The earliest holometabolous insect from the Carboniferous: a "crucial" innovation with delayed success (Insecta Protomeropina Protomeropidae)

André Nel [(1)], Patrick Roques [(2)], Patricia Nel [(1)], Jakub Prokop [(3)] & J. Sébastien Steyer [(4)]

[(1)] CNRS UMR 5202, CP 50, Entomologie, Muséum National d'Histoire Naturelle, 45 rue Buffon, F-75005 Paris, France

[(2)] 1 allée des Myosotis, F-93330 Neuilly sur Marne, France

[(3)] Department of Zoology, Charles University, Viničná 7, CZ-128 44, Praha 2, Czech Republic

[(4)] CNRS UMR 5143, CP 38, Paléobiodiversité, Muséum National d'Histoire Naturelle, 57 rue Cuvier, F-75231 Paris, France

Abstract. Insects dominate Earth by their diversity, and the most are Holometabola. Therefore, the holometabolous development characterised by a pupal stage between larvae and adult seems to be linked with the extensive radiation of insects. Holometaboly is suspected to appear in the carboniferous period, however until now fossils have not brought univocal evidence. The discovery in the Carboniferous (Early Langsettian, circa 310 mya, Bashkirian Stage) of France of the earliest Holometabola attributed to the Permian amphiesmenopteran or antliophoran family Protomeropidae brings the first irrefutable evidence that holometaboly existed in the Carboniferous. Given the climatic data of France at this period, this discovery contradicts the traditional scenarii of a relation between the acquisition of endopterygote pupal stage and climatic global cooling during Late Carboniferous and Early Permian. This example illustrates the hypothesis that a new, apparently more efficient, biological innovation is not always sufficient to guarantee the 'evolutionary success' of the concerned clade. Ecological opportunities have to be considered as well for this innovation success.

Résumé. Le plus ancien insecte holométabole du Carbonifère : une innovation cruciale au succès retardé (Insecta : Protomeropina : Protomeropidae). Les insectes dominant la Terre par leur diversité et les plus diversifiés sont les Holometabola. Le type de développement holométabole caractérisé par un stade pupal entre la larve et l'adulte semble lié à cette réussite radiative. L'holométabolie est suppose apparaître au Carbonifère, mais aucun fossile non équivoque n'est encore connu. La découverte dans le Carbonifère (Langséttien inférieur, environs 310 M.a., Bashkirien) de France du premier Holometabola non ambigu, attribué à la famille Protomeropidae, Amphiesmenoptera ou Antliophora permiens, apporte la première preuve irréfutable que l'holométabolie existait au Carbonifère. Etant donné les conditions climatiques en France à l'époque, cette découverte contredît les scenarii traditionnels d'une relation entre l'acquisition du stade pupal endoptérygote et le refroidissement climatique global de la fin du Carbonifére et du Permien inférieur. Cet exemple illustre l'hypothèse qu'une innovation biologique en apparence plus 'efficace' n'est pas toujours suffisante pour expliquer le succès évolutif du clade concerné.

Keywords: Insecta, Holometaboly, Carboniferous, earliest record, evolutionary process, delayed success.

The historical "success" of a clade can be evaluated indirectly through phylogenetic analyses and directly in the fossil record through abundance, species diversity, disparity, and presence in numerous (palaeo)-environments. Holometaboly is considered as a major innovation in insect evolution, after the wings. The Holometabola is the most successful group of recent terrestrial organisms (Whiting 2003). A "modern" composition of the entomofaunas starts from the Permian/Triassic extinction, and during the Triassic dominant groups at least at ordinal level, are the same as nowadays, viz. Coleoptera, Diptera, Hymenoptera, and Amphiesmenoptera. Triassic and modern faunas are over-dominated by holometabolous insects, characterized by a dramatic modification of morphology, diet, and partition habitats between adults and juveniles, occurring when individuals become reproductively mature (Whiting 2003). But the situation is viewed as different during the Late Carboniferous, with "primitive" dominant groups of the paleopteran and polyneopteran lineages that became extinct by the end of the period and of the Palaeozoic era. Dating the origin of holometaboly with accuracy could allow us to determine which factors contributed to this innovation, present in about 80% of overall living insect species (Whiting 2003). But this has been an issue for long time. Many authors presumed that the origin of holometabolous insects dates from the Late Carboniferous (Kristensen 1991). However, other authors stated that 'there is no univocal evidence' of Carboniferous Holometabola (Grimaldi & Engel 2005). Kukalová-Peck (1991) figured an alleged

