



**Moscovian fossils put light on the enigmatic
polyneopteran families Cacurgidae and Eoblattidae
(Insecta: 'Eoblattida', Archaeorthoptera) Journal of
Systematic Palaeontology**

Thomas Schubnel, Dawn Roberts, Patrick Roques, Romain Garrouste, Laure
Desutter-Grandcolas, André Nel

► **To cite this version:**

Thomas Schubnel, Dawn Roberts, Patrick Roques, Romain Garrouste, Laure Desutter-Grandcolas, et al.. Moscovian fossils put light on the enigmatic polyneopteran families Cacurgidae and Eoblattidae (Insecta: 'Eoblattida', Archaeorthoptera) Journal of Systematic Palaeontology. Journal of Systematic Palaeontology, In press, 10.1080/14772019.2019.1627595 . hal-02294662

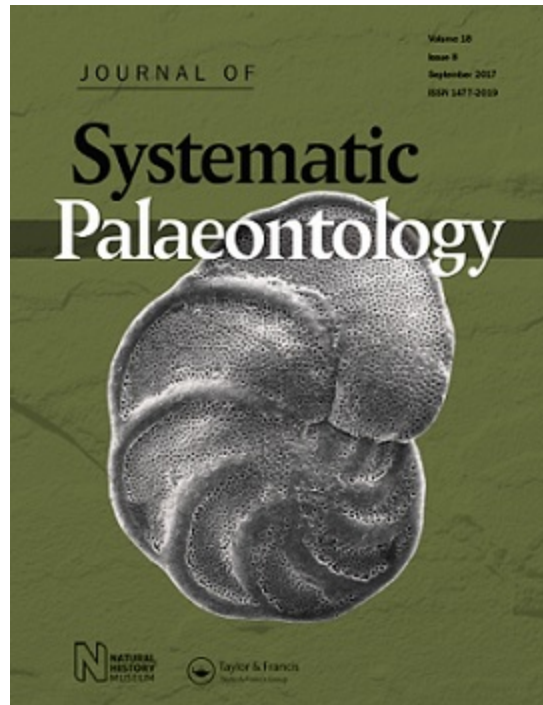
HAL Id: hal-02294662

<https://hal.sorbonne-universite.fr/hal-02294662>

Submitted on 23 Sep 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Moscovian fossils put light on the enigmatic polyneopteran families Cacurgidae and Eoblattidae (Insecta: 'Eoblattida', Archaeorthoptera)

Journal:	<i>Journal of Systematic Palaeontology</i>
Manuscript ID	TJSP-2018-0122.R1
Manuscript Type:	Original Article
Keywords:	Insecta, Polyneoptera, Eoblattida, Archaeorthoptera, wing venation, phylogeny

SCHOLARONE™
Manuscripts

Journal of systematic palaeontology

**Moscovian fossils put light on the enigmatic polyneopteran families
Cacurgidae and Eoblattidae (Insecta: ‘Eoblattida’, Archaeorthoptera)**

Thomas Schubnel^a, Dawn Roberts^b, Patrick Roques^c, Romain Garrouste^a, Laure Desutter-Grandcolas^a and André Nel^{a*}

^a*Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, 57 rue Cuvier, CP 50, 75005 Paris, France;* ^b*The Chicago Academy of Sciences / Peggy Notebaert Nature Museum, 2430 North Cannon Drive, Chicago, IL 60614, USA;* ^c*allée des Myosotis, Neuilly sur Marne, F-93330, France.*

* Corresponding author. Email: anel@mnhn.fr

On the basis of the new species *Cacurgus gallicus* sp. nov., the genus *Cacurgus* and the family Cacurgidae are revised, excluded from the Gerarida, and restored in the Panorthoptera. The Cacurgidae are restricted to the sole genus *Cacurgus*. *Protodictyon pulchripenne* is redescribed, excluded from the Cacurgidae, and put in the archaeorthopteran stem group of the Panorthoptera. We also restore the two genera *Kochopteron* and *Protoblattina* in the Paoliidae. *Suksunus*, *Ideliopsis*, and *Kitshuga*, currently in Cacurgidae, are not Archaeorthoptera but Polyneoptera of uncertain positions to be revised in the future. The type genus *Eoblatta* of the family Eoblattidae and of the super-order Eoblattida, is also restored in the Archaeorthoptera. The whole set of taxa Eoblattida needs a complete revision on accurate homologies of wing venation. Lastly *Aviologus* is excluded from the ‘Cnemidolestina’ and

restored in the Archaeorthoptera. *Westphalopsocus* is restored in the Acercaria: Psocodea. We propose *Paleoischnoptera* nom nov. as replacement name for *Ischnoptera* Béthoux and Nel, 2005 (non *Ischnoptera* Burmeister, 1838).

Keywords: Insecta; Polyneoptera; Eoblattida; Archaeorthoptera; wing venation; sp. nov.; phylogeny

Introduction

A strong controversy occurred a few years ago between O. Béthoux, A.V. Gorochov, and A. Rasnitsyn about the homologies of the wing venation in the polyneopteran insects and especially in the Orthoptera and the so-called ‘Prothoptera’ (Gorochov 2005; Béthoux 2007, 2008; Rasnitsyn 2007). The main problem between the two approaches is that Béthoux, after Béthoux & Nel (2002), proposed to determine the homologies of the wing veins on the basis of the relative positions of the veins plus their relative convexities, while the ‘Russian’ school (Gorochov, Rasnitsyn and more recently Aristov) ignored and/or denied any value to the convexity arguments. They consequently accepted to have a concave or a convex CuA in different polyneopteran insects they put together in the same family (see below). Recently, in a study of the stridulatory apparatus of the Orthoptera: Ensifera using a new 3D-imaging X-ray tomography approach based on the examination of the basivenale bullae from which the main veins emerge at wing base, Desutter-Grandcolas et al. (2017) demonstrated that the concave vein CuP of these extant Orthoptera has several concave branches, that the veins M and CuA are basally fused and appressed or fused to R, and re-separate distally, and that the most anterior concave branch of CuP is ending into the distal part of the convex CuA. These results are congruent with those obtained by Béthoux & Nel (2002) on the basis of the joint observation of the relative positions and relative convexities of the main veins in fossil

Polyneoptera. The ‘arculus’ (see remark below) of the orthopteroid insects is the re-emergence of M+CuA from R+M+CuA, instead of being a convex posterior branch ‘M5’ of M, as supposed by the Russian school; these arguments proved useful to review the position of several fossil Orthoptera. One of us (Schubnel 2018) recently showed with the same tools of X-ray tomography that the extant Dictyoptera have a pattern of venation very different from those of the ‘orthopteroids’, in particular in the presence of a concave stem Cu from which emerges a convex CuA and a concave CuP. We could observe the same situation in the Phasmatodea and Embiida. Furthermore some Palaeozoic roachoids, like *Miroblattites costalis* (Laurentiaux-Vieira & Laurentiaux 1987), have also a strongly convex crossvein m-cua (the so-called ‘M5’ of Russian school). Thus the ‘orthopteroid’ insects can be separated from the other Polyneoptera in the presence of a concave branched CuP, with the most anterior branch ending in a strongly convex vein (CuA or M+CuA). The other polyneopteran clades have a stem of Cu divided into an anterior convex CuA and a posterior concave CuP (generally simple).

