ORIGIN AND EVOLUTION OF HEXAPODA

André Nel and **Romain Garrouste**
CNRS UMR 7205, Muséum national d'Histoire naturelle, Paris, France

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Contents

Summary

The Hexapoda is the most diverse clade of the history of life. They cannot be considered as the oldest terrestrial animals and the first Hexapoda were small apterous animals of the Devonian soil fauna, apparently not very diverse and 'dominated' by myriapods and arachnids at that time. Things dramatically changed during the Early Carboniferous with the appearance and the expansion of the winged insects. This crucial innovation allowed this clade to diversify in a spectacular way in the Late Carboniferous. The main clades were already present at the end of this period, viz. Paleoptera, 'Polyneoptera', Paraneoptera and Holometabola.

The latter two groups became truly diverse and began to dominate the animal kingdom after the major Permo-Triassic biodiversity crisis. Nevertheless no one can really judge a causal link between the two phenomena. After the Triassic, all insect orders are present and many modern families are as old as the Jurassic, a situation completely

different from that of the terrestrial vertebrates. The last major change in the hexapods occurred about 100 Ma ago, and may be linked with the mid-Cretaceous angiosperm diversification, but apparently not with the supposed major crisis of diversity at the end of the Cretaceous. Cenozoic insects are mainly characterized by the extension all over the continents of the warm-adapted faunas, but these animals belong to modern genera in their great majority. Lastly the Pleistocene history of insects is linked to the climatic degradations. The destructive impact on the hexapods due to the humans begins to be visible during the 20th century but becomes more and more sensible and worrying.

1. Introduction

1.1. Hexapod Diversity

The Hexapoda (or six-legged arthropods) is the most diverse clade of animals, with more than one million species described and perhaps five to nine millions still awaiting description, representing over half of all described species. Numerous explanations have been proposed to explain this phenomenon, viz. their relative age, giving time for diversification to take place, supposed low extinction rates, flight or properties resulting from it like enhanced dispersal, wing folding, complete metamorphosis in the most diverse clades, small body size, and mouthpart diversity.

The tests of these hypotheses and consequent search for explanations of this phenomenon need joint phylogenetic analyses (using both molecular and morphological data) and a better knowledge of the fossil record. Our knowledge in both fields has greatly developed during the period 1990-2010, with the new tools in phylogeny (cladistics, maximum likelihood, Bayesian analyses) and the discoveries and studies of new, very rich and diverse fossil hexapod assemblages, especially in countries where these ancient organisms were previously unknown (Brazil, China, India, etc.). New gene sequencing technologies (genomics) have strongly increased molecular data and revolutionized phylogenetics. However molecular trees need fossil calibrations to be dated. New fossils or re-interpretations of the previously described taxa are more than ever necessary.

Until the 1990s, the hexapods had the bad reputation of fossilizing only in exceptional cases. Thus, these supposed very rare fossils were considered useless for the reconstruction of the history of this taxon. The situation has completely changed thanks to the increasing collaborations between the Russian, Chinese, American, and European researchers that took place in the years 1998-2000. The discovery and study of very rich outcrops all over the World, dated from the Carboniferous to the Neogene have also dramatically changed the situation. If some crucial gaps remain in the fossil record, now the past entomofaunas and their evolution are well documented for the period from the Late Carboniferous to Recent.

1.2. Quality of the Fossil Record

Fossil insects can be found as compressions in lacustrine or fluviatile rocks, or included in fossil resins (ambers). Compressed fossils are generally preserved in two dimensions, which is not a real problem for the study of the wing venation but can render very difficult that of the body structures. Inclusions in amber have the great advantages of being three-dimensional and sometime exquisitely preserved (Figure 1, 2B), even with internal organs such as genital structures, now observable with the modern tools of the X-ray tomography.

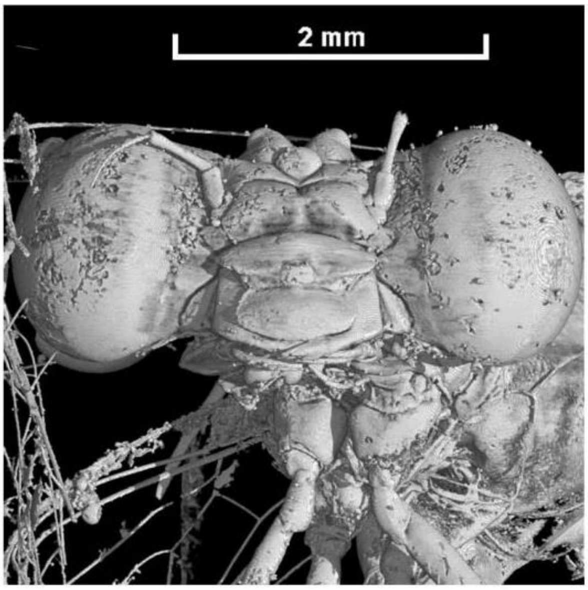

Figure 1. X-ray microtomography of the head of a small damselfly in Cenomanian (100 Ma ago) opaque amber of France.