holometabolous larva from the Late Carboniferous of Mazon Creek (Illinois, USA), without formal description. Several authors expressed doubts and discussed the interpretation and assignment of this fossil that could in fact be a myriapod (Willmann 1998; Rasnitsyn & Quicke 2002; Grimaldi & Engel 2005). A number of indirect evidence such as wood-borings (Rasnitsyn & Quicke 2002), and galls (Cichan & Taylor 1982; Lesnikowska 1990; Labandeira & Phillips 1996) suggested the existence of holometabolous insects in the Carboniferous. However, life-habits of Carboniferous non-holometabolous insects are poorly known, hence there is a significant uncertainty concerning the identity of the origin (if insects are involved) of these wood-borings and galls. Galls could have been made by other arthropods such as mites, or extinct groups of unknown life habits. Lastly, Uchman (2005) supposed that the Carboniferous *Treptichnus*-like traces in lake sediments could have been made by dipteran larvae, but the same author added that these traces could have been made by some other unknown organisms of similar behaviour. These indirect 'evidences' are based
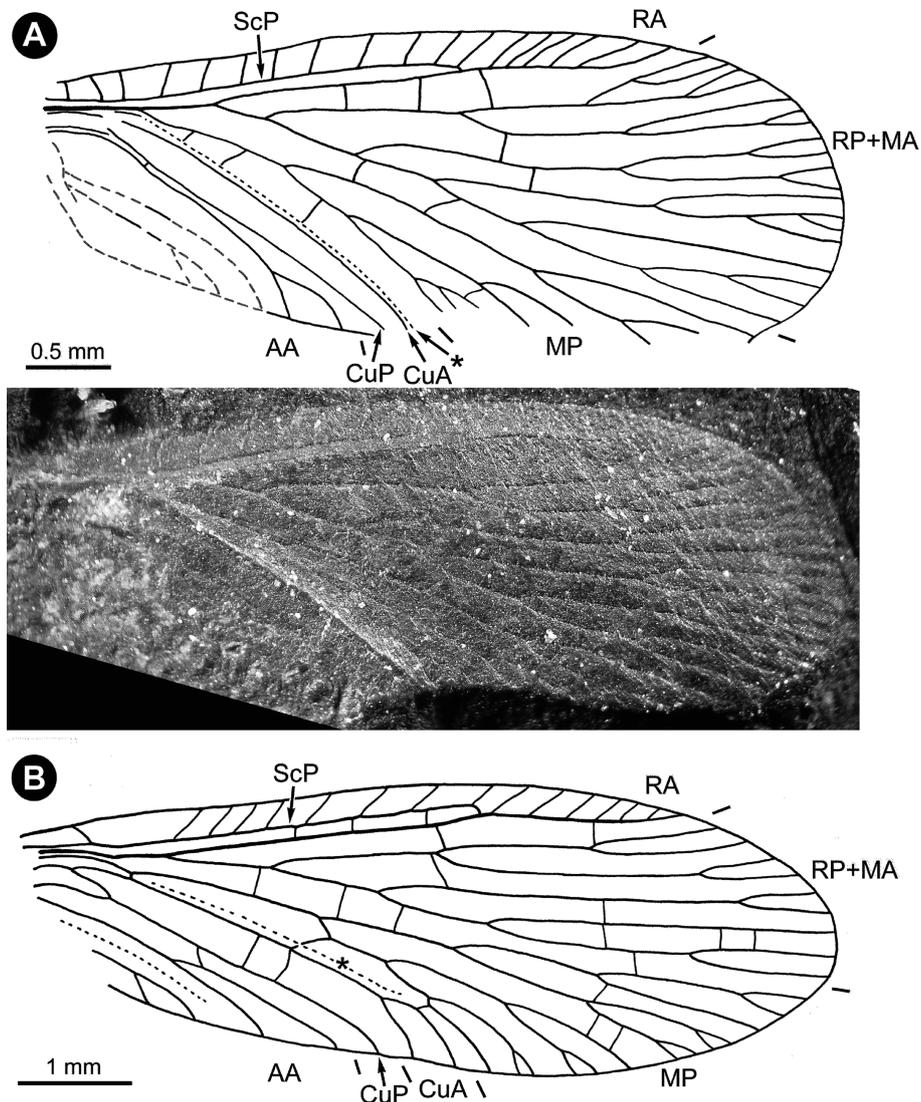
Figure 1
Early Langsettian (Bashkirian) and Early Permian Protomeropidae, hind wings. **A,** *Westphalomerope maryvonneae* n. sp., holotype R.55181, drawing and photo, scale bar, 0.5 mm; **B,** *Pseudomerope mareki* Kukalová-Peck & Willmann 1990, (paratype 4/1989, modified from Kukalová-Peck & Willmann 1990: fig. 4), scale bar, 1 mm. Abbreviations: ScP, subcosta posterior; RA, radius anterior; RP + MA, radius posterior + media anterior; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; AA, analis anterior.

on poorly supported inferences of recent biological data to 300 mya old biotas (for the theoretical methods of 'actualism', see Nel 1997).

Many authors treated the Carboniferous order Miomoptera (known as adult wings and body) as a stem-group of Holometabola (Kukalová-Peck 1991), but its position is, indeed, unclear (Grimaldi & Engel 2005; Beutel & Pohl 2006). The assignment of this order is made uncertain by the absence of apomorphic characters (Rasnitsyn & Quicke 2002). This issue is obviously related to the fact that there is no known external character diagnostic for adult Holometabola (Kristensen 1999), although recent holometabolous orders are sufficiently derived to allow identification of fossil representatives. It is uncertain whether or not miomopterans are holometabolous.

