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Reassigned and new basal Archaeorthoptera from the Upper Carboniferous of Mazon Creek (IL, USA)

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Abstract

Lobeatta schneideri gen. and *sp. nov.*, *Anegertus cubitalis* Handlirsch 1911, and *Nectoptilus mazonus gen.* and *sp. nov.*, from the deposit of Mazon Creek (IL, USA; Upper Carboniferous), are described. They are shown to be close relatives of the genera *Eoblatta* Handlirsch 1906 and *Ctenoptilus* Lameere 1917. The latter genera, from French deposits nearly contemporaneous with Mazon Creek (Commentry, Montceau-les-Mines), have been previously assigned to Archaeorthoptera Béthoux and Nel 2000. Additional evidence of archaeorthopterid affinities of the Mazon Creek species is provided. Ongoing reviews of North American and European Upper Carboniferous insect faunas might reveal more similarities than expected in their respective composition, although at a suprageneric taxonomic level.

Key words

Archaeorthoptera, Westphalian D, Pennsylvanian, Commentry, *Eoblatta*, *Ctenoptilus*

Introduction

The Konservat Lagerstätte ("preservational gold mine") of Mazon Creek (Westphalian D, Upper Carboniferous; *c.* 310 my) yielded a numerous and diverse insect fauna. Carpenter (1997) and Hay (1997) both refer to 150 described species. However, a compendium of Mazon Creek insect fauna is as yet out of reach. Several revisions demonstrate that an extensive taxonomic update is necessary, because a significant number of described taxa are synonyms (*e.g.*, Burnham 1986, Carpenter & Richardson 1976). Additionally, new taxa remain to be described.

Herein I redescribe *Anegertus cubitalis* Handlirsch 1911, and describe *Nectoptilus mazonus gen.* and *sp. nov.*, and *Lobeatta schneideri gen.* and *sp. nov.*, all from Mazon Creek. These taxa are related to the genus *Eoblatta* Handlirsch 1906, assigned by Rasnitsyn (2002) to the order Eoblattida Handlirsch 1906, itself considered as the 'ancestral stock' of the whole Polyneoptera. However, it has now been demonstrated that generic taxonomy and affinities of the taxa placed by Rasnitsyn (2002) into Eoblattida were partly erroneous. Many show the typical feature of the Archaeorthoptera, *i.e.*, CuA fused with M, then free, and further fused with a branch of CuP (Béthoux 2003, Béthoux & Nel 2005, further evidence below). Besides the fact that most 'eoblattid' insects are more closely related to Orthoptera than to any other modern polyneopterous insect order, Rasnitsyn's definition of Eoblattida is insufficient, due to his acceptance of paraphyletic natural groups.

Some eoblattid taxa cited by Rasnitsyn are now assigned to the clade Cnemidolestodea Handlirsch 1937, a basal group of Archaeorthoptera (Béthoux 2005). The affinities of remaining 'eoblattid' Carboniferous genera such as *Eoblatta* Handlirsch 1906 and *Ctenoptilus* Lameere 1917 (see revision in Béthoux & Nel 2005), although belonging to Archaeorthoptera, are yet unclear. Although taxa described herein are certainly relatives of the latter, the creation of a new major clade of basal Archaeorthoptera is premature, with respect to the current lack of knowledge of wing morphology of most basal Archaeorthoptera. For example, the branching pattern of CuA + CuPa, the location of the branching of R into RA and RP, the location of the first branching of M, and the branching of CuPb, are all characters as yet difficult to polarize.

Since the term 'eoblattid' has been used in a wider sense, and in order to prevent confusion between Rasnitsyn's sense and mine, I will provisionally refer to the subset of archaeorthopterid insects described herein, plus *Eoblatta* and *Ctenoptilus*, as 'lobeattid' insects, a group whose monophyly remains to be demonstrated.

Systematic paleontology

Drawing and photographic procedures described in Béthoux *et al.* (2004) were followed. I used the wing venation nomenclature elaborated by Béthoux & Nel (2002) for Archaeorthoptera, itself based on that of Orthoptera (Béthoux & Nel 2001), repeated herein for convenience: ScA, anterior Subcosta; ScP, posterior Subcosta; R, Radius; RA, anterior Radius; RP, posterior Radius; M, Media; MA, anterior Media; MP, posterior Media; Cu, Cubitus; CuA, anterior Cubitus; CuP, posterior Cubitus; CuPa, anterior branch of CuP; CuPb, posterior branch of CuP; AA1: first anal.