Figure 2. Bees fossilized as compression in lacustrine rocks (A) or embedded in amber (B). A. *Paleohabropoda oudardi* from the Palaeocene of Menat; B. *Paleomacropis eocenicus* from the Earliest Eocene amber of Oise.

But inclusions in fossil resins are generally small fossils due to the size of the amber pieces and to the facility with which large and powerful living insects can escape from fresh resin. Also, fossil resins with significant arthropod faunas are rather young (Early Cretaceous of Lebanon) compared to the antiquity of the Hexapoda (Devonian). On the contrary, compressed fossils (Figure 2A) can be very large, and in some outcrops also exquisitely preserved with very delicate details (as is typical of the Middle Jurassic volcanic ash of Inner Mongolia, China).

Some fossil insects are preserved in more 'exotic' ways, included in selenite, salts, gypsum, cave stalactite, or sedimentary quartz. They can be three-dimensional replicas in silica, phosphate, or iron hydroxide (Cenozoic of Quercy, France; Early Cretaceous Crato Formation, Brazil).

Even some continental outcrops that were supposed to be azoic recently yielded a very rich entomofauna, as in the case of the red Permian of Lodève, France. Lastly, traces of activities (ichnofossils and plant attacks) can be of great help in some outcrops where the fossil animals are lacking.

For all these reasons, fossil insects are much more frequent than what was supposed before the 1990s. It is now possible to use them as direct witnesses of the hexapod evolution, to complete, date, and test phylogenies based on recent taxa.

1.3. Deceiving Attempts to Use Ancient Molecules

In the 1990s, some papers (in 'good' journals) announced the possible use of fossil inclusions in amber to obtain very ancient DNA. This is also at the origin of the scenario of the film Jurassic Park. However the ancient DNA is unlikely to survive intact more than 100000 years. In consequence it won't be possible to use directly old fossil insects in the molecular analyses.

2. The Hexapoda: An Ancient Story

2.1. Antiquity of the Hexapoda

Hexapod affinities have long been controversial, with two putative sister-groups being Myriapoda and Crustacea, but the recent morphological and molecular advances support a Hexapoda – Crustacea clade. The monophyly of the Hexapoda is also well supported.

The Hexapoda is a very ancient group, as the oldest records are from the Early Devonian. Among animals, arthropods have been considered to be the earliest colonizers of land based on fossil evidence. However, it is possible that other animal taxa (e.g. nematodes, tardigrades, and annelids) colonized land even earlier, but these groups have relatively poor fossil records. Nevertheless, the hexapods are far from being the oldest terrestrial animals as the first traces of a possible terrestrial arthropod are from the Cambrian or Ordovician of Australia. Ordovician and Silurian terrestrial arthropods are represented by arachnids and myriapods. Nevertheless a molecular time for the divergence of hexapods and crustaceans estimated as 666 ± 58 Ma was recently proposed, which is well before the Cambrian. This hypothesis is not supported by the fossil record of the early Hexapoda, based on taxa described from very few Devonian outcrops. Indeed, the fossil record indicates that the Hexapoda are younger than the other terrestrial arthropods. Thus their antiquity, which is about the same as Tetrapoda (which has about 20 000 extant species), is not a plausible argument to explain their high diversity.

These Devonian apterous hexapods belong to two main lineages (Figures 3-4), the Entognatha (Collembola, Protura, Diplura) with mouthparts hidden in the cephalic capsule, and the Insecta, a clade that comprises the two apterous orders Archaeognatha and Zygentoma, plus the winged forms or Pterygota (Zygentoma and Pterygota are characterized by dicondylic mandibles). All these clades are known in the Devonian or the Carboniferous and are still living, except perhaps the controversial order Monura that comprises the sole extinct family Dasyleptidae, recorded from the Late Carboniferous to the Triassic. This situation is extraordinary compared to the fact that many of the Early Palaeozoic major vertebrate clades are now extinct (Thelodonti, Osteostraci, Placodermi, Embolomeri, etc.). Even the oldest Collembola *Rhiniella praecursor* has a very modern habitus similar to those of the modern springtails.