Finally, there is no accurate record of holometabolous insects earlier than Early Permian. But the Permian Holometabola are already rather diverse with representatives of the Coleoptera, Neuropterida, and some taxa attributable to the Antliophora (Mecoptera-like insects).

Herein we describe a specimen discovered in the Carboniferous Early Langsettian deposit of North France. It is a hind wing extremely similar to hind wings of representatives of the Early Permian Protomeropidae, especially *Pseudomerope mareki* Kukalová-Peck & Willmann 1990 or *Permomerope ramosa* Sukatsheva 1976, i. e. compare figs 1–2 with Kukalová-Peck & Willmann (1990) and Ivanov & Sukatscheva (2002).

The Protomeropidae Tillyard 1926 (and Microptysmatidae Martynova 1958), are considered by Willmann (1989) and Kukalová-Peck & Willmann (1990) as "mecopteroid-like" Holometabola, the "oldest representatives of wings of a mecopteroid type, which appeared suddenly in the Permian" (see also Tillyard 1926; Laurentiaux 1953; Martynova 1959), but not to the Mecopteroidea or Panorpida (= Amphiesmenoptera and Antliophora) (Grimaldi &Engel 2005; Beutel & Pohl 2006). Sukatscheva (1982), Ivanov & Sukatscheva (2002), and Novokshonov (1993) included the Protomeropidae within the order Trichoptera (caddisflies) as type-family of a fossil suborder Protomeropina Sukatscheva, 1982, that would be closely related ('ancestor') to true Trichoptera (see below). Grimaldi & Engel (2005) considered the Protomeropeidae (sic) as distantly related to the Amphiesmenoptera. Thus the Protomeropidae are currently considered as true Holometabola.

Several studies have been published on the entomofauna of the Bolsovian (= Westphalian C, Moscovian Stage) of North France (Pruvost 1912, 1914; Laurentiaux 1949a,b, 1953, Laurentiaux & Laurentiaux-Vieira 1979, among others) but little is known on the insects of the Early Langsettian from the same locality.

Material and method

The wing venation nomenclature of Kukalová-Peck & Willmann (1990) is used.

The measurements are made using a stereobinocular Olympus SZX9.

Description

Westphalomerope n. gen.

Type species. *Westphalomerope maryvonneae* n. sp.

Etymology. From the Westphalian age of the specimen, and 'Merope', as suffix in general use for 'mecopteroid-like' genera; feminine in gender.

Diagnosis. It is based on hind wing venation. MP and CuA completely separated, without any basal strut or brace between them; convex fold between MP and CuA crossing wing from Median stem to posterior wing margin; CuA simple; no distal vein between CuA and Median vein; a distinctly oblique cross-vein between posterior branch of RP + MA and MP present.

Westphalomerope maryvonneae n. sp.

Holotype. MNHN-LP-R.55181 (n° 3, coll. Roques), Laboratory of Palaeontology, National Museum of Natural History, Paris, France. The fossil is an imprint of a hind wing collected France, Pas-de-Calais, Bruay-la-Bussière, in the "Terril n° 5bis", black Carboniferous shales, "Faisceau de Modeste", "Veine Maroc" (Corsin 1932), 50°28'56"N 2°32'50"E. It is dated from the Pennsylvanian, Early Langsettian (= Early Westphalian A, Bashkirian Stage), Vicoigne Series.

Etymology. After Maryvonne Roques, wife of one of the authors (Patrick Roques).

Description. Positive imprint of a nearly complete hind wing (see below), without trace of original colouration; wing length, 4.8 mm; width, 1.9 mm; width of costal area, 0.2 mm; twelve cross-veins in costal area between C and ScP, basal of fusion of ScP and RA; second basal cross-vein (probably humeral cross-veins hcv) very obliquely directed towards base; distally, ScP + RA with six short costal branches; no visible cross-vein between ScP and RA; ScP concave and RA convex; stems of M and of R basally not separable; concave vein MP emerging from basal stem 0.5 mm from wing base; concave vein RP+MA separated from RA 0.5 mm distally; three cross-veins between RA and RP; RP+MA bifurcated 0.3 mm distad of its base; costal branch bifurcated 1.1 mm distally, with seven main branches reaching apical part of wing; posterior branch of RP+MA with four main branches divided into twelve branches reaching posterior wing margin; area covered by RP+MA very broad; length of part of posterior margin of wing covered by RP+MA, about 1.7 mm; MP divided into two main branches, and together with seven branches reaching posterior wing margin; length of part of posterior margin of wing covered by MP, 1.7 mm; two or three faint cross-veins between MP and CuA; a very strongly convex and straight fold between MP and CuA, beginning very close to stem of Media and reaching posterior wing margin; vein Cu

