and centipedes); hexapods (containing insects) and predominantly aquatic ‘crustaceans’ (for example crabs and prawns), which are collectively known as pancrustaceans; and include important extinct groups, such as the trilobites (**Figure 1**). Their abundance makes arthropods ecologically essential; for example, myriapods are important processors of detritus in forests, and termites consume such large amounts of cellulose that they are significant for the carbon cycle and atmospheric gas composition ^[3]. Without arthropods, life and ecosystems on Earth would be radically different. Their surprising diversity (which exceeds 75% of all living species described ^[4]) can help to elucidate the patterns and processes of macroevolution.

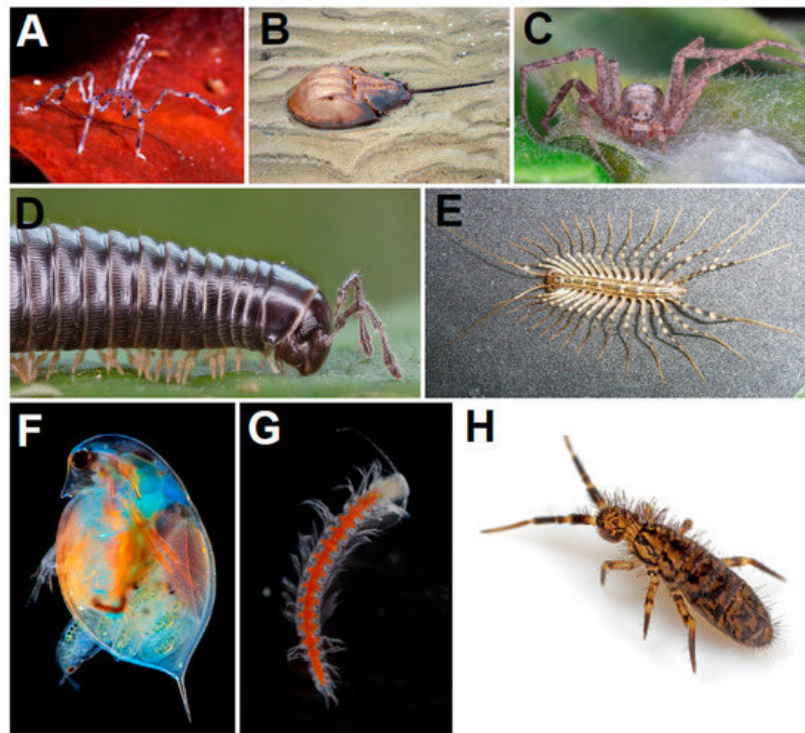


Figure 1. Present diversity of arthropods (A) pycnogonid *Endeis flaccida* (chelicerate); (B) xiphosuran *Limulus polyphemus* (chelicerate); (C) spider *Philodromus aureolus* (arachnid: chelicerate); (D) millipede *Cylindroiulus caeruleocinctus* (myriapod); (E) centipede *Scutigera coleoptrata* (myriapod); (F) branchiopod *Daphnia* sp. (pancrustacean); (G) remipede *Morlockia williamsi* (pancrustacean); (H) hexapod *Orchesella villosa* (pancrustacean). Image sources: Wikimedia Commons; (G) Jørgen Olesen.

The earliest animals people know as land-dwelling were arthropods [5]. Evaluating the earliest fossil evidence of arthropod life on land can rely on two approaches—phylogenetic bracketing and direct anatomical evidence. Under the former approach, the discovery of a fossil representative belonging to an entirely terrestrial clade can be deemed to provide evidence of life on land, even when the state of preservation of the individual fossils is not particularly impressive. The second, more direct approach, relies on identifying unambiguous terrestrial adaptations in fossil specimens to conclude that these indeed lived on land.