At the light of these recent advances, it is important to re-evaluate some fossils, crucial for the general classification of the other Palaeozoic Polyneoptera. It is especially the case for the two taxa *Eoblatta robusta* (Brongniart, 1885) type species of the super-order ‘Eoblattida’ sensu Aristov (2017) and *Cacurgus* Handlirsch, 1911, type genus of the family Cacurgidae (in super-order Archaeorthoptera). The recent discovery by of us (PR) of a very well-preserved forewing attributable to *Cacurgus* is the occasion to make these revisions.

Material and methods

The recently discovered outcrop at Avion in the department of Pas-de-Calais, France, is especially rich in small to very small wings mixed with thousands of plant fragments. It has led a very diverse entomofauna that comprises Palaeodictyoptera (including larvae),

Odonatoptera, Archaeorthoptera, Caloneurodea, Paoliida, Dictyoptera, and the oldest representatives of the clades Acercaria and Holometabola (Nel *et al.* 2013, 2018; Prokop *et al.* 2013, 2014; Coty *et al.* 2014). It is dated to the Moscovian (Westphalian C/D or equivalent Bolsovian/Asturian). These fossil insects were found in ‘Terril N 7’, which contains rocks from the slag heap of coal mines 3 and 4 of Liévin, Bolsovian (Westphalian C, 308–311 Ma, ‘faisceaux de Ernestine’) /Asturian (Westphalian D, 306–308 Ma, ‘veines Arago, Dusouich, Marthe’; Bruno Vallois 2013 pers. comm.). The new fossil was collected in sampled rocks, using systematic observation of the pieces of rocks under a lens. The fossil is stored in the collection of the Muséum National d’Histoire Naturelle, Paris (MNHN), France. The fossil was studied in a dry state using Olympus SZX-9 and Nikon SMZ 1500 stereomicroscopes. Photographs were taken at the MNHN using a Nikon D800 digital camera with Nikon AF-S Micro NIKKOR 60mm f/2.8G ED. Original photographs were processed using the image-editing software Adobe Photoshop CS. Photographs were also taken at the PIN using a Leica M165C microscope with Leica DFC425 digital camera and Kolor Autopano Giga 3.5 software. We follow the wing venation nomenclature of Béthoux and Nel (2002), as it was confirmed by a recent study (Desutter-Grandcolas *et al.* 2017). The venational symbols used here are specified as follows: symbols in capitals denote the longitudinal veins (CP: costal posterior, ScP: subcostal posterior; RA/RP: radial anterior/posterior; MA/MP: medial anterior/posterior; CuA/CuP: cubital anterior/posterior; AA/AP: anal anterior/posterior).

Remark. The ‘arculus’ is a composite structure frequently observed in the basal third of the wing. The arculus reinforces the base of the wing, as noted by Wootton (1992), but it is not homologous in the several insect Orders where it occurs: in Odonatoptera, the arculus is a transverse structure made by RP+MA and a posterior crossvein; in ‘orthopteroids’, it is M+CuA plus anterior branch of CuP; in Acercaria, it is M+CuA plus a modified crossvein

cua-cup; in Dictyoptera, Paoliida, Plecoptera, and Holometabola, it is a crossvein m-cua (Béthoux 2005a; Nel et al. 2012; Prokop et al. 2014b).

Systematic palaeontology

Class Insecta Linnaeus, 1758

Superorder **Archaeorthoptera** Béthoux & Nel, 2002

Subclade **Panorthoptera** Crampton, 1928 (sensu Béthoux & Nel 2002)

Family **Cacurgidae** Handlirsch, 1911

Included taxa. Only the type genus *Cacurgus* Handlirsch, 1911

Type species. *Cacurgus spiloapterus* Handlirsch, 1911 (Moscovian, Mazon Creek, USA).

Other species. *Cacurgus gallicus* Schubnel et al. sp. nov. (Moscovian, Avion, France).

Carpenter (1992: 120-121) listed the genera *Cacurgus*, *Heterologus* Carpenter, 1944, *Protodictyon* Melander, 1903, and *Spilomastax* Handlirsch, 1911 in Cacurgidae. Kukalová-Peck & Brauckmann (1992: 2463) included the genera *Cacurgus*, *Archimastax* Handlirsch, 1906, *Spilomastax*, *Cacurgellus* Pruvost, 1919, *Antracoris* Richardson, 1956 (sic, in fact *Anthrakoris*), and *Axiologus* Handlirsch, 1906 in Cacurgidae. The same authors also listed *Axiologus* in Geraridae in the same paper. Béthoux & Nel (2002) argued that *Cacurgus* could be a Panorthoptera. Béthoux (2006) revised the genus *Cacurgus*, but with some errors of interpretation due to the incompleteness of the type material. Aristov (2012) indicated that Béthoux & Nel (2002) listed the following genera in Cacurgidae: *Cacurgus*, *Archimastax*, *Spilomastax*, and *Cacurgellus*. In fact, Béthoux & Nel (2002) did not attributed *Archimastax*, *Spilomastax*, and *Cacurgellus* to the Cacurgidae, but considered them as possible Archaeorthoptera. Aristov (2017) listed the following genera in the Cacurgidae: *Cacurgus*, *Ideliopsis* Carpenter, 1948, *Kochopteron* Brauckmann, 1984, *Kitshuga* Aristov, 2012, and

Suksunus Aristov, 2015. As some of these taxa strongly differ in their patterns of wing venations, we discuss on them below.

Remark. Following the revisions and keys to the ‘Eoblattina’ sensu Aristov (2012, 2017), *Cacurgus* and the Cacurgidae would be characterized by the following characters: wings developed; ‘M5’ present; ‘SC’ ends in ‘C’; ‘M’ is divided into ‘MA’ and ‘MP’ at the middle of the wing or distally. These characters are not sufficient to define the clade because they are present in a majority of Polyneoptera.

Amended diagnosis (modified from Béthoux 2006). Forewings: branches of ScP strongly oriented towards wing apex, with few cross-veins between them; ScP reaching anterior wing margin near second third of wing length; RA with many anterior branches; RP arising near last third of wing length; MA basally fused with R and re-merging from R distal of basal third of wing (unique character and putative apomorphy); MP branched distal to middle of wing, with many branches (at least five); a concave posterior branch CuPa β basal of fusion of CuP with CuA; CuA+CuPa α without a defined branching pattern, with many branches (at least 8 to 12); CuPb forked. Hind wings: RP with many branches (at least five).

Genus **Cacurgus** Handlirsch, 1911

Type species. *Cacurgus spilopterus* Handlirsch, 1911

Cacurgus avionensis Schubnel et al. sp. nov.

(Figs. 1-2)

Material. Holotype MNHN.F.A70497, parnt and counterpart of a nearly complete wing, collected by Patrick Roques; MNHN, Paris, France.

Age and outcrop. Moscovian (315.2 ± 0.2 – 307.0 ± 0.1 ; Westphalian C/D equivalent to Bolsovian/Asturian), ‘Terril N 7’, Avion, Pas-de-Calais, France.

Etymology. Named after Avion, type locality of the fossil.

Diagnosis. Forewing characters only. Wing long (59.5 mm long) and narrow (16.0 mm wide); a short brace between most anterior branch of MA and RP.

