

Remipedia and the Evolution of Hexapods

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Advanced article

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With more than a million species that have already been described, the hexapods (insects and allies) constitute the largest animal group. Still their origin and phylogenetic affinities are matter of intense debate. Although previous morphological work generally considered the millipedes as sister taxon of the hexapods, molecular phylogenetic analyses agree that hexapods are actually closely related to crustaceans. Recent studies have provided evidence that the Remipedia, enigmatic crustaceans that have been discovered only 30 years ago in anchialine cave systems, may be the closest living relatives of hexapods. Support for this hypothesis comes from similar brain architecture, presence of an insect-type respiratory haemocyanin in remipedes and phylogenomic studies. Thus hexapods may have evolved from a Remipedia-like marine crustacean. These data evokes doubt on the generally described hypotheses in textbooks that might present an outdated picture of arthropod phylogeny.

Introduction

Arthropods constitute the most species-rich animal phylum on our planet and include four subphyla: Chelicerata (spiders, scorpions, mites, ticks, horseshoe crabs and allies), Myriapoda (centipedes, millipedes and allies), Crustacea (crabs, shrimps and others) and Hexapoda (insects and allies). The phylogenetic relationships and the evolutionary history of the Arthropoda are notoriously debated. This controversy already commenced in the nineteenth century

(Pocock, 1893; Lankester, 1904) at the time of Charles Darwin and still persists in evolutionary biology until today (Figure 1). See also: [Arthropoda \(Arthropods\)](#)

For a long time it had been assumed that annelids are the closest living relatives of arthropods. However, increasing molecular and morphological data support the hypothesis that Arthropoda are rather member of the superphylum ‘Ecdysozoa’, which also includes other moulting phyla, that is Onychophora (velvet worms), Tardigrada (water bears), Nematomorpha (horsehair worms), Priapulida (priapulid worms) and Kinorhyncha (mud dragons) (Aguinaldo *et al.*, 1997; Dunn *et al.*, 2008). A sister group relationship of Onychophora (velvet worms) and Arthropoda has become widely accepted and is well supported by molecular phylogenetic studies (e.g. Roeding *et al.*, 2007; Dunn *et al.*, 2008).

Based on a number of shared morphological characters (synapomorphies), it has long been thought that Hexapoda are allied with Myriapoda in a taxon named ‘Tracheata’ or ‘Atelocerata’ (Brusca and Brusca, 2003). These supposed synapomorphies include reduced second antennae, mandibles without palp, both maxillae with two endites, uniramous thoracopods, the Tömösvary organs and segmental pairs of spiracles (Brusca and Brusca, 2003). Deoxyribonucleic acid (DNA) and protein sequence data, however, have provided strong evidence that Hexapoda are actually closely related to the crustaceans (Friedrich and Tautz, 1995; Dunn *et al.*, 2008), thus forming the taxon referred to as ‘Pancrustacea’ (Zrzavý and Štys, 1997) or ‘Tetraconata’ (Richter, 2002). Within recent years this concept also gained support from comparative morphology (Fanenbruck and Harzsch, 2005). Morphological characters as well as some molecular phylogenetic studies have suggested that Pancrustacea are most closely related to the Myriapoda (e.g. Rota-Stabelli and Telford, 2008; Regier *et al.*, 2010), with the Pancrustacea in a taxon Mandibulata (Brusca and Brusca, 2003). However, other molecular approaches have provided evidence for a common clade of Myriapoda and Chelicerata (‘Myriochelata’ or ‘Paradoxopoda’ hypothesis; e.g. Pisani *et al.*, 2004; Dunn *et al.*, 2008). Morphological evidence for such relationship is poor and restricted to similarities of early neurogenesis (Kadner and Stollewerk, 2004).