Lobeattid insects have a peculiar branching pattern of CuA + CuPa. This composite vein is abundantly branched, posteriorly pectinate, with a first posterior main branch that is stronger and with more branches than any other posterior branch of CuA + CuPa (debatable in *Ctenoptilus*, in which several basal posterior branches are abundantly branched). However, in some lobeattids (*Ctenoptilus*, *Anegertus* Handlirsch 1911, *Lobeatta gen. nov.*), basal to this main posterior branch, CuA + CuPa emits weaker and simple branches that vanish in the area between CuA + CuPa and CuPb, or reach CuPb. Since these branches can be absent (*Nectoptilus gen. nov.*, *Eoblatta*) I distinguish the first main posterior branch of CuA + CuPa from these branches of secondary importance.

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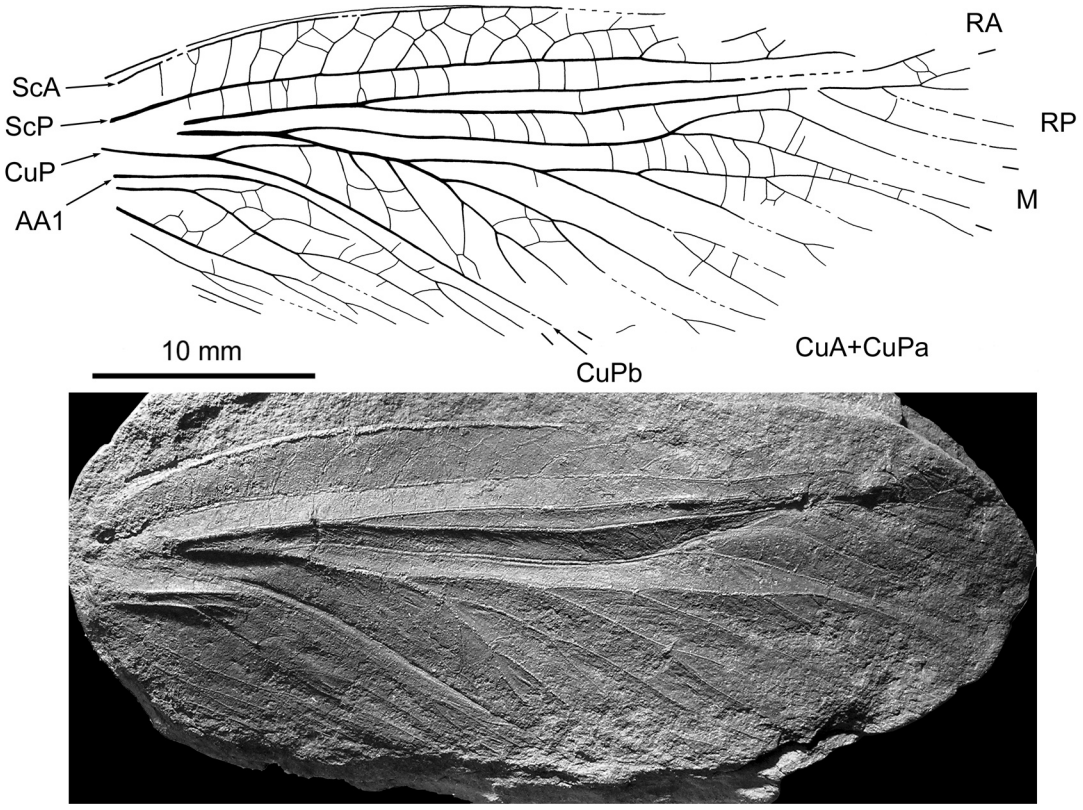


Fig. 1. *Lobeatta schneideri gen.* and *sp. nov.* (holotype specimen ROM 45568): drawing and photograph (right forewing, positive imprint, see text for vein nomenclature).

Archaeorthoptera Béthoux & Nel 2002

Lobeatta *gen. nov.*

Type species.— *Lobeatta schneideri sp. nov.*

Etymology.— Anagram of '*Eoblatta*', a related genus.