Description. Part and counterpart of a well preserved forewing with only extreme base missing and a brake in the area between RP and M; wing elongate, ca. 59.5 mm long; 16.0 mm wide; area between anterior wing margin and ScP broad, 3.5 mm wide; most anterior branches of ScP simple distal to point of divergence of RA and RP, two of them being forked; few cross-veins between them; ScP reaching anterior wing margin near second third of wing length; MP+CuA appressed to R near wing base but distinctly separated from distally, stem R+MA clearly a double vein; distinctly convex MA emerging from R 15.0 mm distally; independent stem of MP+CuA 7.4 mm long; R forked into a convex RA and a concave RP 13.0 mm distal of point of emergence of MA; RP strong and forked; MA clearly more convex than MP and RP, 13.9 mm long before its first branching; MA with five branches; a rather strong veinlet between anterior branch of MA and RP; MA and anterior branch of MP connected by a strengthened crossvein; distal free part of M concave, long, 27.2 mm long, before its first branching; distal part of MP poorly preserved but probably with 2-3 branches; MP+CuA, CuA, and CuA+CuP α strongly marked and convex; distal free part of CuA relatively short, 2.6 mm long; CuPa long before ending in CuA, 10.4 mm long; CuA+CuP α divided into two main veins, both divided into four branches; area between CuPa and CuPb broad with many cells; a clearly concave longitudinal vein CuP β emerging from CuPa basal of its fusion with CuA; CuPb concave, distally forked; AA1 convex, with a weak distal branch; all crossveins convex; except in area between anterior wing margin and ScP, crossveins generally irregular.

Discussion. The preserved parts of this forewing and of the forewing of *Cacurgus spilopterus* Handlirsch, 1911 are extremely similar, in the convexity of the veins, their relative positions

and branches, even in the presence of two strong posterior veins emerging from R (MA and RP). The unique differences are the presence of a short brace between the most anterior branch of MA and RP; forewing narrower (16.0 mm wide, instead of ca. 25 mm in *C. spiloferus*, the wings of *C. spiloferus* are incomplete with unknown lengths), and presence of a clearly concave longitudinal vein emerging from CuPa basal of its fusion with CuA (Béthoux 2006). Thus we consider that it corresponds to a new species in the genus *Cacurgus*.

Béthoux (2006: 32) indicated the presence of a longitudinal vein emerging from CuPa basal of its fusion with CuA in *Cacurgus spiloferus*, but he considered it as convex. Nevertheless it is clear after the photograph of the holotype that this vein is clearly less convex than CuA and as 'convex' as the concave main branch of CuPa. He concluded that *Cacurgus* is an Archaeorthoptera but not a Panorthoptera.

The new fossil is helpful to complete the redescription of the genus *Cacurgus* made by Béthoux (2006). This author interpreted the convex vein MA re-emerging from R+MA as the 'RP' and the true RP as a 'posterior branch of RA'. In the photograph of the holotype of *Cacurgus spiloferus* of Béthoux (2006: fig. 2), it is clearly visible that the alleged 'anterior branch of RA' and 'RP' are more convex than, respectively, the vein 'M' and the 'posterior branch of RA', in complete accordance with the new fossil. In any case, *Cacurgus* has a very particular pattern of the radial vein with two distinct posterior veins emerging from the radial stem (either MA and RP, or RP and distal posterior branch of RA).

The pattern of wing venation of *Cacurgus* corresponds exactly to that of the clade Archaeorthoptera Béthoux & Nel, 2002, as verified by Desutter-Grandcolas et al. (2017) on extant Ensifera. Its pattern of venation is typical of the Archaeorthoptera: basal fusion of M with CuA, both appressed to R, a distal re-emergence of a convex M(P)+CuA, a separation of M(P)+CuA into a concave M(P) and a strongly convex CuA (the M5 sensu Aristov), a concave CuP that divides into CuPa (considered as CuA by Aristov) and CuPb, and CuPa

ending into the convex CuA. *Cacurgus* has the main synapomorphy of the Panorthoptera, viz. a concave posterior branch CuPa β of CuPa separating basal of fusion of the other branch CuPa α of CuPa with CuA. Thus we restore the Cacurgidae in the Panorthoptera, in accordance with Béthoux & Nel (2002).

Cacurgus has also a putative apomorphy not present in Orthoptera and the majority of the Archaeorthoptera, viz. presence of two main posterior veins emerging from the radial stem, viz. either vein MA basally fused with R and re-emerging distally as a convex vein, plus RP (our preferred hypothesis for the relative convexities of these veins); or RP and distal posterior branch of RA (Béthoux & Nel (2002)' hypothesis). Its vein CuPa is also quite long before ending into CuA (the extreme wing base is not preserved in the holotype of *Cacurgus spilopterus*).

‘Group’ **Archaeorthoptera nec Panorthoptera** (stem group of Panorthoptera)

Genus *Protodictyon* Melander, 1903

Protodictyon pulchripenne Melander, 1903

Figs. 3-4

Holotype. CHAS PALEO 4749 (part and couterpart of a body with wings attached), stored in the collection of the Chicago Academy of Sciences.

Age and outcrop. Moscovian, Mazon Creek, Illinois, USA.

New diagnosis. Forewings and hind wings nearly homonomous, hind wings with reduced anal area; CuPa ending in CuA; no CuPa β ; no anterior branches and few posterior branches of CuA+CuPa; fork of M into MA and MP close to base of M; MA touching RP; a short, strong and convex crossvein at level of base of M, between M+CuA and R.

Redescription. This taxon has never been revised since Melander (1903). The original description and figures are too incomplete to determine its affinities. A redescription is necessary.

Body poorly preserved, 27.5 mm long; head in a very poor condition, thorax 10.8 mm long, 4.6 mm wide; abdomen 13.0 mm long, 3.7 mm wide, with apex in a very poor state, no cerci visible, probably not preserved.

Forewings with apices missing, elongate, preserved part 23.0 mm long; 9.3 mm wide; area between C and ScP narrow, 1.0 mm wide, with two rows of cells; ScP reaching anterior wing margin near second third of wing length; M+CuA appressed to R near wing base but distinctly separated from it 4.0 mm distally, M+CuA 1.7 mm long; a short but strong convex crossvein between R and M+CuA at the level of base of M; RP separating from RA 2.7 mm distal of this crossvein, more concave than RA, with at least three branches; M more concave than CuA, 2.0 mm long before its first branching, MA fused with RP for a short distance but separating distally, MP with three visible posterior branches; M+CuA, CuA and CuA+CuPa strongly marked and convex; distal free part of CuA relatively short, 0.5 mm long; CuPa weaker than M+CuA, concave, 3.0 mm long before ending in CuA; CuA+CuPa with four posterior branches; area between CuA+CuPa and CuPb broad with 2-3 rows of cells; no clear longitudinal vein emerging from CuPa basal of its fusion with CuA; CuPb concave and simple; anal veins not preserved, but anal area certainly not very broad, at most 1.0 mm wide. crossveins generally irregular.

Forewing and hind wing nearly homonomous, as it is visible on the superimposed left wings: hind wing with a reduced anal area, not fan-like, wings of same sizes, and of nearly the same venation. The most important difference between the fore- and the hind wing is the more basal position of the base of RP in the hind wing than in the forewing, only 2.5 mm distal of

point of separation of M+CuA and R. The small convex crossvein situated at this last point is clearly visible.