Figure 3. A modern Diplura Japygidae.

The great subclades of Entognatha and the true Insecta (Archaeognatha, probably Zygentoma and dicondylic insects, see Figure 4) were certainly already diversified during the Late Devonian times. A record from Gilboa (Givetian, Middle Devonian, New York, a portion of head capsule with a globose compound eye) could correspond to an Archaeognatha. *Leverhulmia*, from Rhynie (Early Devonian, Scotland) is reminiscent of the Archaeognatha and Zygentoma, but its exact affinities within the Hexapoda remain unclear. An Archaeognatha is recorded from the Emsian of Gaspé, Eastern Quebec. Nevertheless the Devonian record of undoubted Insecta is restricted to the incomplete *Rhyniognatha* from Rhynie, only known by body fragments with dicondylic mandibles, and the Late Devonian *Strudiella* from Strud in Belgium. *Rhyniognatha* fits in the stem group of the Pterygota, but without any evidence of presence of wings in this taxon. The oldest winged insects are recorded from the Early Namurian of the Late Carboniferous.

The Devonian record of the Hexapoda remains very scarce. The Hexapoda were clearly not a dominant clade in term of diversity or abundance, even if it was already morphologically very disparate. These oldest Hexapoda were very small apterous animals of the soil fauna, eating organic remains. The first evidence of direct interactions between living plants and hexapods dates from the Carboniferous. If some very small Devonian coprolithes have been found inside plants stems, they were probably caused by mites. There were no predators either among the Devonian hexapods, this role being filled by some Arachnida and Myriapoda.

2.2. The Enigma of the Carboniferous

The situation completely changed after the Early Carboniferous with an explosion of diversity that affected the winged insects, but not the apterous hexapod lineages. The oldest known outcrops with Pterygota are dated from the Namurian of Germany, Czech Republic, and China. These localities provided very rich and diverse entomofaunas, with species belonging to extant taxa (cockroaches, Orthoptera or grasshoppers, Odonatoptera or dragonflies, etc.), but also other that correspond to extinct, strictly Palaeozoic groups as Paoliida a neopteran group dominating in the earliest Late Carboniferous deposits, and the most famous one being the Palaeodictyoptera.