Diagnosis.— Forewing: branches from ScP simple, most apical ones more oblique than basal ones; MA oriented towards RP at its origin, further curved and oriented toward posterior wing margin; area between MP and anterior branch of CuA + CuPa very narrow; cross-vein network loose.

Discussion.— The diagnostic characters of the Archaeorthoptera are clearly visible on the holotype of the type species of the genus (Fig. 2). In that respect, it is probably the Mazon Creek specimen that most clearly demonstrates the archaeorthopterid affinities of lobeattid insects.

Lobeatta differs from all lobeattid insects, except *Eoblatta*, by its MA oriented towards RP and its narrow area between MP and the anterior stem of CuA + CuPa. It differs from all lobeattids by its branches of ScP spaced out, simple, and/or less oblique. It also has relatively fewer branches of CuA + CuPa. It differs from *Eoblatta* by a less narrow area between RA and RP, a lesser extent of cross-vein reticulation, and the occurrence of simple and weak posterior branches of CuA + CuPa (basal to the first main posterior branch).

Lobeatta schneideri *sp. nov.*
Figs 1-3

Etymology.— In honor of Prof. J. W. Schneider, a tireless and valuable Late Paleozoic paleontologist and geologist.

Diagnosis.— By monotypy, that of the genus.

Material.— ROM 45568, Royal Ontario Museum, Toronto, Ontario, Canada.

Description.— Positive and negative imprint of a right forewing; apex, part of the anterior wing margin, posterior wing margin, and wing base missing; preserved length about 41 mm, estimated width about 15 mm; ScA convex, parallel but distinct from the anterior wing margin for a long distance; branches from ScP simple, apical branches more oblique than basal ones; ScP probably reaches RA; RA simple in preserved part; RP branched 20.4 mm distal of its origin, with 4 branches in preserved part; M branched 17.5 mm distal of its origin; MA oriented towards RP at its origin, further curved and oriented toward posterior wing margin; a fold that mimics a main vein occurs in the area between RP and MA (Fig. 3); MA and MP simple in preserved part; area between MP and the anterior branch of CuA + CuPa very narrow; CuA (from M + CuA) oblique at its origin; CuA + CuPa with several weak and simple posterior branches, basal to its first main posterior branch; first main posterior branch of CuA + CuPa with 5 branches in preserved part; 6 other distal branches of CuA + CuPa in preserved part; CuP, CuPa and CuPb strongly concave and readily visible (Fig. 2); CuPb simple; AA1 strongly convex, distally forked; cross-vein network loose.

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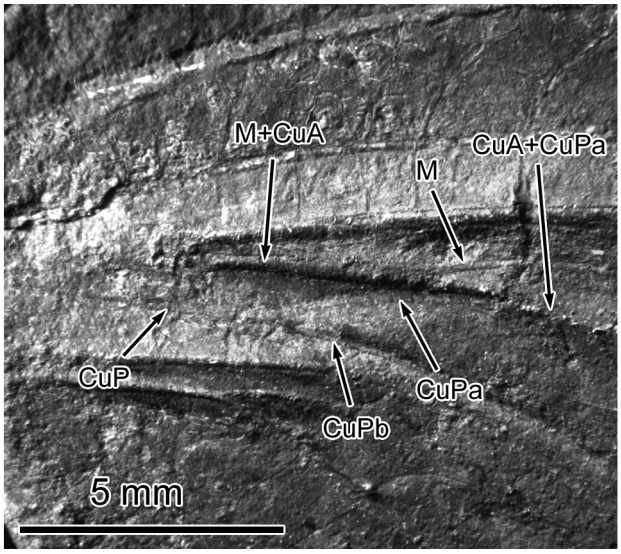


Fig. 2. *Lobeatta schneideri gen.* and *sp. nov.* (holotype specimen ROM 45568): detail of the wing base, photograph (right forewing, positive imprint, composite).