basally well separated from stem of M; Cu concave; Cu divided into CuA and CuP about 0.3 mm from base of wing but point of separation not preserved; CuA concave and distinctly separated from MP, no basal strut or brace between MP and CuA, i.e. minimal distance between MP and CuA, 0.1 mm; CuA long, simple, and distally straight, reaching posterior wing margin; no distal vein between CuA and MP; CuA parallel to the convex 'cubito-median fold' and very close to it; free part of concave vein CuP very short, 0.1 mm long, fused with convex vein AA_{1+2}; $CuP+AA_{1+2}$ long, simple, straight, parallel to CuA, and reaching posterior wing margin; basal part of anal vein parallel with anal margin of wing; anal vein divided into AA_{1+2}, AA_{3+4}, and two other veins (AP_{1+2} and AP_{3+4}?); anal area rather poorly preserved, thus the presence or absence of cells in this area cannot be verified; length of anal area, 2.2 mm; width, 0.6 mm.

Discussion

Systematic relationships

As this wing is very similar to the hind wings of *Pseudomerope mareki*, we consider it as a hind wing (costal area narrow, presence of a convex "cubito-median fold", no convex strut between CuA and median vein).

As there is no clear wing venation synapomorphy of the Holometabola, we have to try to attribute this fossil to a subgroup of this clade.

The diagnosis of Protomeropidae provided by Sukatscheva (1976) is "CuA is directly connected with M and is negative, but a convex, heavily sclerotized fold runs in front of it and disappears in the wing membrane". As this character is present in *Westphalomerope*, this taxon can be attributed to this family. Novokshonov (1993) considered this fold as a branch M5 of the median vein but Kukalová-Peck (1991) indicated that it is not a true vein. Since this structure is divided into two non-connected parts near the median stem in *Westphalomerope*, we agree with the opinion of the latter author.

Westphalomerope shares with the Protomeropidae the following diagnostic characters sensu Kukalová-Peck & Willmann (1990): narrow costal area; presence of a humeral cross-vein hcv; narrow ScP-RA area; prominent convex fold approximating, parallel, and anterior to CuA; CuA and CuP diverge close to base of wing; CuA more concave than convex fold; CuP uniformly concave; hind wing anal branches probably not looped. *Westphalomerope* differs from *Pseudomerope* in the complete absence of a MP-CuA strut or brace because the convex fold between MP and CuA reaches the median stem.

Westphalomerope has the "apomorphy" of the Protomeropidae as proposed by Ivanov & Sukatscheva (2002), viz. "ScP distally fused with RA" which might well be a plesiomorphy at the level of Holometabola (if not of the whole Pterygota). It also has characters that are plesiomorphies of the family with respect to the Trichoptera, which are "ScP with more than six branches", "RP and M with more than seven branches".

Nevertheless, *Westphalomerope* differs from the Protomeropidae and Amphiesmenoptera in its hindwing CuA simple, instead of being forked. The forked CuA is probably a plesiomorphic character in Holometabola as it is present in Neuropterida (Raphidioptera, Neuroptera, and Megaloptera). Hymenoptera have their CuA simple (or distally forked but CuA_{1+2} distally fused with MP_{3+4} after Kukalová-Peck & Lawrence (2004), but their interpretation needs confirmation). Alate Antliophora (Mecoptera and Diptera) have a simple CuA (Grimaldi & Engel 2005), (or anterior branch of CuA, CuA_{1+2} captured and fused with MP_4, after the interpretation of Kukalová-Peck & Lawrence 2004: figs 10, 12).

Note that Kukalová-Peck & Lawrence (2004) proposed the distal fusion of MP_{3+4} with CuA_{1+2} as a synapomorphy of their clade Mecopterida (= Mecoptera + Amphiesmenoptera), and the distal fusion of MP_{3+4} with CuA_1 as a character of the Neuropterida. Their interpretation of a crossvein between CuA and MP as a branch of CuA is not obvious in Neuroptera and Mecoptera, very dubious in Amphiesmenoptera, and absent in the hind wing of *Westphalomerope* and (at least) of *Permomerope ramosa* Sukatscheva 1976 (Kukalová-Peck & Willmann 1990) because of the presence of a fold between MP and CuA. Therefore the situation in the Protomeropidae contradicts Kukalová-Peck & Lawrence's hypothesis concerning this distal fusion, otherwise poorly supported.

The simple CuA of the antliophoran lineage would suggest that *Westphalomerope* could belong to this clade rather than to the Amphiesmenoptera. But there is no vein (branch of CuA or crossvein) between CuA and M in their distal parts in *Westphalomerope*, as in Permian Protomeropidae. Thus the distal structure of CuA in *Westphalomerope* and Protomeropidae appears to be different to those of Amphiesmenoptera and Antliophora, and could constitute a synapomorphy of the Protomeropidae.