Discussion. *Protodictyon* has a wing venation of archaeorthopteran type with a basal stem M+CuA appressed to R, a concave M and a convex M+CuA, and concave vein CuPa ending into convex CuA (Fig. 4). Nevertheless, the absence of a CuPa β between CuPb and CuA indicates that it is not related to *Cacurgus* and the Cacurgidae, and is not a Panorthoptera.

Because of the lack of phylogenetic analysis or even of a key to the taxa currently in the Archaeorthoptera nec Panorthoptera, we have to compare *Protodictyon* with all these taxa. The vein CuPa ending on CuA rather than on M+CuA excludes affinities with *Cymenophlebia* Pruvost 1919, *Bethouxia* Prokop et al., 2015, *Eoblatta* Handlirsch 1906, and some species of the genus *Miamia* Dana 1864 (Béthoux & Nel 2005; Prokop et al. 2015). Affinities with the Cnemidolestodea are excluded because of the absence of anterior concave branches of CuA. *Protodictyon* shares with *Aviohapaloptera* Prokop et al. 2014 the presence of a basal branch of M fused with RP for a short distance, but it differs from this genus in the presence of more numerous branches of CuA+CuPa (Prokop et al. 2014a). It also differs from *Aenigmatodes* Handlirsch, 1906 in the same character (Handlirsch 1906). In *Omalia* van Beneden & Coemans, 1867, the fork of M into MA and MP is much more distal than in *Protodictyon*. *Coselia* Bolton, 1922, the Narkeminidae Pinto & Pinto de Ornellas, 1991, Carpenteropteridae Pinto & Pinto de Ornellas 1991, and Taiophlebiidae Martins-Neto in Martins-Neto et al., 2007 have anterior branches of CuA+CuPa. *Proedischia* Pinto & Pinto de Ornellas, 1978 differs from *Protodictyon* in the presence of anterior branches of CuA+CuPa and the absence of fusion between RP and MA (Pinto & Pinto de Ornellas 1978; Pinto, 1992). *Pachytylopsis* de Borre, 1875 has no fusion of MA with RP (Laurentiaux & Laurentiaux-Vieira 1981). *Palaeomastax* Handlirsch, 1904, *Hapaloptera* Handlirsch 1906, *Archaeologus* Handlirsch, 1906, *Archimastax* Handlirsch, 1906, *Endoiasmus* Handlirsch 1906, *Omaliella*

Béthoux & Nel, 2005, *Gerarulus* Handlirsch, 1911 have a long stem of M, unlike *Protodictyon* (Handlirsch 1906, 1911; Carpenter 1992; Béthoux & Nel 2005). *Emphyloptera* Pruvost, 1919 and *Tshecalculus* Novokshonov, 2000 have a simple CuA + CuPa (Pruvost 1919; Novokshonov 2000). In general, the Hapalopteridae Handlirsch, 1906 have different branching of CuA+CuPa and M (Rasnitsyn et al. 2004). *Protodictyon* differs from *Miamia* Dana, 1864 (sensu Béthoux et al. 2012) in the very long stem CuA+CuPa, basal of the first branch of this vein. *Protodictyon* differs from *Etotabla* Béthoux & Jarzembowski, 2010 in the clearly less numerous branches of CuA+CuPa, while it differs from *Westphaloblattinopsis* Béthoux and Jarzembowski, 2010 in the more regular pattern of branching of CuA+CuPa and a fusion between RP and MA (Béthoux & Jarzembowski 2010). *Ctenoptilus* Lameere, 1917, *Lobeatta* Béthoux, 2005, *Anegertus* Handlirsch, 1911, *Nectoptilus* Béthoux, 2005, *Ischnoptera* Béthoux & Nel, 2005 (note that the genus name *Ischnoptera* is preoccupied by the extant blattodea genus *Ischnoptera* Burmeister, 1838, thus we propose *Paleoischnoptera* nom nov. as replacement name for *Ischnoptera* Béthoux & Nel, 2005), *Protophasma* Brongniart, 1879, *Nosipteron* Béthoux & Poschmann 2009, *Sinopteron* Prokop & Ren, 2007 and *Chenxiella* Liu et al., 2009 have much more numerous branches of CuA+CuPa (Béthoux 2003, 2005b; Béthoux & Nel 2005; Prokop & Ren 2007; Béthoux & Poschmann 2009; Liu et al. 2009; Béthoux & Schneider 2010). *Forfexala* Béthoux & Herd, 2009 differs from *Protodictyon* in its branching pattern of M+CuA, with CuPa reaching the point of separation between MP and CuA (Béthoux & Herd 2009). *Cymenophlebia* Pruvost, 1919 differs from *Protodictyon* in CuA+CuPa ending on MP, vein MA not fused with RP, and vein M separating from CuA (+CuPa) distal of the fusion of CuPa with CuA, and not basal as in *Protodictyon* (Béthoux 2007). The Chinese Namurian *Longzhua* Gu et al., 2011 differs from *Protodictyon* in the MP simple, MA with two branches (Gu et al. 2011). *Lodevolongzhua*

Prokop et al., 2015 differs from *Protodictyon* in the shape of MA strongly approximating RP but fused to it very distally.

The presence in *Protodictyon* of a short, strong and convex crossvein at level of base of M, between M+CuA and R, is remarkable. Together with CuA and CuPa, it constitutes a very particular ‘arculus’. Also the homonomous forewings and hind wings are remarkable, as the ‘orthopteroids’ have generally a distinctly broader anal area in the hind wings than in the forewings. Among the Archaeorthoptera, only the Caloneurodea have also homonomous wings (Béthoux et al. 2003). Nevertheless in this order there are well-developed CuPa β veins in all wings, unlike in *Protodictyon*. Also, the Caloneurodea have a simple CuA+CuPa α in all wings, unlike *Protodictyon*. Thus *Protodictyon* cannot be attributed to this order. The wing homonomy (reduction of the hind wing anal fan) could represent a synapomorphy of *Protodictyon* with the Caloneurodea, but this hypothesis would imply that the convergent development of the vein CuPa β between the Orthoptera (that have retained a hind wing anal fan) and the Caloneurodea. Otherwise the hind wing anal fan was convergently reduced in *Protodictyon* and the Caloneurodea. As the ‘orthopteroid’ clade Titanoptera has also a strong reduction of the hind wing anal fan, but less pronounced than in these taxa, this second solution seems to be more probable.

Protodictyon remains an Archaeorthoptera of uncertain position. It is highly probable that it corresponds to a new family, potentially different from all others by the homonomy of the four wings. But it is premature to erect a new family because several other Archaeorthoptera are only known by their forewings.

Other putative Cacurgidae

After the photograph of the holotype (Fig. 5), *Kitshuga ryzhkova* Aristov, 2012 is based on a counterpart of a forewing. The relative convexities of the different veins are hardly

discernable. The portion of 'CuA' basal of the convex 'arculus' (crossvein between R and CuA) seems to be weaker than the portion 'CuA' distal of 'arculus', but both portions seem to have the same convexity. Thus CuA would be separated from M, corresponding to a pattern of venation quite different from those of the Archaeorthoptera, and of *Cacurgus*. Also, there is a clear RP but no MA re-emerging from R. *Kitshuga* does not belong to the Cacurgidae. Also it seems that it does not belong to the Archaeorthoptera, after what can be seen of the veins' convexities. Its M is progressively diverging from R and at 'arculus' level there is a short transverse vein between them. This last character is quite interesting because the 'arculus' of *Kitshuga* is very similar to that of *Protodictyon*, composed by this short crossvein between R and M and a short crossvein between M and CuA. This strong similarity questions the interpretation of the veins' convexities and the attribution of this enigmatic taxon.