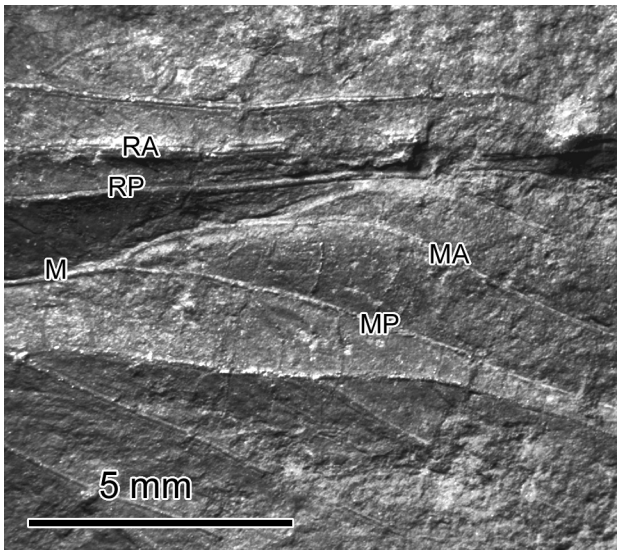


Fig. 3. *Lobeatta schneideri gen.* and *sp. nov.* (holotype specimen ROM 45568): detail of the area between RP and MP, photograph (right forewing, positive imprint, composite).

Geological settings.— Mazon Creek, IL, USA (Handlirsch 1911); Westphalian D, Upper Carboniferous (Rasnitsyn & Zherikhin 2002).

Anegertus Handlirsch 1911

Type species.— *Anegertus cubitalis* Handlirsch 1911.

Diagnosis.— Forewings: branches from ScP numerous, mostly with several branches; occurrence of simple, weak posterior branches from CuA + CuPa, basal to the main fork of this vein; dense network of cross-veins.

Discussion.—The diagnostic characters of Archaeorthoptera are not preserved in the available material of *Anegertus cubitalis*, type species of the genus. However this taxon shares with lobeattid insects a very basal divergence of RP from R, a long and narrow area between RA and RP, a distal branching of RP, and a first main posterior branch of CuA + CuPa abundantly branched. Hence it is assigned to the Archaeorthoptera. Hind wing morphology does not differ significantly from that known in *Ctenoptilus* (see Béthoux & Nel 2005, their Fig. 9).

Anegertus differs from all other lobeattids by its denser network of cross-veins. It also has branches of ScP that are more frequently branched (in an area known only in *Eoblatta* and *Lobeatta gen. nov.*, see below). Additionally, it has MA regularly curved, unlike in *Eoblatta* and *Lobeatta*. Finally it differs from *Ctenoptilus* by its more distal branching of M (closer to first branching of RP than to the origin of the first main posterior branch of CuA + CuPa).

Anegertus cubitalis Handlirsch 1911
Figs 4-5

Diagnosis.— By monotypy, that of the genus.

Material.—YPM 43, Yale Peabody Museum, New Haven, CT, USA.

Description.— Negative imprint of an individual in dorsal view; no clearly defined remains except wings and fragments of thorax and head; wings folded in resting position, hind wings largely hidden by forewings; wing apices missing and bases poorly preserved.
Forewings: area between anterior wing margin and ScP wide; branches from ScP numerous, dense, mostly with several branches; divergence of RA and RP basal to the origin of the first main branch of CuA + CuPa; RA and RP simple, close and parallel for a long distance; M forked 12.1 mm/11.5 mm (respectively LFW / RFW) distal of the main fork of CuA + CuPa; CuA + CuPa with simple, weak posterior branches basal to the divergence of its main posterior branch; CuA + CuPa abundantly branched; CuPb very weak, hence hardly discernible; AA veins strongly convex; in all well-preserved areas of the wing cross-veins very dense and reticulated, with 1-3 rows of cells.
Left forewing: preserved length about 32 mm; estimated width about 14 mm; ScP probably reaches RA; RP branched 22.2 mm distal of its origin; first posterior main branch of CuA + CuPa with 7 branches reaching posterior wing margin; other branches accounting for at least 8 distal branches.
Right forewing: width 14.0 mm; ScA, convex, close and parallel but distinct from anterior wing margin at length; first posterior main stem of CuA + CuPa with 9 branches reaching the posterior wing margin; other branches accounting for at least 5 distal branches; AA1 distally forked.
Hind wings: RP branched.
Right hind wing: CuA + CuPa branched.

Geological settings.— Mazon Creek, IL, USA (Handlirsch 1911); Westphalian D, Upper Carboniferous (Rasnitsyn & Zherikhin 2002).