The Permian Protomeropidae (i.e. *Permomerope ramosa* Sukatscheva 1976) are supposed to have one of the wing venational synapomorphies of the Amphiesmenoptera, viz. the anal veins of the forewing looping up into a double-Y configuration (Kristensen 1984; Kristensen & Skalski 1999; Ivanov & Sukatscheva 2002). This character is not available in the type hindwing of *Westphalomerope*. Furthermore,

several Protomeropidae have this double-Y anal loop rather rudimentary if not very reduced (i.e. *Pseudomerope oborana* Kukalová-Peck & Willmann 1990). Thus the attribution of the Protomeropidae to the Amphiesmenoptera sensu stricto remains rather weakly supported. Kukalová-Peck & Willmann (1990) considered the Protomeropidae as a 'side branch of meco-hymenopteroid stem group, if Mecopteroidea and Hymenopteroidea are sister groups'.

The Protomeropidae and the Permian Neuroptera: Permithonidae Tillyard 1923 show great similarities in their wing venation. Some Permian taxa currently attributed to the Permithonidae have a forewing venation very similar to that of the Protomeropidae, i.e. *Permosysira* Martynov 1933, with a shortly forked CuA and a rather similar double-Y anal loop (Novokshonov 1996: fig. 4). *Permosysira* could well be erroneously placed in Neuroptera. Other Permithonidae (and more generally the Neuroptera) have CuA with branches longer and more numerous (plesiomorphy) than in Protomeropidae, the Hymenoptera, Amphiesmenoptera, and the Antliophora.

In conclusion, some uncertainty remains on the exact relationships of the Protomeropidae and *Westphalomerope* within the Holometabola, both can be considered as belonging either to the crown group of the Amphiesmenoptera, to that of the Antliophora, or to the crown group of the 'meco-hymenopteroid' lineage, but possible relations with the Neuroptera are more unlikely than the other possibilities.

Holometaboly of *Westphalomerope*

The Carboniferous protomeropid species we describe here is based on a wing, the question is to attest it had a holometabolous development. The Amphiesmenoptera and Antliophora are in advanced positions within all the currently proposed phylogenies of Holometabola (Whiting 2003; Beutel & Pohl 2006). Thus, whichever lineage should include the new Carboniferous Protomeropidae (crown group of the 'meco-hymenopteroid' lineage, Mecopteroidea, Antliophora, Amphiesmenoptera, Trichoptera, or even Neuropterida), the probabilistic phylogenetic inference of a recent character to a fossil taxon (Nel 1997) attests that this fossil had a developmental cycle including a pupal stage.

Hence the earliest holometabolous insects are clearly present on the boundary of Early and Late Carboniferous, thus about 30 mya earlier from their previous record, a rather long period.

This record is nearly contemporaneous to the earliest direct evidence of winged insect (Brauckmann & Schneider 1996; Prokop *et al.* 2005). However,

various authors predicted that the acquisition of wings occurred during the Early to Middle Devonian (Gaunt & Miles 2002; Engel & Grimaldi 2004; Grimaldi & Engel 2005). It is then very unfortunate that we have no record of Devonian or Early Carboniferous pterygote insects, a critical period of time when flight and holometaboly were acquired by insects, *i.e.* the two adaptations that unarguably had the highest impact on continental biodiversity as we know it nowadays. Although few Early Carboniferous fossils of earlier faunas are identified (Brauckmann & Schneider 1996; Grimaldi & Engel 2005), they constitute an insufficient record. Determining under which conditions acted the evolutionary processes that led to the aforementioned major acquisitions requires the discovery of appropriate deposits, and abundant collects, which should become a priority.

Age and origin of holometaboly

Climate during the early Upper Carboniferous in France is supposed to have been warm, humid, but with dry seasons (Furon 1972). Thus, it contradicts the scenario of the 'acquisition' of the pupa in this group in relation to an adaptation to climatic degradations during the Permian (Permo-Carboniferous ice-age or arid conditions) (Handlirsch 1920-21; Schwarzbach 1950). Following authors indicated that the 'pupal stage cannot be regarded as primarily designed to ensure survival of the insect over periods of adverse seasonal changes' because the pupae of the most basal recent Holometabola (Neuropterida, Mecoptera, Trichoptera) have free legs and poor sclerotization (Granger & Bollenbacher 1981; Sehnal *et al.* 1996). Furthermore, the dry desert conditions or extreme monsoon of the red Permian has been recently questioned (Sheldon 2005).

Other authors proposed a different scenario in which the 'pupa' of Holometabola is the result of the reduction of the nymphal stage of the non-holometabolous insects to a single instar between a 'pronymph-larval' stage and the adult stage (Truman & Riddiford 2000, 2002). This reduction is related to the development of the short pronymphal stage of the non-holometabolous insects into a long larval stage of the Holometabola. This last phenomenon would have been related to the exploitation of resources that might not be available to the nymph and the adult. Another scenario would be the shortening of the life span of immatures, less exposed to predation (Grimaldi & Engel 2005). These scenarii are not dependent on Permian climatic coolings, but to exploitation of resources. Thus it is compatible with an earlier, Carboniferous or Devonian acquisition of holometaboly.