The earliest fossil assemblage preserving arthropods belonging to terrestrial clades is the Přídolí-aged Ludlow bone bed Member exposed at Ludford Lane, near Ludlow in Shropshire, western England [6][7][8][9]. This site contains a range of myriapods, including scutigermorph centipedes in the genus *Crussolum* [9], the arthropleurid *Eoarthropleura* [9], and a singular specimen of the trigonotarbid arachnid *Eotarbus jerami* Dunlop 1996 (= *Palaeotarbus jerami*, junior synonymy resolved by Dunlop [10]). Any of these can be confidently considered to be the oldest terrestrial arthropod body fossils, albeit the fidelity of their preservation does not permit the observation of anatomical adaptations for life on land—most are represented by small shreds of cuticle or, in the case of *Eotarbus*, a dark carbonised specimen. U-Pb zircon dating of the Ludlow bone bed at Ludford Lane in Shropshire constrained the age of the deposit to ~420 Ma [11].

The earliest animal possessing unambiguous terrestrial adaptations is the millipede *Pneumodesmus newmani* from the Lower Devonian Cowie Harbour near Stonehaven in Aberdeenshire, Scotland [12], which is preserved with more fidelity. The terrestrial character of this organism is indisputable since it possesses spiracles, openings on the cuticle that allow air to enter the tracheal system. Two other diplopod species were reported from the locality, all described by Wilson and Anderson [12]. The *Dictyocaris* Member of the Cowie Formation at Cowie Harbour was initially considered to be Silurian based on palynological evidence (~426.9 Ma [13][14][15]), but isotopic dating confidently constrained its age to the lowermost Devonian (Lochkovian; ~414 Ma [16]), making it some 6 Mya younger than the Ludford Lane assemblage. Recently, the scorpion *Palaeoscorpion devonicus* [17][18] from the Lower Devonian Hunsrück Slate Lagerstätte in Germany (~405 Ma) was interpreted as possessing adaptations for life on land, namely probable book lungs, indicating that it was likely terrestrial [19].

2. Arthropod Phylogeny

The evolutionary relationships among the major arthropod groups have always been a subject of debate, such that by the start of the 21st century virtually all conceivable topologies for the group had been proposed [20]. Identifying the closest

relatives of each terrestrial lineage is crucial, not only for comparative studies dealing with adaptation strategies for life on land, but also to understand the potential terrestrialization routes and constrain their timing. To infer these phylogenies, the anatomical structures of living and fossil species provide a treasure trove of comparative data that has been expanded even further during the last few decades by vast quantities of molecular data [21]. In their adaptation to land, arthropods have undergone convergent evolution (independent origins of similar biological systems in different lineages), which has often complicated efforts to assess kinship relationships between them [4]. For example, trachea (respiratory structures adapted to terrestrial environments) are found in several lineages that have conquered the land independently during the Palaeozoic: in a few arachnids, myriapods, isopods, and hexapods. The introduction of genome-scale phylogenetic analyses—phylogenomics—has greatly narrowed down the number of hypotheses on hexapod phylogeny, but crucially, some nodes of the arthropod tree remain difficult to resolve. Such challenging nodes often represent ancient and rapid radiations that are complex to address with any dataset, molecular or morphological, and represent the major lasting controversies in reconstructing the process of the arthropod invasion of land [15][22][23][24][25].

3. Myriapods

According to a classical phylogenetic hypothesis, the exclusively terrestrial myriapods, have been regarded as the sister group of the hexapods. This hypothetical clade, called Tracheata (or Atelocerata), is supported mainly by the presence of tracheae in both groups to carry out gas exchange (reviewed in [26]). Current studies based on molecular data, and also a re-examination of more subtle morphological characters of the nervous system and ommatidia [23][27], discard this hypothesis, and attribute this coincidental morphological convergence to independent convergence [28]. A second hypothesis recovered by early analyses of molecular data implicated myriapods as a sister group to the chelicerates (Myriochelata or Paradoxopoda). However, these results are now considered as caused by a phylogenetic reconstruction bias due to the rapid evolutionary rates of pancrustaceans attracting to the outgroup and pushing myriapods and chelicerates into an artefactual clade when using simpler models of molecular evolution [29]. Today, there is a certain consensus on the main relationships between arthropods, supported by phylogenomic data [28]. The myriapods, the first of the three large terrestrial lineages, are generally accepted as a sister group to the pancrustaceans (hexapods and all crustacean lineages), and the chelicerates as the closest relative of this clade (**Figure 2**). Thus, the basic division between arthropods consists of those that have mandibles (myriapods and pancrustaceans) and chelicerae. The internal phylogeny of myriapods, though, is currently more contentious. Several recent phylotranscriptomic analyses disagree on the exact relationship between their main lineages [28][30][31][32][33] but they do not have an impact on the single terrestrialization event inferred for the group.