Nectoptilus *gen. nov.*

Type species.— *Nectoptilus mazonus sp. nov.*

Etymology.— Anagram of '*Ctenoptilus*', a related genus.

Diagnosis.— Forewings: first branching of M near the middle of the wing; absence of simple posterior branches of CuA + CuPa basal to the divergence of the first main posterior branch of this vein;

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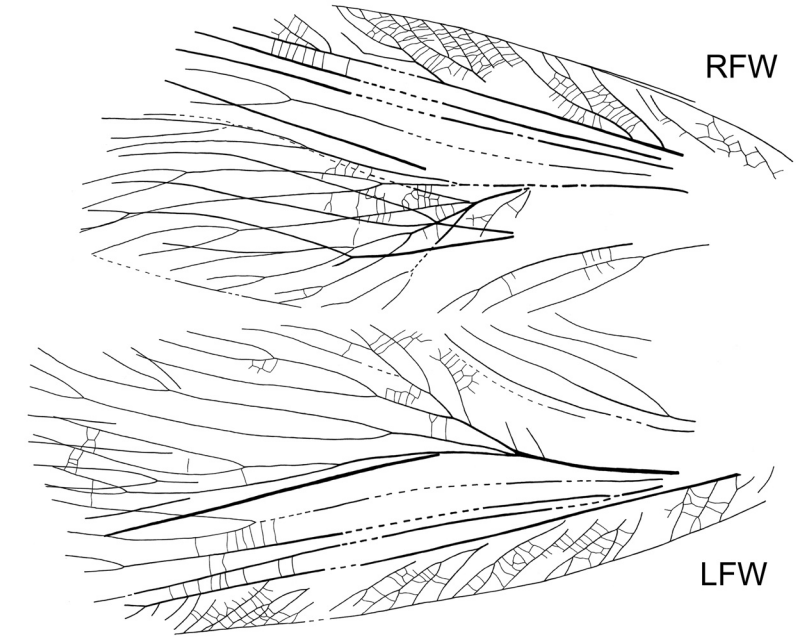
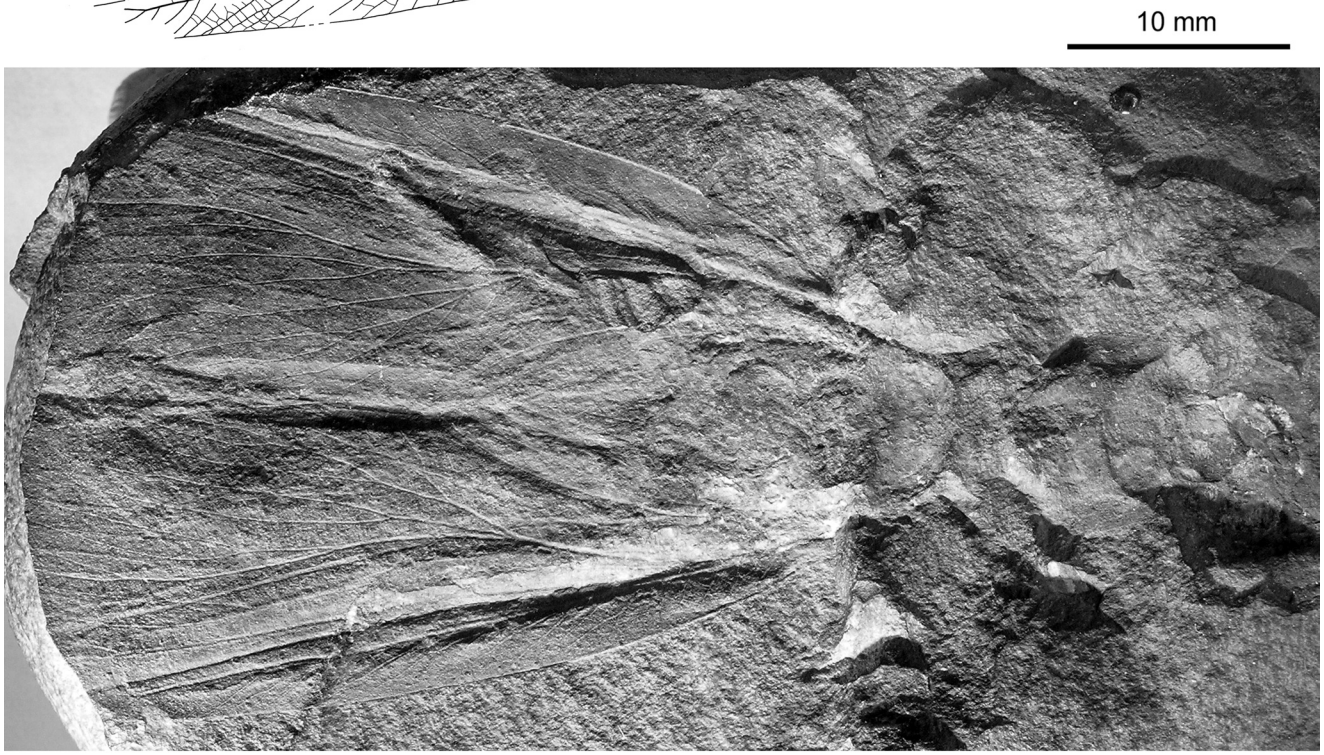