Radiations dependent on extinctions

The presence of very few holometabolous insects in the Carboniferous demonstrates that the evolutionary success of the Holometabola in term of diversity and global presence in all terrestrial ecosystems is not a direct consequence of the acquisition of their particular, apomorphic pattern of postembryonic development and of a pupal stage. Even the Coleoptera, which is now the most diverse insect group, remain unrecorded in some Late Permian insect ecosystems (i.e. the French Lodève Basin), which is not the case during the Triassic and younger ecosystems. Thus, they clearly began to diversify after the extinctions at Permian-Triassic boundary.

The first major, Permian to early Triassic radiations within the Holometabola concern Neuropterida, Coleoptera, and basal lineages of the 'Mecopterida' (or Amphiesmenoptera and Antliophora), but the Holometabola remain minoritary in the Permian outcrops (Beckemeyer & Hall 2007). Other radiations have occurred later, during the Middle-Late Triassic and the Jurassic and concerned Coleoptera, Diptera, Hymenoptera, and Lepidoptera, in relation to phytophagy (Kristensen 1999). The last radiation of holometabolous insects is much more recent, related to the angiosperms Cretaceous diversification.

The presence of a Carboniferous Holometabola is not surprising as this clade was already diversified, but of minor importance in the entomofauna, during the Early Permian with representatives of the neuropteroid, mecopteroid, amphismenopteran and coleopteran clades.

The recent discovery of one Carboniferous representative of the typical Late Permian/Triassic Odonatoptera: Protozygoptera in the Late Carboniferous of England supports a similar pattern of evolution, viz. long co-existence of an ancient flourishing lineage with a more modern one represented by very few species, and the development of the latter that followed the extinction of the former (Jarzembowski & Nel 2002).

In the vertebrate evolution, several major clades also develop 'crucial' innovations with delayed successes, occurring after major extinctions. These delays often correspond to the time meanwhile the innovation function shifts from a primary exaptation into a secondary adaptation. As for the tetrapods for example (about 40,000 living species), the limb with digits (a 'crucial' synapomorphy of the clade (Anderson 2002)) appeared in the Late Devonian (near 370 mya), but the clade really radiated from the Early Carboniferous, i.e. about 15 mya later with the first terrestrial representatives, and after the Frasnien-Fammenian (Late Devonian) extinction. But the longest delayed success in vertebrate evolution is related to the amniotic egg: the first amniotic egg must have existed at leat 310 mya ago (Laurin & Girondot 1999), but the amniote clade diversified explosively from the Early Triassic, after the Permian-Triassic extinction (Carroll 1964), i.e. about 60 mya after. As for the mammalian clade,

its representatives were in minority during the late Mesozoic, and they did not occupy many ecological niches (the main terrestrial niches being already occupied by the non-avian dinosaurs). The mammals really diversified after the changes in the ecosystems, especially for the multituberculates, plesiadapiforms and 'archaic' ungulates at the end of this era, because they had the opportunity to occupy partly empty ecosystems (Bininda-Emonds *et al.* 2007).

More generally, it seems that the development of a new, apparently more efficient, biological structure is not always sufficient to guarantee the 'evolutionary success' of the concerned lineage. 'Struggle for life', i.e. direct competition between two organisms is necessary but not sufficient to explain evolution. One or more ecological opportunities can be necessary as well, in concordance to environmental changes related to extinctions in other groups. There can be a long period between the development of a new structure and the opportunities for its ecological development, leading to an evolutionary success.

References

Anderson J. S. 2002. Use of well-known names in phylogenetic nomenclature: a reply to Laurin. *Systematic Biology* **51**(5): 822-827.

Beckemeyer R. J., Hall J. D. 2007. The entomofauna of the Lower Permian fossil insect beds of Kansas and Oklahoma, USA. *African Invertebrates* **48**: 23-39.

Beutel R. G., Pohl H. 2006. Endopterygote systematics – where do we stand and what is the goal (hexapoda, Arthropoda)? *Systematic Entomology* **31**: 202-219.

Bininda-Emonds O. R. P., Cardillo M., Jones K. E., MacPhee R. D. E., Beck R. M. D., Grenyer R., Price S. A., Vos R. A. Gittleman J. L., Purvis A. 2007. The delayed rise of present-day mammals. *Nature* **446**: 507-512.

Brauckmann C., Schneider J. 1996. Ein unter-karbonisches Insekt aus dem Raum Bitterfeld/Delitz (Pterygota, Arnsbergium, Deutschland). [A Lower Carboniferous insect from the Bitterfeld/Delitz area (Pterygota, Arnsbergian, Germany).] *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1996**(1): 17-30.

Carroll R. L. 1964. The earliest reptiles. *Zoological Journal of the Linnean Society* **45**: 61-83.

Cichan M. A., Taylor T. N. 1982. Wood-boring in *Premnoxylon*: plant-animal interactions in the Carboniferous. *Palaeogeography, Palaeoclimatology, Palaeoecology* **39**: 123-127.