Béthoux & Nel (2002) already noticed that *Anthrakoris* is a Panorthoptera and *Axiologus* is a Polyneoptera *incertae sedis*. Béthoux & Nel (2002) assigned *Heterologus* to the Panorthoptera, but this taxon has only one posterior vein emerging from R, instead of *Cacurgus*.

Kochopteron hoffmannorum Brauckmann, 1984 has also a pattern of venation completely different from that of *Cacurgus*, with a common stem Cu of CuA and CuP that divides into a convex CuA and a concave CuP (CuA has exactly the same shape basal and distal to the arculus). Thus it has no fusion of CuA with R; also its M is not fused with R but appressed to it, as already noticed by Prokop et al. (2014b: Fig. 4H). These authors put *Kochopteron* in the Paoliidae because of its very broad area between CuA and CuP, together with the shape of RA and RP very similar to the situation in *Paolia*. Aristov (2015) did not give any arguments against the hypothesis of Prokop et al. (2014), a paper he listed in his references but did not cite in the text of the paper. His unique arguments in 2017 to separate *Kochopteron* from the Paoliidae are as follows: ScP ending into C (this character is highly

variable in many insect groups, for instance the extant Plecoptera can have ScP ending into RA or not, or the Neuroptera: Chrysopidae can have ScP ending into C or RA depending of the genera, even the species, thus it cannot be used to separate families or groups of higher ranks); presence of paranota (this character is of little value as it is certainly a plesiomorphy, as it is shared by the paleopteran clades, many Dictyoptera and Archaeorthoptera). The same argument is given in Rasnitsyn & Aristov (2016: 3): ‘The only difference of cacurids (sic) from paoliids in characters of the body is the presence of paranota on the pronotum’. Paranota are also present in at least another taxon that Prokop et al. (2014b) put into the Paoliidae, *Protoplattina bouvieri* Meunier, 1909, but excluded from this clade by Rasnitsyn & Aristov (2016: 7) on the basis of the following characters: ‘hind wing of Protoplattinidae is unknown, but the presence of paranota, forewing not narrowing towards the apex and lacking blind branches of RS and CuA, SC ending on C, rather proximally branching M and rather distally branching CuA make it impossible to assign this family to Paoliida’. As the presence vs. absence of paranota in *Paolia* is unknown, it is not possible to exclude *Protoplattina* from Paoliidae on the basis of the *a priori* hypothesis of its absence in paoliids. The ‘genuine’ paoliid *Kemperala* seems to have narrow paranota even if its pronotum is rather poorly preserved. The shape of the forewing of *Protoplattina* is not especially different from those of the Paoliidae. The apex of ScP is not preserved in *Protoplattina*. The Paoliidae have not special ‘blind’ branches of RP, but veinlets, and this area is poorly preserved in *Protoplattina*. The area between CuA and CuP is also poorly preserved, but there seems to be some weak posterior branches of CuA ending in CuP. As only the distal anterior branches of CuA are well-preserved in *Protoplattina*, it is not really possible to say that it has only distal branches. The only difference between *Protoplattina* and the other Paoliidae that remains valid in the relative basal branching of M, which is not sufficient to exclude it. Even this character alone is not sufficient to support a different family. Rasnitsyn & Aristov (2016: 3) ignored the main

synapomorphy of the Paoliidae, viz. the presence of concave anterior branches of CuA and of convex posterior ones, present in *Protoplattina*. We restore *Kochopteron* and *Protoplattina* in the Paoliidae, considering that the arguments of Aristov (2015, 2017) and Rasnitsyn & Aristov (2016) are not sufficient to exclude them. We also formally synonymize the Protoplattinidae with the Paoliidae.

Dalduba faticana Storozhenko, 1996 has the same pattern of venation as *Kochopteron*, with a common stem Cu of CuA and CuP that divides into a convex CuA (clearly visible after a patterns of fossilization similar to its R and RA, fossilized a wide ‘double’ dark vein), and a concave CuP (that has not the same pattern of fossilization, less marked in the sediment, appearing as a white vein similarly to M). Thus it has no fusion of CuA with R; also its M is not fused with R but appressed to it (visible in the photograph of the type in Aristov 2012: pl. 7, figs 3, 5). It has also a convex arculus (reinforced crossvein m-cua, or ‘M5’). There is no difference in its CuA basal and distal to the arculus, which is not the case for *Gerarus* (under Aristov’s interpretation). Thus *Dalduba* is not related to the Archaeorthoptera and *Cacurgus*. *Dalduba* is probably a Paoliidae too.

The relative convexity vs. concavity of the veins of *Ideliopsis* remain difficult to establish because the fossil seems to be very ‘flat’ (Aristov 2012: pl. 7, fig. 1). Thus, the exact position in or outside the Archaeorthoptera cannot be accurately established now. Nevertheless, it has not the important cacurgid apomorphy of the basal fusion of MA with R and its distal re-emergence. It only shows a clear RP separating from RA. It is not a Cacurgidae.

Suksunus bicodex Aristov, 2015 is based on a very incomplete wing, with all the crucial structures of the wing base lacking. It clearly shows a broad area between distal part of CuA and CuP, but all the structures basal of the arculus (and the arculus itself) are unknown. Thus it is not possible to know if it had a venation of ‘orthopteroid’- or of ‘paoliid’ type. It is

a Polyneoptera *incertae sedis*. After Aristov (2015: fig. 4), *Suksunus* has not a MA basally fused with R and distally re-emerging. It is not a Cacurgidae.

Relative positions of Eoblattidae and Cacurgidae

As Aristov (2017) considered that *Cacurgus* belongs to the superorder ‘Eoblattida’, a comparison with *Eoblatta robusta*, type species of this set of taxa, is necessary. Béthoux (2006: 33) indicated that the ‘Pennsylvanian genera *Eoblatta* Handlirsch, 1906, and *Ctenoptilus* Lameere, 1917, share a narrow area between RA and RP (see Béthoux & Nel 2005), unlike *Cacurgus*’, but this difference is based on an error in the position of RP in *Cacurgus*. In *Eoblatta* MA is not fused with R and the base of RP is very basal, while in *Cacurgus*, MA is fused with R and RP emerges in a very distal position. Aristov (2017) separated the two families Eoblattidae and Cacurgidae on the sole basis of the ScP ending into R in the former and in C in the later. As indicated above, this character is highly variable even in extant insect families, thus it is of weak value in fossils too. The type specimen of *Eoblatta robusta* has the apex of ScP not preserved, even if it is very close to R, but as in some extant Chrysopidae or Sysiridae, ScP can strongly approximate RA and finally ends into C. Béthoux & Nel (2005) revised in detail *Eoblatta*, and concluded that its venation is of ‘orthopteroid’ type, with the convex CuA basally fused with M, distally re-emerging, and a concave CuPa ending into CuA (Fig. 6). Thus *Eoblatta robusta*, type species of the type genus of the type family of the (super-)order ‘Eoblattida’ that contains an impressive set of families, including the ‘Grylloblattida’ sensu Storozhenko (2002), is in fact an Archaeorthoptera. It is absolutely not related to the Dictyoptera, the Paoliida, and the fossil taxa currently included in the set ‘Grylloblattodea’. The whole concept of the order ‘Eoblattida’ should be reconsidered on the basis of more accurate homologies of the main wing veins, based not only on their relative positions, but also on their relative convexities.