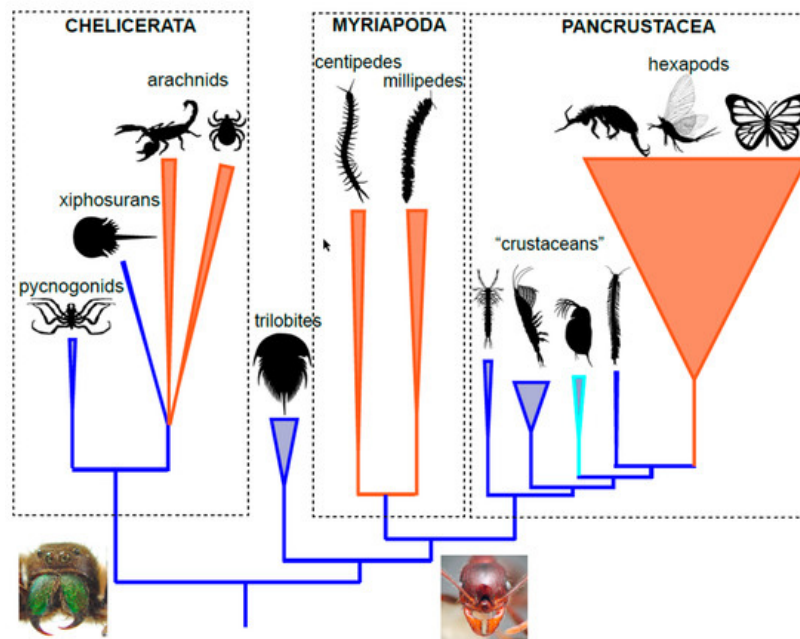


Figure 2. Cladogram with the current consensus on the phylogenetic relationships between the main groups of arthropods. The terrestrial groups are represented in orange colours while the marine clades in blue and turquoise for Branchiopoda (fresh water). The thickness of the terminal branches corresponds to a proportional approximation of the number of described species. At the base of the cladogram, image with detail of chelicerae and mandibles, the defining structures of the two groups. Some of the silhouettes come from Phylopic (phylopic.org/; accessed on 5 November 2022).

4. Pancrustacea (Hexapoda)

There is strong molecular and morphological evidence that favours the position of hexapods as nested within the 'crustaceans' (as the clade Pancrustacea, or Tetraconata), and myriapods as the sister group of pancrusteans forming the Mandibulata group, characterized by the presence of this distinctive oral structure ^{[34][35][36]}. In contrast, the exact relationships of hexapods within the Pancrustacea are still unclear, and it is not obvious which is their aquatic sister group. Phylogenomic datasets have variously lent support to the mostly freshwater-dwelling branchiopods ^[37], or the species-poor and enigmatic remipedes ^{[17][19]}. Establishing which 'crustacean' group is the most closely related to hexapods has a great impact on whether the latter group presumably colonised terrestrial environments directly from the sea, or whether they first colonized freshwater environments and later moved to land. Most recent phylogenomic studies, though, using hundreds of molecular markers, have shifted the balance in favour of Remipedia ^{[34][36]}. Remipedia are a class of blind and predatory crustaceans that live in coastal aquifers that contain saline groundwater. They were discovered less than 40 years ago ^[38], and have a very restricted distribution, with fewer than 30 known species described from the anchialine caves in the Caribbean Sea, two species from the Canary Islands and one from Western Australia. Very little is known about the biology of these organisms, which makes it difficult to understand their significance for hexapod terrestrialization.