Corsin P. 1932. Guide paléontologique dans le terrain houiller du nord de la France. *Travaux et Mémoires de l'Université de Lille, Album* **5**: 1-44.

Engel M. S., Grimaldi D. A. 2004. New light shed on the oldest insect. *Nature* **427**: 627-630.

Furon R. 1972. *Eléments de paléoclimatologie.* Collection «De l'enseignement à la recherche, Sciences de la Terre». Vuibert, Paris, 216 p.

Gaunt M. W., Miles M. A. 2002. An insect molecular clock dates the origin of the insects and accords with palaeontological and biogeographic landmarks. *Molecular Biology and Evolution* **19**(5): 748-761.

Granger N. A., Bollenbacher W. E. 1981. Hormonal control of insect metamorphosis, p. 105-137 *in*: **Gilbert L. I., Frieden E. (eds).** *Metamorphosis. A problem in developmental biology.* Plenum, New York.

Grimaldi D. A., Engel M. S. 2005. *Evolution of the insects.* Cambridge University Press, Cambridge, UK, 15 + 755 p.

Handlirsch A. 1920-21. Geschichte, Literatur, Technik, Palaeontologie, Phylogenie, Systematik, p. 117-306 *in*: **Schröder C. (ed.).** *Handbuch der Entomologie*, Gustav Fisher, Jena, **3**, 8 + 1202 p.

Ivanov V. D., Sukatscheva I. D. 2002. Order Trichoptera Kirby, 1813 - The caddisflies, p. 199-219 *in*: **Rasnitsyn A. P., Quicke L. J. (eds.)** *History of Insects*. Kluwer Academic Publishers, Dordrecht, The Netherlands, 517 p.

Jarzembowski E. A., Nel A. 2002. The earliest damselfly-like insect and the origin of modern dragonflies (Insecta: Odonatoptera: Protozygoptera). *Proceedings of the Geologist's Association* **113**: 165-169.

Kristensen N. P. 1984. Studies on the morphology and systematics of primitive Lepidoptera (Insecta). *Steenstrupia* **10**: 141-191.

Kristensen N. P. 1991. Phylogeny of extant Hexapods, p. 125-140 *in*: **Naumann I. D. (ed.).** *The Insects of Australia. A Textbook for Students and Research Workers*. Second edition, **1**, CSIRO (publ.), Cornell University Press, Melbourne University Press, Ithaca, Melbourne, 542 p.

Kristensen N. P. 1999. Phylogeny of endopterygote insects, the most successful lineage of living organisms. *European Journal of Entomology* **96**(3): 237-253.

Kristensen N. P., Skalski A. W. 1999. Phylogeny and Palaeontology. Chapter 2, p. 7-25 *in*: **Kristensen N. P. (ed.).** Lepidoptera, moths and butterflies. Volume 1: evolution, systematics, and biogeography. *Handbook of Zoology*, **4**, *Arthropoda: Insecta, (35).* Walter de Gruyter, Berlin, New York, 487 p.

Kukalová-Peck J. 1991. Chapter 6: Fossil history and the evolution of hexapod structures, p. 141-179 *in*: **Naumann I. D. (ed.).** *The insects of Australia. A textbook for students and research workers* Second edition, **1**, CSIRO (publ.), Cornell University Press, Melbourne University Press, Ithaca, Melbourne, 542 p.

Kukalová-Peck J., Lawrence J. F. 2004. Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters *European Journal of Entomology* **101**(1): 95–144.

Kukalová-Peck J., Willmann R. 1990. Lower Permian 'mecopteroid-like' insects from Central Europe (Endopterygota). *Canadian Journal of Earth Sciences* **27**(3): 459-468.

Labandeira C. C., Phillips T. L. 1996. A Carboniferous insect gall: insight into early ecological history of the Holometabola. *Proceedings of the National Academy of Sciences of the United States of America* **93**: 12278-12282.

Labandeira C. C., Phillips T. L. 2002. Trunk borings and rachis galls of tree ferns from the Late Pennsylvanian (Kasimovian) of Illinois: implications for the origin of the galling functional feeding group and holometabolous insects. *Palaeontographica*, (A) **264**(1-4): 1-84.

Laurentiaux D. 1949a. Un insecte nouveau (Breyeriidae) du terrain houiller du Pas-de-Calais. *Annales de la Société Géologique du Nord* **69**: 47-54.

Laurentiaux D. 1949b. Les insectes Cacurgidae du terrain houiller du Nord de la France. *Annales de la Société Géologique du Nord* **69**: 55-65.

Laurentiaux D. 1953. Classe des insectes (Insecta Linné, 1758), p. 397-527 *in*: **Piveteau J. (ed.)** *Traité de Paléontologie. Les formes ultimes d'invertébrés, morphologie et évolution, Onychophores, Arthropodes, Echinodermes, Stomocordés*. Masson et Cie, Paris.

Laurentiaux D., Laurentiaux-Vieira F. 1979. Un type singulier d'insecte Protorthoptera du Westphalien supérieur du Pas-de-Calais. *Annales de la Société Géologique du Nord* **99**: 407-413.