Remarks. We take the opportunity of this paper to comment on the positions of two fossil insects (also found at the locality of Avion) that Aristov (2017) transferred into the ‘Eoblattida’.

Aviologus Coty et al., 2014 was originally described in the clade Panorthoptera. Aristov (2017) transferred this taxon into the Spanioderidae Handlirsch, 1906 in the set of taxa ‘Cnemidolestina Handlirsch, 1937’ sensu Aristov (2017), without argument. Du et al. (2017) considered that it could be an Archaeorthoptera (but not Panorthoptera, subclade of the Archaeorthoptera), close to the genus *Protomiamia*, on the basis that ‘the origin of a CuPa β , which would be diagnostic of the group Panorthoptera, was damaged by preparation [sic, in fact originally damaged], hence the nature of the corresponding vein is not evident ...’ It remains that the vein in question clearly exists and does not correspond to CuPb or to CuPaa, thus it is more likely a CuPa β . At least *Aviologus* is an Archaeorthoptera, and not a ‘Cnemidolestina’.

Westphalopsocus Azar et al., 2013 (in Nel et al. 2013) was originally described in the clade Acercaria. Aristov (2017) transferred this taxon into the Spanioderidae, on the basis of this argument: ‘However, venation of this species is quite typical for spanioderid, to which we refer *Westphalopsocus*. The genus is most similar to *Xixia* from which, as from all the other Spanioderidae is distinguished by its small size and bi-branched CuA’. This author completely ignored the discussion in Nel et al. (2013) to justify the attribution of *Westphalopsocus* into the Acercaria, in the basis of the presence of an areola postica (the ‘bi-branched CuA’), and of anal veins fusing apically and thus forming an inverted ‘Y-vein’, etc. There is strictly no synapomorphy that would justify its attribution to the Spanioderidae and to the set of taxa ‘Cnemidolestina Handlirsch, 1937’ sensu Aristov (2017). Thus we restore *Westphalopsocus* and the family Westphalopsocidae in the Acercaria. Furthermore, Béthoux

et al. (2012) revised *Miamia*, type genus of the Spanioderidae, and demonstrated it is an Archaeorthoptera on the basis of the relative convexity/concavity of the cubital veins, an argument also ignored by Aristov (2016, 2017), who put them in a superorder Perlidea Latreille, 1802. This confusing situation is due to the conflict mentioned above between two schools for the homology of the polyneopteran wing venation.

Conclusion

Cacurgus and the Cacurgidae can be restored in the Panorthoptera. The only accurate cacurgid genus is *Cacurgus*. The two genera *Dalduba* and *Kochopteron* are not Cacurgidae, but Paoliidae. Also *Suksunus*, *Ideliopsis*, and *Kitshuga* are not Cacurgidae but Polyneoptera of uncertain positions to be revised in the future. *Protodictyon* is an Archaeorthoptera nec Panorthoptera (stem group), without direct relationships with *Cacurgus*. *Eoblatta* and the Eoblattidae are Archaeorthoptera nec Panorthoptera (stem group). It is quite interesting to see that very different patterns of venations can be superficially similar within the Palaeozoic Polyneoptera (‘orthopteroid’ pattern versus ‘dictyopterid-paoliid’ pattern). Fossils with relative convexities of veins or with wing base not preserved cannot be accurately placed.

Acknowledgements

We thank a lot two anonymous referees for their helpful comments on the first version of the paper. We sincerely thank Pr. Alexander Rasnitsyn for the photograph of the holotype of *Kitshuga ryzhkovae*. We also thank Mr. Stéphane Carlier, Eiffage Route Nord Est, for their kind authorization to collect fossil insects in the terril of Avion.

References

- Aristov, D. S.** 2012. Composition and distribution of the family Cacurgidae (Insecta; Grylloblattida). *Paleontological Journal*, **46**, 250–257.
- Aristov, D. S.** 2015. Classification of the order Eoblattida (Insecta: Blattidea) with description of new taxa. *Far Eastern Entomologist*, **301**, 1–56.
- Aristov, D. S.** 2016. New suborder of the Paleozoic-Mesozoic order Cnemidolestida (Insecta: Gryllones). *Far Eastern Entomologist*, **311**, 13–22.
- Aristov, D. S.** 2017. *Palaeozoic evolution of the Insecta Gryllones*. PhD Thesis, Moscow, 238 pp. [in Russian]
- Béthoux, O.** 2003. *Protophasma dumasii* Brongniart 1879, a link between Orthoptera and the ‘dictyopterid’ orders? *Journal of Orthoptera Research*, **12**, 57–62.
- Béthoux, O.** 2005a. Wing venation pattern of Plecoptera (Insecta: Neoptera). *Illiesia*, **1**, 52–81.
- Béthoux, O.** 2005b. Reassigned and new basal Archaeorthoptera from the Upper Carboniferous of Mazon Creek (IL, USA). *Journal of Orthoptera Research*, **14**, 121–126.
- Béthoux, O.** 2006. Revision of *Cacurgus* Handlirsch, 1911, a basal Pennsylvanian Archaeorthoptera (Insecta: Neoptera). *Bulletin of the Peabody Museum of Natural History*, **47**, 29–35.
- Béthoux, O.** 2007. Archaeorthoptera wing venation nomenclature: a reply to Gorokhov. *Paleontological Journal*, **41**, 338–340.
- Béthoux, O.** 2008. Groundplan, nomenclature, homology, phylogeny, and the question of the insect wing venation pattern. *Alavesia*, **2**, 219–232.
- Béthoux, O., Gu, Jun-Jie, Yue, Yan-li & Ren, D.** 2012. *Miamia maimai* n. sp., a new Pennsylvanian stem-orthopteran insect, and a case study on the application of cladotypic nomenclature. *Fossil Record*, **15**, 103–113.

- Béthoux, O. & Herd, K.J.** 2009. Discovery of an enigmatic and gigantic Pennsylvanian Archaeorthoptera. *Journal of Orthoptera Research*, **18**, 23–28.
- Béthoux, O. & Jarzembowski, E.A.** 2010. New basal neopterans from Writhlington (UK, Pennsylvanian). *Alavesia*, **3**, 87–96.
- Béthoux, O. & Nel, A.** 2002. Venation pattern and revision of Orthoptera sensu nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov. *Zootaxa*, **96**, 1–88.
- Béthoux, O. & Nel, A.** 2005. Some Palaeozoic 'Protorthoptera' are 'ancestral' orthopteroids: major wing braces as clues to a new split among the 'Protorthoptera': *Journal of Systematic Palaeontology*, **2**, 1–25.
- Béthoux, O., Nel, A. & Lapeyrie, J.** 2003. The extinct order Caloneurodea (Insecta: Pterygota: Panorthoptera): wing venation, systematics and phylogenetic relationships. *Annales Zoologici*, **54**, 287–300.
- Béthoux, O. & Poschmann, M.** 2009. A new lobeattid insect from the Permo-Carboniferous of Niedermoschel, southwestern Germany (Archaeorthoptera). *Journal of Orthoptera Research*, **18**, 139–143.
- Béthoux, O. & Schneider, J.W.** 2010. Description of a hind wing of a new basal Archaeorthoptera (Mazon Creek, IL; Pennsylvanian). *Alavesia* **3**, 81–85.
- Bolton, H.** 1922. A monograph of the fossil insects of the British coal measures. *Palaeontographical Society Monograph London*, **74**, 81–156.
- Borre, P. de** 1875. Note sur des empreintes d'insectes fossiles découvertes dans les schistes houillers des environs de Mons. *Annales de la Société Entomologique de Belgique (Comptes-Rendus)*, **18**, 49–52.