5. Pancrustacea (Isopods)

The suborder Oniscidea (woodlice) represents the most diverse isopod crustacean group, with over 3700 described species ^[39]. It is the only pancrustacean group besides the hexapods composed almost entirely of terrestrial species; its members are found in almost all terrestrial habitats, ranging from nearshore settings to forests ^[40]. In particular, the intertidal genus *Ligia* inhabiting shorelines is often regarded as a transitory group ^[41]. Given their varying degrees of adaptations for life in semi-aquatic and terrestrial environments, woodlice provide a rewarding model group for understanding the transition from marine to terrestrial habitats, which hinges on an understanding of their phylogeny ^[41] ^[42]. Morphological studies implicate Ligiidae as the basalmost woodlouse clade, implying a single invasion of land directly from the marine realm ^[43], although some molecular studies have challenged the monophyly of the group (e.g., ^{[44][45]}). Overall, isopods remain probably the least-studied terrestrialization event among arthropods. Their fossil record is fragmentary and scarce, with their oldest occurrence from the Cretaceous (summarised in ^[41]). If terrestrial isopods originated in the late Palaeozoic, potentially the Carboniferous ^[41], they would represent the most recent arthropod terrestrialization event.

In some sense, other pancrustacean clades such as amphipods and the decapods, also invaded semi-terrestrial habitats (e.g., supralittoral zone of beaches, moist soil and leaf litter, edges of freshwater habitats) and these have been considered as terrestrialization events by some (e.g., ^[46]). Here, the researchers refrain from treating these groups as fully terrestrial, since their adaptation to life is not as developed as in the case of the woodlice. Nonetheless, these taxa represent important study groups for future research in arthropod adaptation to semi-terrestrial habitats.

6. Arachnids

Among terrestrial arthropods, only insects outnumber arachnids in terms of the number of described species (1 million versus 112,000, respectively; ^[47]). The clade Arachnida includes all terrestrial chelicerates, composed mainly of predatory groups such as spiders and scorpions, and parasites such as ticks. However, chelicerates also include marine taxa such as the pycnogonids (sea spiders) and xiphosurans (horseshoe crabs). Neither the currently available morphological nor molecular data have unequivocally resolved the internal kinship relationships between chelicerates ^[45]. Arachnids have traditionally been regarded as a monophyletic group, implying that a single and irreversible ancestral colonization of land paved the way to this group's evolutionary success. Some recent studies including genome-scale and morphological phylogenies, however, do not support this relationship, instead placing the marine Xiphosura within terrestrial arachnids, and not as a sister group to it ^{[24][48]}. The focus of this debate is whether there has been a single common ancestor for all terrestrial arachnids, a single terrestrialization event within a common ancestor of terrestrial arachnids + xiphosurans (with the later transitioning again into aquatic environments soon after), or whether arachnid terrestrialization occurred on two or more separate occasions. Resolving this puzzle is enormously significant, as it rewrites the researchers' perception of the evolution of terrestrial adaptations (e.g., the respiratory system, sensory and reproductive systems, and the locomotor appendages). The physiological demands of life on land require a significant modification of these anatomical features, which is probably best illustrated by the respiratory organs, a great variety of which are present in extant chelicerates (book lungs and tracheae in terrestrial groups, and book gills in marine forms) ^{[49][50]}. If xiphosurans were a group of marine arachnids, this may suggest that the remaining lineages colonized land independently. A second option would be that xiphosurans recolonized the marine environment from a terrestrial ancestor. Of these two options, the first would be

considered more plausible, since the fossil record of Xiphosura extends back more than 400 Ma with exclusively aquatic forms, without traces of a potential terrestrial or amphibious ancestors ^[51]. Furthermore, no widespread losses of terrestrial respiratory organs in arthropods are known, once acquired, in line with the predictions of Dollo's law ^[52].

In addition, even though horseshoe crabs can make momentary incursions into the coasts to spawn eggs, they do not have distinctly terrestrial morphological adaptations and their body structures present great similarity, and probably homology, with that of other aquatic fossil chelicerates ^{[53][54]}. Other recent studies using genome-scale datasets, as well as morphological and fossil evidence suggest that marine chelicerates (pycnogonids and Xiphosura) are successive sister groups of a monophyletic lineage of terrestrial arachnids. These results are compatible with a single colonization of land within chelicerates and the absence of wholly marine arachnid orders ^{[15][55]}.

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