Fig. 4. *Anegertus cubitalis* Handlirsch 1911 (holotype specimen YPM 43); drawing of the wings and photograph (negative imprint, light-mirrored; RFW: right forewing; LFW: left forewing).



cross-veins reticulated along the posterior wing margin, in the distal area of the wing, and between CuA + CuPa and CuPb, otherwise straight, close, and parallel.

Discussion.— Although the diagnostic characters of Archaeorthoptera are not preserved in the available material, *Nectoptilus* shares with lobeattid insects the following characters: RA and RP close together for a long distance, RP branched very distally, M with a low number of branches, CuA + CuPa long, with a first posterior main branch abundantly branched. Moreover, it shares with *Ctenoptilus* a clearly concave MP, a more basal fork of M, and a similar overall shape of the forewing. Hence *Nectoptilus* is assigned to the Archaeorthoptera.
It differs from *Ctenoptilus* by the number of branches of the first main posterior branch of CuA + CuPa, relative to the number of branches accounted for by the rest of the vein: the respective number of branches are more nearly equal in *Nectoptilus* than in *Ctenoptilus*. These 2 genera also differ in cross-vein reticulation. *Nectoptilus* mainly differs from *Anegertus* by its more basal branching of M (but see diagnosis of the latter genus), and from *Eoblatta* and *Lobeatta* by its regularly curved MA.

Nectoptilus mazonus *sp. nov.*
Fig. 6

Etymology.— After the name of the type locality.

Diagnosis.— By monotypy, that of the genus.