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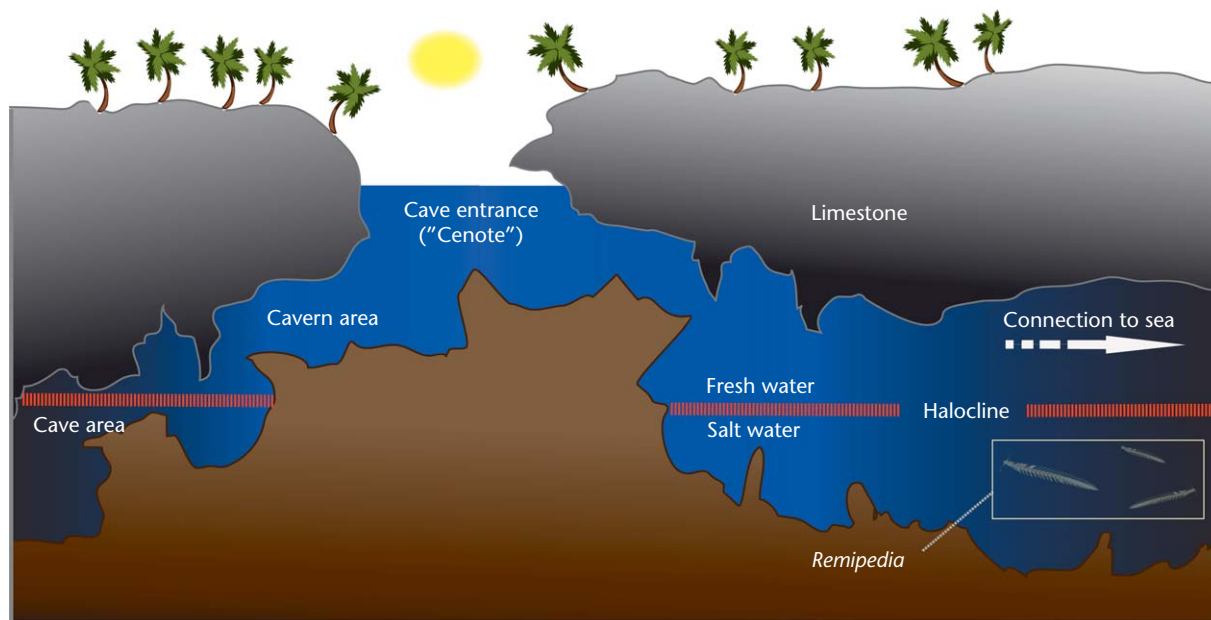


Figure 1 An anchialine cave system as typically found on the Yucatan, Mexico.

Hexapoda

The subphylum Hexapoda includes the ectognathan (with external mouth parts) insects and three orders of entognath, wingless arthropods (Collembola, Diplura and Protura). Hexapods are the dominating animal life form and include at least 80% of all described animal species (more than 1 million). Winged insects are the only arthropods that successfully conquered air.

The evolutionary scenario of hexapod origin is still uncertain, basically because the fossil record of hexapods is sparse (Grimaldi and Engel, 2005). The oldest known unambiguous hexapod fossil is the springtail *Rhyniella praeursor* (Collembola) from the early Devonian Rhynie Lagerstätte in Scotland. However, this fossil harbours poor diagnostic features and thus offers little information on early hexapod morphology. Recently, *Devonohexapodus bocksbergensis*, an enigmatic fossil from the lower Devonian, has been reported as marine hexapod (Haas *et al.*, 2003). However, this view has been challenged (Kühl and Rust, 2009).

A common ancestry (monophyly) of all hexapods has received wide support from morphological studies (Kukalová-Peck, 1998; Brusca and Brusca, 2003). Shared derived characters of hexapods include the tagmosis of the body with a thorax constituted of three, limb bearing segments and an abdomen constituting of originally eleven segments and a telson. However, some phylogenetic studies based on mitochondrial DNA sequences have suggested a paraphyletic origin of hexapods and found the collembolans (Nardi *et al.*, 2003; Lavrov *et al.*, 2004; Hassanin, 2006) or diplurans (Carapelli *et al.*, 2007) nested within the crustaceans. Recent analyses have shown that these

relationships are most likely misinterpretations of the sequence data due to insufficient taxon sampling and inability of mitochondrial sequences to solve internal arthropod relationships (Cameron *et al.*, 2004; Hassanin, 2006). In fact, recent sequence analyses relying on nuclear genes confirm the monophyly of hexapods (Timmermans *et al.*, 2008; von Reumont *et al.*, 2009; Regier *et al.*, 2010).