Laurin M., Girondot M. 1999. Embryo retention in sarcopterygians, and the origin of the extra-embryonic membranes of the amniotic egg. *Annales des Sciences Naturelles* **3**: 1-6.

Lesnikowska A. D. 1990. Evidence of herbivory in tree-fern petioles from the Calhoun Coal (Upper Pennsylvanian) of Illinois. *Palaios* **5**(1): 76-80.

Martynova O. M. 1959. Filogeneticheskie vzaimootnosheniya nasekomykh mekopteroidnogo kompleksa [Phylogenetic relationships of insects in the mecopteroid complex.] *Trudy Instituta Morfologia Zhivotnykh im. A.N. Severtzova* **27**: 221-230. [in Russian.]

Nel A. 1997. The probabilistic inference of unknown data in phylogenetic analysis, p. 305-327 *in*: **Grancolas P. (ed.).** The origin of biodiversity in insects: phylogenetic tests of evolutionary scenarios. *Mémoires du Muséum National d'Histoire Naturelle* **173**: 1-354.

Novokshonov V.G. 1993. The early evolution of the caddisflies (Trichoptera). *Entomological Review* **72** (3): 138-148. [Translated from Russian in **Novokshonov V.G. 1992**, *Zoologicheskij Zhurnal* **71**(12)].

Novokshonov V.G. 1996. Systematic position of some Upper Permian Myrmeleontida (= Neuroptera; Insecta). *Paleontological Journal* **30** (1): 38-45.

Prokop J., Nel A., Hoch I. 2005. Discovery of the oldest known Pterygota in the Lower Carboniferous of the Upper Silesian Basin in the Czech Republic (Insecta: Archaeorthoptera). *Geobios* **38**: 383-387.

Pruvost P. 1912. Les insectes houillers du Nord de la France. *Annales de la Société Géologique du Nord* **41**: 323-380.

Pruvost P. 1914. Nouvelles découvertes d'insectes fossiles dans le terrain houiller du Nord et du Pas-de-Calais. *Annales de la Société Géologique du Nord* **43**: 282-295.

Rasnitsyn A. P., Quicke D. L. J. 2002. *History of insects*. Kluwer Academic Publishers, Dordrecht, Boston, London, 11+517 p.

Schwarzbach M 1950. *Das Klimat der Vorzeit. Eine Einführung in die Paläoklimatologie*. Enke F, Stuttgart, 275 p.

Sehnal F, Švácha P., Zrzavy J. 1996. Evolution of insect metamorphosis, p. 3–58 *in*: **Gilbert L. I., Tata J. R., Atkinson B. G. (eds).** *Metamorphosis, postembryonic reprogramming of gene expression in amphibian and insect cells*. Academic Press, San Diego.

Sheldon N. D. 2005. Do red beds indicate paleoclimatic conditions? a Permian case study. *Palaeogeography, Palaeoclimatology, Palaeoecology* **228**: 305-319.

Sukatscheva I. D. 1976. Caddisflies of the suborder Permotrichoptera. *Paleontological Journal* **10**(2): 198-209.

Sukatscheva I. D. 1982. Istoricheskoye razvitie otryada rucheinikov. [The historical development of the order Trichoptera.] *Trudy Paleontologicheskogo Instituta Akademii nauk SSSR* **197**: 1-112.

Tillyard R. J. 1926. Kansas Permian insects. 7. Mecoptera. *American Journal of Science* (5) **11**: 133-164.

Truman J. W., Riddiford L. M. 2000. The origins of insect metamorphosis. *Nature* **401**: 447-452.

Truman J. W., Riddiford L. M. 2002. Endocrine insight into the evolution of metamorphosis in insects. *Annual Review of Entomology* **47**: 467-500.

Uchman A. 2005. *Treptichnus*-like traces made by insect larvae (Diptera: Chironomidae: Tipulidae), p. 143-46 *in*: **Buta R. J., Rindsberg A. K., Kopaska-Merkel D. C. (eds)**. Pennsylvanian Footprints in the Black Warrior Basin of Alabama. *Alabama Paleontological Society Monograph* **1**: I-IX, 1-380.

Whiting M. F. 2003. Phylogeny of holometabolous insects: The most successful group of terrestrial organisms, p. 345-364 *in*: **Cracraft J., Donoghue M. (eds)**. *Assembling the Tree of Life*. Oxford University Press, New-York, 592 p.

Willmann R. 1989. *Palaeontology* and the systematization of natural taxa, p. 267-292 *in*: **Schmidt-Kittler M., Willmann R. (eds.).** Phylogeny and the classification of fossil and recent organisms. *Abhandlungen Naturwissenschaften Verein Hamburg* (NF) **28**: 267-291.

Willmann R. 1998. Advances and problems in insect phylogeny, p. 269-279 *in*: **Fortey R. A., Thomas R. H. (eds)** *Arthropod relationships*. Systematics Association Special Volume Series 55**,** Chapman & Hall Ltd, London,