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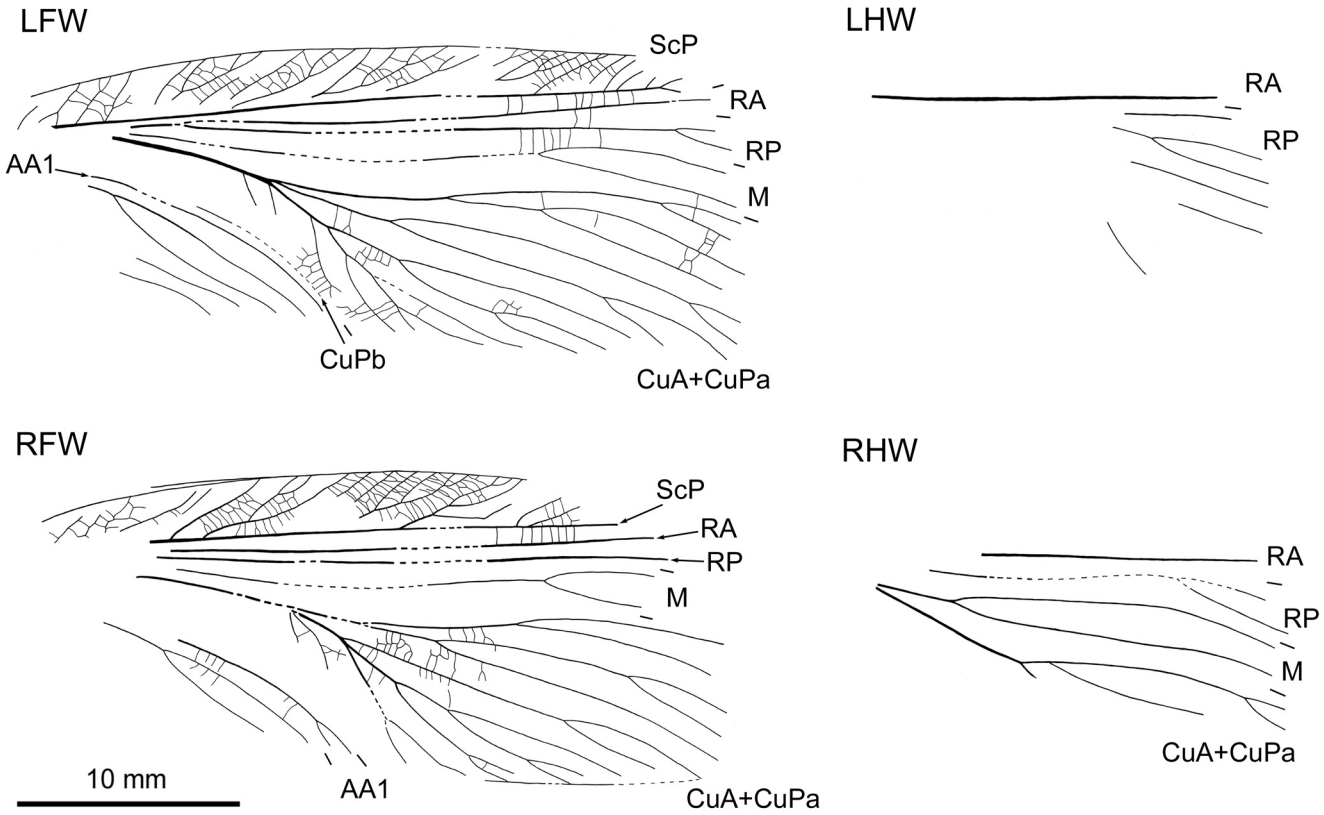


Fig. 5. *Anegertus cubitalis* Handlirsch 1911 (holotype specimen YPM 43); drawing, wings separated, left wings reversed (abbreviations as in Fig. 4 and also RHW: right hind wing; LHW: left hind wing).