- Brauckmann, C.** 1984. Weitere neue Insekten (Palaeodictyoptera: Protorthoptera) aus dem Namurium B von Hagen-Vorhalle. *Jahresberichte des Naturwissenschaftlichen Vereins in Wuppertal*, **37**, 108–115.
- Brongniart, C.** 1879. A new genus of orthopterous insects of the family Phasmidae (*Protophasma dumasii*), from the Upper coal-measure of Commentry, Dept. Allier, France. *Geological Magazine*, (N.S.) (2) **6**, 97–102.
- Brongniart, C.** 1885. Les insectes fossiles des terrains primaires. Coup d’oeil rapide sur la faune entomologique des terrains paléozoïques. *Bulletin de la Société des Amis des Sciences Naturelles de Rouen*, (3) **1885**, 50–68.
- Carpenter, F.M.** 1944. Carboniferous insects from the vicinity of Mazon Creek. *Illinois State Museum, Scientific Papers*, **3**, 1–20.
- Carpenter, F.M.** 1948. A Permian insect from Texas. *Psyche* **55**, 101–103.
- Carpenter, F. M.** 1992. Superclass Hexapoda. In: Moore, R. C. & Kaesler, R. L. (eds). *Treatise on Invertebrate Paleontology. The Geological Society of America and the University of Kansas, Boulder, Colorado, (R), Arthropoda 4, 3/4; xxii + 655 pp.*
- Coty, D., Háva, J., Prokop, J., Roques, P. & Nel, A.** 2014. New archaeorthopteran insects from the Late Carboniferous of the Nord and Pas-de-Calais basins in northern France (Insecta: Cnemidolestodea, Panorthoptera). *Zootaxa*, **3878**, 462–470.
- Crampton, G.C.** 1928. The grouping of the insect orders and their lines of descent. *The Entomologist*, **61**, 82–85.
- Dana, J.D.** 1864. On fossil insects from the Carboniferous formations in Illinois. *American Journal of Science*, (2) **37**, 34–35.
- Desutter-Grandcolas, L., Jacquelin, L., Hugel, S., Boistel, R., Garrouste, R., Henrotay, M., Warren, B. H., Chintauan-Marquier, I. C., Nel, P., Grandcolas, P. & Nel, A.** 2017. 3-

D imaging reveals four extraordinary cases of convergent evolution of acoustic communication in crickets and allies (Insecta). *Scientific Reports*, **7**(1) (7099), 1–8.

Du, Sile, Béthoux, O., Gu, J.-J. & D. Ren, D. 2017. *Protomiamia yangi* gen. et sp. nov. (Early Pennsylvanian; Xiaheyan, China), a sexually dimorphic Palaeozoic stem-Orthoptera. *Journal of Systematic Palaeontology*, **15**, 193–204.

Gorochoy, A. V. 2005. Review of Triassic Orthoptera with descriptions of new and little known taxa: part 1. *Paleontological Journal*, **39**, 178–186.

Gu, J.-J., Béthoux, O. & Ren, D. 2011. *Longzhua loculata* n. gen. n. sp., one of the most completely documented Pennsylvanian Archaeorthoptera (Insecta; Ningxia, China). *Journal of Paleontology*, **85**, 303–314.

Handlirsch, A. 1906. Revision of American Paleozoic insects. *Proceedings of the United States National Museum*, **29**, 661–820.

Handlirsch, A. 1911. New Paleozoic insects from the vicinity of Mazon creek, Illinois. *American Journal of Science*, (4) **31**, 297–326 + 353–377.

Handlirsch, A. 1937. Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme. Teil 1. *Annalen des Naturhistorischen Museums in Wien*, **48**, 1–140.

Kukalová-Peck, J. & Brauckmann, C. 1992. Most Paleozoic Protorthoptera are ancestral hemipteroids: major wing braces as clues to a new phylogeny of Neoptera (Insecta). *Canadian Journal of Zoology*, **70**, 2452–2473.

Laurentiaux, D. & Laurentiaux-Vieira, F. 1981. Nouveau Pachytylopsidae (Insecte Protorthoptère) du Westphalien inférieur belge. *Annales de la Société Géologique du Nord*, **100**, 83–89.

- Laurentiaux-Vieira, F. & Laurentiaux, D.** 1987. Un remarquable Archimylacridae du Westphalien inférieur belge. Ancienneté du dimorphisme sexuel des blattes. *Annales de la Société Géologique du Nord*, **106**, 37–47.
- Linnaeus, C. von** 1758. Systema Naturae per regna tria naturae secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Ed. decima reformata. Holmiae, Laur. Salvii, **1**, 1–823.
- Liu, Y.-S., Ren, D. & Prokop, J.** 2009. Discovery of a new Namurian archaeorthopterid from Ningxia, China (Insecta: Archaeorthoptera). *Zootaxa*, **2032**, 63–68.
- Martins-Neto, R.G., Gallego, O.F., Brauckmann, C. & Cruz, J.L.** 2007. A review of the South American Palaeozoic entomofauna. Part I: the Ischnoneuroidea and Cacurgoidea, with description of new taxa. *African Invertebrates*, **48**, 87–101.
- Melander, A. L.** 1903. Some additions to the Carboniferous terrestrial arthropod fauna of Illinois. *The Journal of Geology*, **11**, 178–198.
- Nel, A., Prokop, J., Nel, P., Grandcolas, P., Huang, Di-ying, Roques, P., Guilbert, E., Dostál, O. & Szwedo, J.** 2012. Traits and evolution of wing venation pattern in paraneopteran insects. *Journal of Morphology*, **273**, 480–506.
- Nel, A., Roques, P., Nel, P., Prokin, A. A., Bourgoin, T., Prokop, J., Szwedo, J., Azar, D., Desutter-Grandcolas, L., Wappler, T., Garrouste, R., Coty, D., Huang, Diying, Engel, M. & Kirejtshuk, A. G.** 2013. The earliest known holometabolous insects. *Nature*, **503**, 257–261.
- Nel, A., Roques, P., Prokop, J. & Garrouste, R.** 2018. A new, extraordinary ‘damselfly-like’ Odonatoptera from the Pennsylvanian of the Avion locality in Pas-de-Calais, France (Insecta: ‘Exopterygota’). *Alcheringa*, <https://doi.org/10.1080/03115518.2018.1489561>
- Novokshonov, V. G.** 2000. New fossil insects (Insecta: Grylloblattida, Ordinis incertis) from the Lower Permian of the Middle Urals. *Paleontological Journal*, **34**, 513–518.