An increasing number of molecular and anatomical data have provided evidence that Hexapoda are allied with Crustacea, thereby forming a pancrustacean assemblage (Friedrich and Tautz, 1995; Roeding *et al.*, 2007; Dunn *et al.*, 2008). Several lines of evidence have suggested that the Crustacea may be paraphyletic in terms of the Hexapoda, meaning that some crustaceans are more closely related to the hexapods than others. However, it had remained uncertain which class is the actual sister group of Hexapoda (Garcia-Machado *et al.*, 1999; Wilson *et al.*, 2000; Hwang *et al.*, 2001). Mitochondrial DNA and protein sequences have suggested a relationship of Hexapoda and malacostracan crustaceans (i.e. crabs, lobsters, shrimps, woodlice) (Garcia-Machado *et al.*, 1999; Wilson *et al.*, 2000; Hwang *et al.*, 2001). This view has received support from comparative studies of brain anatomy and embryonic development (Averof and Akam, 1995). On the contrary, analyses of ribosomal ribonucleic acid (rRNA) found Copepoda as sister group to the Hexapoda (Mallatt and Giribet, 2006; von Reumont *et al.*, 2009). Multigene analyses support a clade consisting of Branchipoda and Hexapoda (Roeding *et al.*, 2007; Dunn *et al.*, 2008). However, most of these studies included only some selected crustacean classes, but did not provide a comprehensive overview taxon sampling. Most recently, three independent lines of molecular and morphological

evidence have pointed to a third crustacean taxon as putative sister group of Hexapoda: the Remipedia (Fanenbruck *et al.*, 2004; Ertas *et al.*, 2009; Regier *et al.*, 2010).

Remipedia

Remipedia are an enigmatic crustacean class that has been discovered by Jill Yager in 1979 (Yager, 1981). These small animals dwell in anchialine cave habitats that feature an underground connection with salt water to the sea, whereas the entrance and surface part is composed of freshwater (Ilfie *et al.*, 1984). Fresh and saltwater form two layers that are separated by a cline-area, the halocline, in which both layers mix (Figure 2). Vertical spreading and dimension of this interface layer is conditioned to the topology in the

cave and varies also depending on characteristics of existing currents. Remipedia have been observed so far only below the halocline (Koenemann *et al.*, 2007). Four hot-spots of remipede cave habitats are currently known: the Canary Islands, Mexico (Yucatan), the Bahamas and West Australia. The origin of the disjunct biogeography of Remipedia is controversial. Some authors have suggested a Mesozoic relict distribution (Ilfie *et al.*, 1984; Humphreys, 1993). However, the Canary Islands are relatively young with estimated 30 million years and this volcanic archipelago evolved rather isolated (Carracedo, 2002). Thus an alternative explanation may be that remipede representatives have lived or still live in deeper water horizons or cave systems, and were or are capable of colonising new habitats. Unfortunately, evidence for such 'deep water horizon' remipede species is still absent.

Adult remipedes are typically 10–45 mm long, lack pigmentation and eyes, and are characterised by a small head