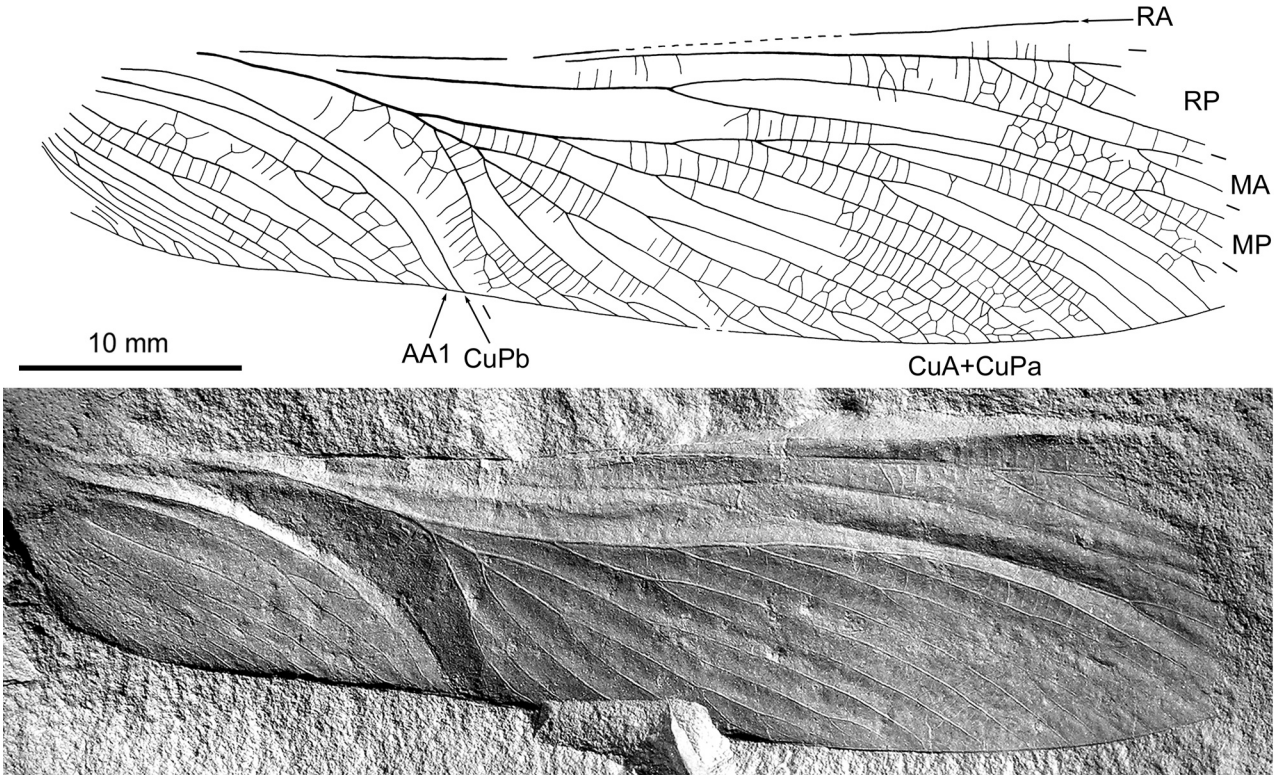


Fig. 6. *Nectoptilus mazonus gen.* and *sp. nov.*. (holotype specimen FMNH PE 31978): drawing and photograph (right forewing; negative imprint, light-mirrored, reversed).

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Material.— FMNH PE 31978, Field Museum of Natural History, Chicago, IL, USA.

Description.— Positive and negative imprint of a right forewing; apex, area between R/RA and the anterior wing margin, and wing base, are missing; preserved length about 53 mm, estimated length about 60 mm, preserved width about 12 mm; RA and RP closely parallel for a long distance; RP posteriorly pectinate, with 3 branches in preserved part; M concave, branched near middle of wing; MA and MP forked in preserved part; MP strongly concave; CuA + CuPa strongly convex, with an anterior main stem, posteriorly pectinate; branches from CuA + CuPa irregularly branched, although the first posterior branch has more branches (13) than others taken together (10); area between CuA + CuPa wide, filled with cross-veins; CuPb strongly concave, simple; AA1 strongly convex, simple; anal area filled with moderately convex veins, mostly simple; cross-veins reticulated along posterior wing margin, in distal area of the wing, and between CuA + CuPa and CuPb, otherwise straight, close, and parallel.

Geological settings.— Mazon Creek, IL, USA (Handlirsch 1911); Westphalian D, Upper Carboniferous (Rasnitsyn & Zherikhin 2002).

Conclusion

Evidence that further, 'protorthopterous' (*sensu* Carpenter 1992) or 'eoblattid' (*sensu* Rasnitsyn 2002), insects are genuine Archaeorthoptera is provided. The archaeorthopterid genera *Eoblatta*, *Ctenoptilus*, *Anegertus*, *Nectoptilus*, and *Lobeatta* share characters that are difficult to polarize. Hence the monophyly of the group is undemonstrated and the relationships of these insects within basal Archaeorthoptera uncertain. Surely, they neither belong to the Cnemidolestodea *sensu* Béthoux (2005) nor to the larger clade Panorthoptera Béthoux & Nel 2002.

It is noteworthy that studying a new deposit (and material) doubled the amount of known lobeattid genera and species: from 2 genera and 3 species (from 2 deposits), lobeattid insects are now known to include 5 genera (2 new) and 6 species (2 new). One could argue it is a rather weak record, with most species known from a single specimen. However, we now know a larger array of morphologies for these insects, which will allow us to identify consistent characters and new relatives, and to assess whether or not they belong to a monophyletic clade.

Step by step, taxonomic review of Carboniferous insects and improved understanding of their phylogeny opens up new prospects. Although identical insect genera are rarely found in any two deposits, Upper Carboniferous faunas might have similarity in higher rank composition, as demonstrated by the pairing of *Ctenoptilus* with *Nectoptilus*, and *Eoblatta* with *Lobeatta*. Faunal composition characteristics could be compared to investigate the taphonomic, ecological, temporal and geographic constraints on fossil assemblages. A better knowledge of these earliest insect faunas might lead to significant improvements in our understanding of the origin of the Late Paleozoic and modern insect biodiversity.

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