- Pinto, I. D. & Pinto de Ornellas, L.** 1978. Carboniferous insects (Protorthoptera and Paraplecoptera) from Gondwana. (South America, Africa and Asia). *Pesquisas (Zoologia)*, **11**, 305–321.
- Pinto, I. D.** 1992. Carboniferous insects from Argentina. 5. Narkeminidae Pinto et Ornellas 1991, Order Paraplecoptera. *Anais do Academia Brasileira de Ciencias*, **64**, 289–292.
- Prokop, J. & Ren, D.** 2007. New significant fossil insects from the Upper Carboniferous of Ningxia in northern China (Palaeodictyoptera, Archaeorthoptera). *European Journal of Entomology*, **104**, 267–275.
- Prokop, J., Toppelová, S., Roques, P. & Nel, A.** 2013. A new genus and species of Breyeriidae and wings of immature stages from the Upper Carboniferous, Nord-Pas-de-Calais, France (Insecta: Palaeodictyoptera). *Insect Systematics & Evolution*, **44**, 117–128.
- Prokop, J., Roques, P. & Nel, A.** 2014a. New non-holometabolous insects from Pennsylvanian of Avion locality in Pas-de-Calais, France (Insecta: 'Exopterygota'). *Alcheringa*, **38**, 155–169.
- Prokop, J., Krzeminski, W., Krzeminska, E., Hörnschemeyer, T., Ilger, J.-M., Brauckmann, C., Grandcolas, P. & Nel, A.** 2014b. Late Palaeozoic Paoliida is the sister group of Dictyoptera (Insecta: Neoptera). *Journal of Systematic Palaeontology*, **12**, 601–622.
- Prokop, J., Szwed, J., Lapeyrie, J., Garrouste, R. & Nel, A.** 2015. New Middle Permian insects from Salagou Formation of the Lodève Basin in southern France (Insecta: Pterygota). *Annales de la Société Entomologique de France (N.S.)*, **51**, 14–51.
- Pruvost P.** 1919. Introduction à l'étude du terrain houiller du Nord et du Pas-de-Calais. La faune continentale du terrain houiller du Nord de la France. *Mémoires pour servir à l'Explication de la Carte Géologique de la France*, Paris, 584 pp.
- Rasnitsyn, A. P.** 2007. On the discussion of the wing venation of (Archae)Orthoptera (Insecta). *Paleontological Journal*, **41**, 341–344.

Rasnitsyn, A. P. & Aristov, D. S. 2016. Revision of the Palaeozoic order Paoliida (Insecta). *Far Eastern Entomologist*, **309**, 1–13.

Rasnitsyn, A. P., Aristov, D. S., Gorochoy, A. V., Rowland, J. M. & Sinitshenkova, N. D. 2004. Important new insect fossils from Carrizo Arroyo and the Permo-Carboniferous faunal boundary. In: Lucas, S. G. & Zeigler, K. E. (eds). Carboniferous-Permian transition at Carrizo Arroyo, Central New Mexico. *Bulletin of the New Mexico Museum of Natural History and Science*, **25**, 215–246.

Richardson, E.S.Jr. 1956. Pennsylvanian invertebrates of the Mazon Creek area, Illinois. Insects. *Fieldiana, Geology*, **12**, 15–56.

Schubnel, T. 2018. Homologie de la nervation des ailes et phylogénie des Dictyoptera actuels et fossiles (Insecta). Master Thesis, MNHN – Sorbonne Université, 1–38 + annex.

Wootton, R. J. 1992. Functional morphology of insect wings. *Annual Review of Entomology*, **37**, 113–140.

Figure 1. *Cacurgus gallicus* sp. nov., holotype MNHN.F.A70497. Photograph of forewing, **A**, part; **B**, counterpart. Scale bars = 5 mm.

Figure 2. *Cacurgus gallicus* sp. nov., holotype MNHN.F.A70497. Photograph of forewing base, part. Scale bar = 5 mm.

Figure 3. *Protodictyon pulchripenne* Melander, 1903, holotype specimen CHAS PALEO 4749. Photograph of forewing and hind wing bases. Scale bar = 1 mm.

Figure 4. *Protodictyon pulchripenne* Melander, 1903, holotype specimen CHAS PALEO 4749. Photograph of habitus. Scale bar = 10 mm.

Figure 5. *Kitshuga ryzhkova* Aristov, 2012, holotype PIN, no. 3840/542. Photograph of forewing, counterpart. Copyright Alexander Rasnitsyn. Scale bar = 5 mm.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Figure 6. *Eoblatta robusta* (Brongniart, 1885), holotype MNHN.F.R51344. Photograph of forewing. Scale bar = 5 mm.

For Review Only



figure 1

172x209mm (300 x 300 DPI)



figure 2

172x137mm (300 x 300 DPI)



figure 3

178x102mm (300 x 300 DPI)



figure 4

172x166mm (300 x 300 DPI)

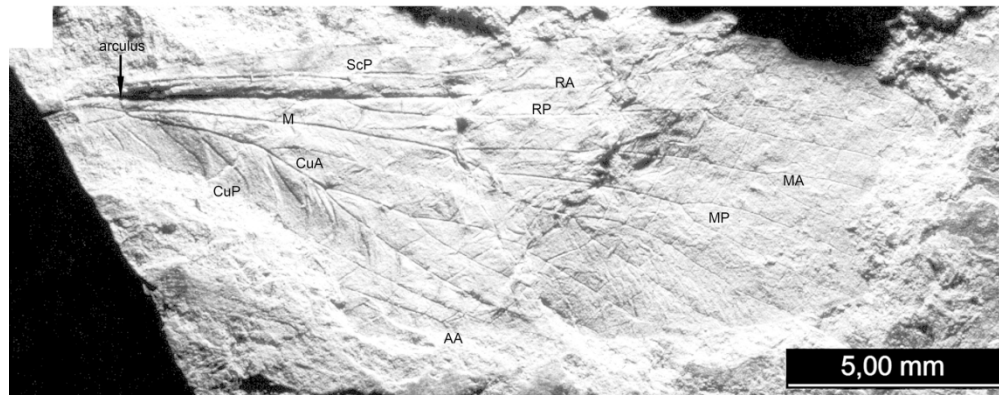


figure 5

172x69mm (300 x 300 DPI)

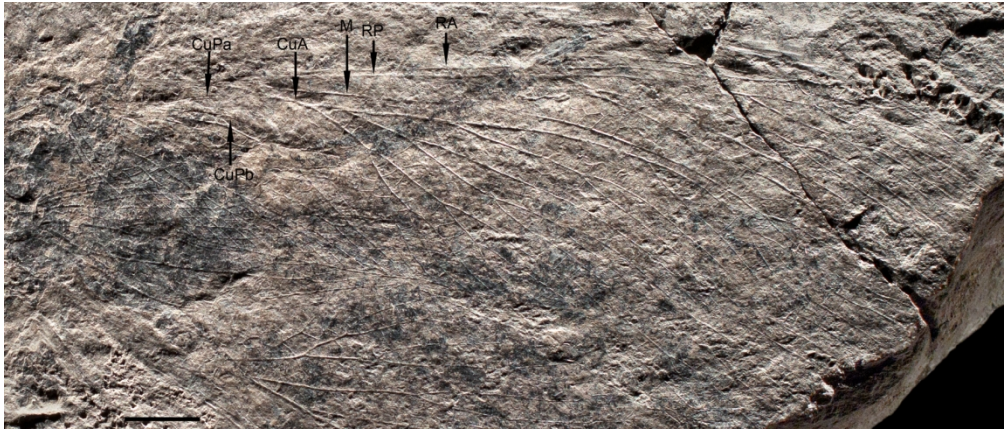


figure 6

153x65mm (300 x 300 DPI)