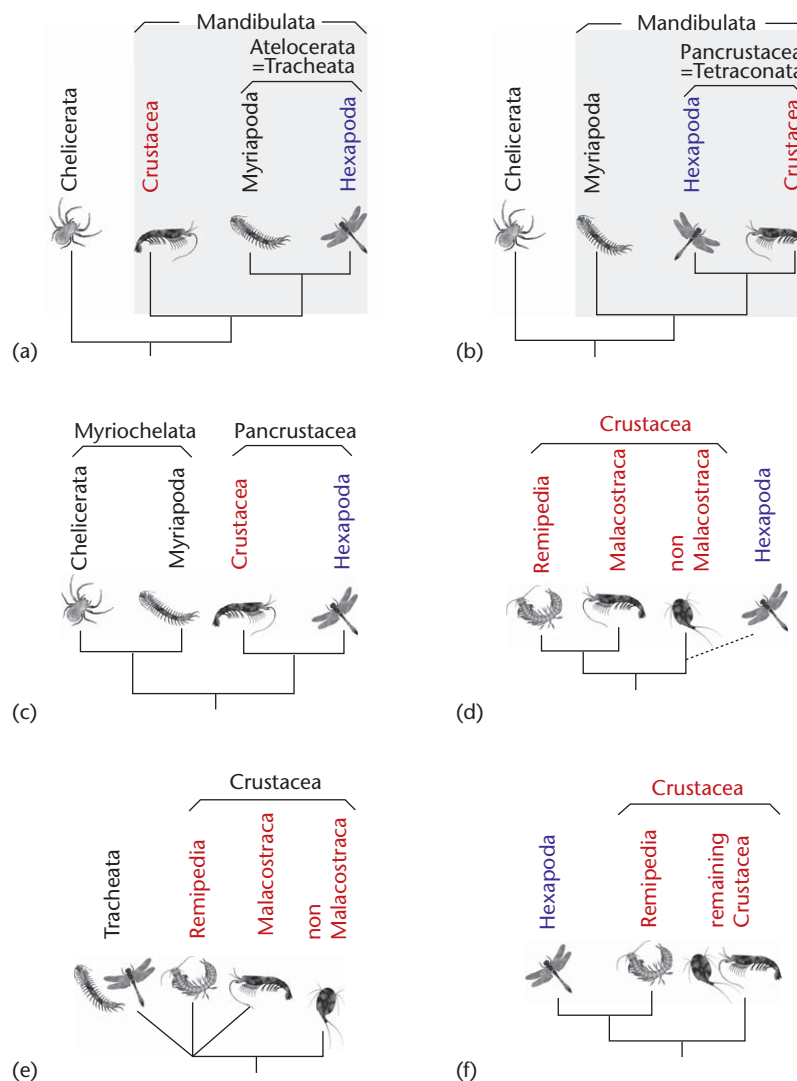


Figure 2 Conflicting hypotheses of remiped and hexapod evolution.

and an elongate, homonomously segmented trunk (Figure 3). Remipedes harbour a number of unique features (autapomorphies), which include the loss of eyes, biramous antennulae, three pairs of postmandibular mouthparts adapted to predatory feeding and the lack of specialisation of body segments (tagmatisation) in the trunk (Schram and Lewis, 1989; van der Ham and Felgenhauer, 2008). The fossil record of Remipedia is poor and restricted to *Tesnusocaris goldichi* and *Cryptocaris hootchi* from the Carboniferous period.

The phylogenetic affinities of Remipedia have been controversial. First analyses had suggested a sister group relationship of Remipedia to all other crustaceans (Schram, 1986). This assumption based on 'primitive' morphological characters that had been presumably inherited from the arthropod ancestor, such as the homonomous segmentation of the trunk, paddle-like appendages and a cephalic shield (Schram, 1986; Brusca and Brusca, 2003). Some authors did not assign remipedes to any other crustacean taxon because of lack of sufficient characters. First molecular studies as well as comparative analyses of limb morphology proposed a relationship of Remipedia and Maxillopoda (Ito, 1989; Spears and Abele, 1997), but the arrangement of mitochondrial genes persuasively excluded Remipedia from maxillopods (Lavrov *et al.*, 2004). Other studies employing DNA sequence data identified Remipedia at various positions within Crustacea, albeit usually with very poor support (Regier *et al.*, 2005; Hassanin, 2006; Carapelli *et al.*, 2007; Koenemann *et al.*, 2010). Neuro-anatomical studies have suggested that remipedes might represent a rather derived crustacean taxon (Fanenbruck *et al.*, 2004; Fanenbruck and Harzsch, 2005). Most recently, remipedes were revealed to be closely related to hexapods based on independent molecular data (Ertas *et al.*, 2009; Regier *et al.*, 2010).

Sister Group Relationship of Hexapoda and Remipedia

Comparative studies of arthropod brains showed that Remipedia represent a derived crustacean taxon that is most closely related to Malacostraca and Hexapoda (Fanenbruck *et al.*, 2004; Fanenbruck and Harzsch, 2005). Several brain structures (glomerular olfactory neuropils, bipartite antenna 1 neuropils, olfactory-globular tracts with characteristic chiasmata and hemiellipsoid bodies) were found only in Remipedia, Malacostraca and Hexapoda, but not in 'lower' crustaceans or chelicerates. Thus these neuro-anatomical studies provide support for a close relationship of Remipedia, Malacostraca and Hexapoda. This polytomy and thus the exact relation among these three taxa could not be resolved in that study. Interestingly, the recently identified larval forms of remipedes most closely resemble those of malacostracan crustaceans (Koenemann *et al.*, 2007, 2009).

