



Enigma of hexapod evolution

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Abstract

Modern hexapod diversity represents summation of over 400 million years of high speciation rates and low levels of natural extinction. It seems that nature loves six legs. Out of the million documented species of hexapods, approx 83% are holometabola and largest group (38%) is of Coleoptera (beetles). The gap in the hexapod fossil record is called Hexapod gap. Their origin and evolution is highly debated because there are not enough fossils that directly connect them to the arthropods. Only few fossils found are not enough to precisely solve the mystery of hexapod evolution. There is no doubt that ability of flight gives them power to explore new niches and enhance their biodiversity. Origin and evolution of hexapods is somewhat more complex than it seems. Phylogenetics is not much useful because it requires a previous database to compare things and we do not have database of extinct hexapods. If we want to solve the enigma of hexapod evolution we must find another way which correlate hexapod adaptations with their contemporary environments.

Keywords: hexapods, arthropods, brachiopods, myriapods, crustacean, devonian

Introduction

Hexapods are the arthropods having six legs and are the most diverse group of animals on terrestrial earth occupying multiple niches. One of the fossil dragonflies has a wing spread of more than two feet. Most common features of hexapods are linear series of rings or segments, external chitinous exoskeleton, median and ventral nervous system with ganglions and obviously jointed appendages. They obtain flight before any organism on earth. Their origin and evolution is highly debated because there are not enough fossils that directly connect them to the arthropods. Recent molecular evidence suggests that hexapods are closely related to Brachiopods such as water fleas and also suggests that evolutionary origin of hexapods in freshwater around 410 million years ago. The successful colonization of the terrestrial environment by hexapods coincides with other terrestrial animals such as Chelicerates and Myriapods in the Late Silurian and the tetrapods in the Late Devonian. All these events appear to have occurred through a freshwater dwelling phase in their evolutionary transition from marine to true terrestrial animals. The Devonian is believed to have been a time of drought, which might have forced these animals on to land as their freshwater habitats vanished. When insects enter their terrestrial habitats their crustacean ancestors had already occupied all potential niches, which could prevent hexapods from colonizing the sea subsequently [1, 9, 10].

Results and Discussion

Modern hexapod diversity represents summation of high speciation rates and low levels of natural extinction. It seems that nature loves six legs. Out of the million documented species of hexapods approx 83% are holometabola and largest group (38%) is of Coleoptera (beetles). The gap in the hexapod fossil record is called Hexapod gap. According to one hypothesis, hexapods were limited by the amount of oxygen (below 15%) available on Earth's atmosphere during the late Devonian. Another

hypothesis is that hexapods were abundant but don't seen in fossil record due to bad rocks that does not preserve them. There is no doubt that ability of flight gives them power to explore new niches and enhance their biodiversity. It is assumed that hexapods originated about 480 mya in Ordovician period at about same time terrestrial plants appeared. It is assumed that hexapods evolved from group of crustaceans. The oldest hexapod fossil has been proposed to be *Rhyniognatha hirsti*. The pterygotes undergo divergent radiation in Carboniferous while Endopterygotes undergo divergent radiation in the Permian period. Most extant orders of Hexapods developed during the Permian period. Many of the early groups became extinct during the P-T extinction. Many hexapod groups like Diptera, Lepidoptera, Coleoptera, Hymenoptera etc co-evolved with flowering plants during Cretaceous [1, 9].

Only a few fossils provide insight into the earliest stages of insect evolution. The most well known is the springtail *Rhyniella praecursor* (Entognatha), long considered to be oldest hexapod. Michael and David [2] sheds light on the fragmentary fossil *Rhyniognatha hirsti* (Ectognatha) that is the true insect and has derived characters shared with winged insects, suggesting that the origin of wings may have been earlier than it is believed. Timothy *et al* [3] describes four major episodes of hexapod evolution *viz.* first one is terrestrialization, second one is flight, third one is metamorphosis and fourth one is eusociality. No doubt that terrestrialization required waxy cuticle, tracheal system, excretory system composed of malpighian tubules and cryptonephridia to reduce water loss. Origin of flight required refinement of the pterelia at the base of the wing and of tough wing muscles. Earlier there were two assumptions about origin of wings. First was that wingless insects such as *Thysanura* (Silverfish) termed as Apterygota evolved after the origin of insects. Second was that insects were winged and that all wingless insects are secondarily evolved. Second assumption was seen more relevant due to conviction that insects arose directly from Trilobites and

lateral lobes of which became functional wings. Metamorphosis allows them to survive in all niches and skips adverse climatic conditions. The basal pterygote orders Ephemeroptera and Odonata have nymphs that live in freshwater and for this reasons, it is assumed that insects evolved from and aquatic ancestors. Eusociality includes key criteria such as generation overlap, cooperative brood care and reproductive division of labor.

Romain *et al* ^[4] report *Strudiella devonica* gen. et. Sp. nov. as first complete late Devonian insect which was probably a terrestrial species. Its mandibles are of an omnivorous type. This discovery narrows the 45 million years gap in the fossil record of Hexapoda and suggests that the pterygota diversified before and during Romer's gap (360-345 mya). This insect fossil was recovered from the Famennian Strud locality, Namur province, Belgium. Martin *et al* ^[5] provide a phylogenomic solution to the origin of hexapods by resolving crustacean-hexapod relationships. Their study specifically addresses the origins of hexapods including transcriptomes for two species each of Cephalocarida and Remipedia. Phylogenetic analyses of selected matrices clearly rejects a sister group relationship between Hexapoda and Brachiopoda. Further analysis assessing targeted taxon exclusion support Remipedia as the sole sister taxon of Hexapoda and suggest that the prior grouping of Remipedia and Cephalocarida is an artifact, possibly due to heterogeneity. They further proposed that terrestrialization of Hexapoda probably occurred in the late Cambrian to early Ordovician, that is independent of their proposed sister group.

Conclusions:

Molecular phylogenetics when combined with morphological data and evidences from the fossil record can provide much more robust understanding of hexapod evolution. Our extant insect fauna is only a small fragment of the total insect aggregation that has occupied the earth during the past 250 million years ^[6]. We do not have enough knowledge of extinct insect species as well as fossil records. The early fossil record of hexapods is scarce with only few finds in the Devonian. All these fossils appear dubious, problematic and controversial partly due to incomplete preservation and challenging interpretation of many structures. Phylogenetic analyses of the last decades have produced many presumed sister groups for hexapods. Whole concept of origin and evolution of hexapods is based on few presumed Devonian fossils viz. *Rhyniella praecursor*, *Rhyniognatha hirsti*, *Eopterum devonicum*, *Eopteridium striatum*, *Devonohexapodus bocksbergensis*, *Wingerstshellicus backesi*, *Cambranatus brasseli*, *Leverhulmia mariae*, *Strudiella devonica* etc ^[8].

These fossils are not enough to precisely solve the mystery of hexapod evolution. It is somewhat more complex than it seems because of rapid speciation occurs in hexapods during geological time scale. Phylogenetics is not much useful because it requires a previous database to compare things and we does not have database of extinct hexapods. If we want to solve the enigma of hexapod evolution we must find another way which correlate hexapod adaptations with their contemporary environments. After all the review I can say that yet there are no plausible explanations for origin and evolution of hexapods and the enigma remain unsolved.

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