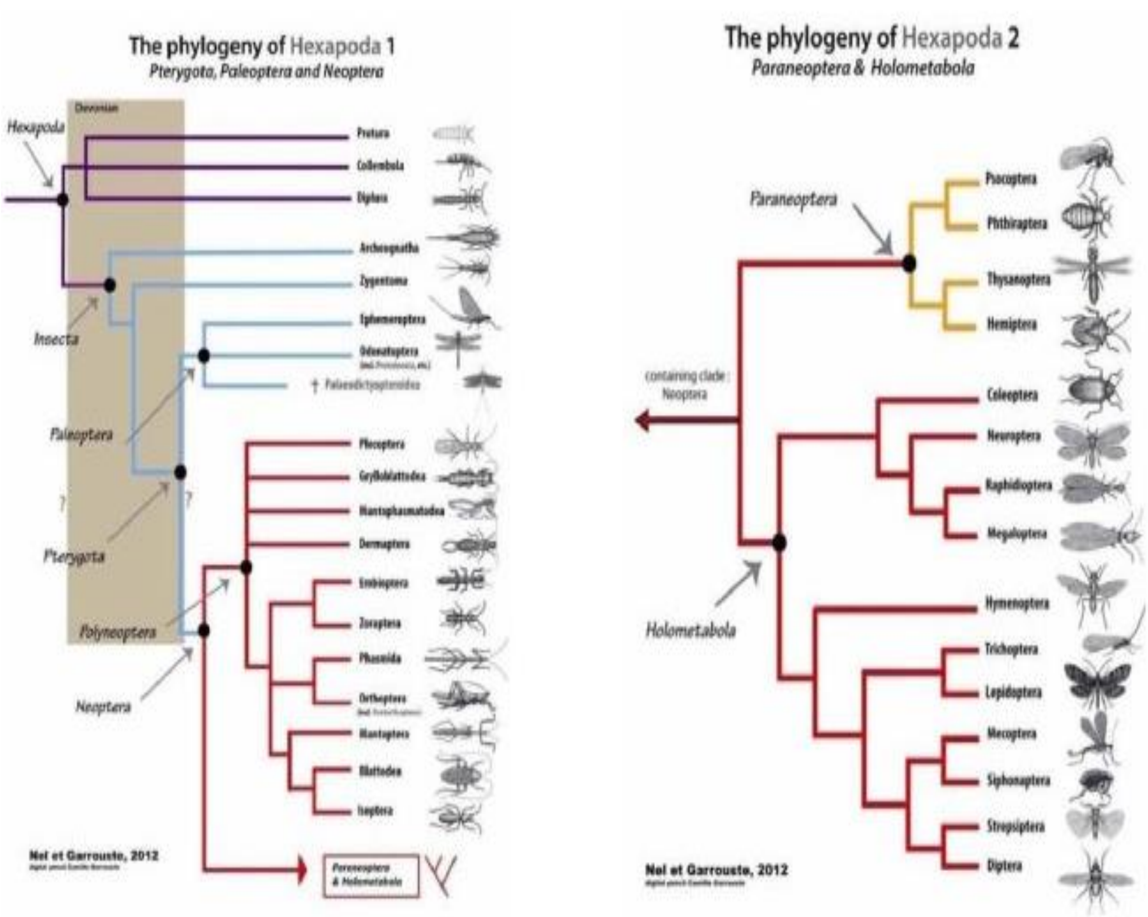

Figure 4. Consensus of the current phylogenetic hypotheses for the Hexapoda. A, basal clades. B, Paraneoptera and Holometabola.

Our knowledge on these earliest winged insects has greatly increased during these last years. These insect assemblages comprise taxa with a high morphological disparity corresponding to very different ecological niches, comprising detritivorous, herbivorous, and carnivorous insects. Interestingly the terrestrial plants seem to have diversified quite earlier than the phytophagous insects. Forests with arborescent forms are recorded in the Late Devonian of Gilboa (USA) and of Svalbard. Unfortunately the crucial period between the Late Devonian and the Late Carboniferous is without any described fossil hexapod. This gap of ca. 50 Ma seems to correspond to Romer's Gap for vertebrates, it is currently explained by a low-oxygen interval with a depauperate spectrum of major arthropod and vertebrate taxa before a major Late Paleozoic colonization of terrestrial habitats, although some (few) terrestrial tetrapods, myriapods and scorpions have been very recently discovered in Scotland. Another explanation is the lack of field research of hexapods in the Early Carboniferous plant outcrops, but it seems that fossil insects are really not frequent in sediments from this period, after the rather negative results of two field trips that the authors made in the potentially favorable outcrops of Svalbard.

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Biographical Sketches

André Nel is a researcher at the UMR 7205 MNHN/ CNRS, in the Systematics and Evolution Department of the Museum National d'Histoire Naturelle (MNHN) in Paris (France), in entomology and palaeoentomology, where he has been working since 1993. He obtained his Agrégation of Mathematics in 1983, his PhD in Palaeoentomology in 1991, and his Habilitation Thesis in 1995 at the University of Reims-Champagne-Ardennes. He has published 481 scientific papers concerning fossil insects, phylogeny, palaeoecology between 1983 and 2012. He currently works on fossils of the following insect groups: Odonata, Neuroptera, Diptera, Hymenoptera, Heteroptera (mainly aquatic), Neuroptera, Trichoptera. He is Curator for the terrestrial arthropods collection at the MNHN. He is a member of the Société Entomologique de France, Associate Editor for *The Annales de la Société Entomologique de France* and *Cretaceous Research*, and Reviewing Editor for the *Comptes Rendus Palevol* and *Insect Systematic & Evolution*.

Romain Garrouste is a researcher at UMR 7205 MNHN/ CNRS, in the Systematics and Evolution Department of the Museum National d'Histoire Naturelle (MNHN) in Paris (France), in entomology and palaeoentomology. He specializes in insect tropical ecology, systematics and palaeoentomology of the Hemiptera and the palaeobiology of the Palaeozoic hexapods, as well as of new imaging technologies (3D CT Scan, SEM) in palaeoentomology. He obtained his Ph D in Ecology in 1995 and a Habilitation Thesis in Life Sciences in 2008. Romain is also Associate Researcher and Assistant Professor at the Université du Sud-Toulon-Var (USTV, PROTEE Lab.). He was head of the French Guyana Office of the MNHN and had teaching activities in ecology and evolution (new courses) in French Guyana-West Indies University, during the period 2003-2009. He participated in field trips in several areas in the world (Neotropics, Polar, Mediterranean, South East Asia, Australian, and Pacific regions) to collect extant and fossil insects. He is a member of the International Palaeoentomological Society and the International Heteropterist Society, the French Explorers Society, and several French societies and scientific committees. RG is author and co-author of 91 papers and communication, including popularization. He is Associate Editor for The Annales de la Société Entomologique de France.