A molecular phylogenetic study on arthropod haemocyanins also came to the conclusion that remipedes are closely related to hexapods (Ertas *et al.*, 2009). Haemocyanins are copper-containing, respiratory proteins that serve for the transport of oxygen in the haemolymph (Markl and Decker, 1992). Haemocyanins form hexamers or oligo-hexamers ($n \times 6$) that consist of identical or similar subunit types. The subunit composition is typically conserved between related taxa. For example, malacostracan haemocyanins consist of three subunit types (α , β and γ) (Markl and Decker, 1992), whereas two other distinct subunit types (1 and 2) form the hexapod haemocyanins (Pick *et al.*, 2009). The remipede species *Speleonectes tulumensis* (Figure 3) harbours three distinct haemocyanin subunit types (Ertas *et al.*, 2009). In phylogenetic these sequences do not group with malacostracan haemocyanins, but form common clades with hexapod subunit type 1 (*S. tulumensis* haemocyanin subunits 1 and 3) and hexapod subunit type 2 (*S. tulumensis* haemocyanin subunit 2), respectively. The phylogenetic tree is supported by a unique shared sequence motif insertion in *S. tulumensis* haemocyanin 2 and hexapod type 2 subunits. Together, remipede and hexapod haemocyanins are in the sister-group position to the haemocyanins of malacostracan crustaceans. However, a major drawback of this study is the absence of haemocyanins in other crustaceans ('Entomostraca'), which usually harbour haemoglobins.

Most recently, Regier *et al.* (2010) used an alignment of 68 nuclear genes (~41 kb) to infer the relationship among 75 arthropod species. They reconstructed a taxon named 'Xenocarida' that consists of the crustacean classes Remipedia and Cephalocarida. Cephalocarida are small, benthic crustaceans (2–4 mm). Only 10 cephalocarid species are hitherto described. Although there is little morphological similarity of Remipedia and Cephalocarida, a close relationship has already been recovered in some previous



Figure 3 *Speleonectes tulumensis* pictured in a frontal-ventral photography.

studies (Spears and Abele, 1997; Regier *et al.*, 2005, 2008; Koenemann *et al.*, 2010). However, this relationship has not been trusted because of possible 'long branch attraction' artefacts due to highly divergent sequences in Remipedia and Cephalocarida (Spears and Abele, 1997; Koenemann *et al.*, 2010). Xenocarida were the sister group of Hexapoda, a taxon the authors referred to as 'Miracrustacea' (Regier *et al.*, 2010).

Remipede Perspective of Hexapod Evolution

Understanding hexapod origin and biodiversity requires identification of the closest relatives. Although all hexapods known today are terrestrial, there is little doubt that they have evolved from a marine or freshwater ancestor. Major concerns also address the problem how arthropods conquered land and have developed the diversity we find today. Palaeontological evidence of the putative crustacean ancestor of hexapods is essentially absent because for almost a century scientists believed in the existence of 'Tracheata' and thus tried to identify a myriapod as predecessor of hexapods. Recently, the early Devonian fossil *D. bocksbergensis* was proposed as putative marine hexapod (Haas *et al.*, 2003). Putative hexapod-like structures include the leg-like palps of maxillae, the absence of a second pair of antennae and three pairs of long uniramous thoracopods with six podomeres. Interestingly, *D. bocksbergensis* also harbours remipede-like characters such as a homonomous trunk with 38 segments and 'abdominal' leglets. However, a recent study suggests that *D. bocksbergensis* does not represent a hexapod but rather an undefined euarthropod species (Kühl and Rust, 2009).

Nevertheless, several lines of evidence now suggest that the Remipedia represent the long sought hexapod sister taxon, or are at least closely related to it (see the earlier discussion). Thus Remipedia occupy a key position for the understanding of morphological and functional innovations eventually resulting in the emergence of Hexapoda. These may include physiological features like a unique haemocyanin or anatomical characters like an advanced brain structure. Remipedia are very rare animals that are difficult to access in their anchialine cave habitats. However, given their importance for understanding hexapod origins they deserve more interest in science.

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