Revision of the Enigmatic Insect Family Anthracoptilidae Enlightens the Evolution of Palaeozoic Stem-Dictyopterans

Authors: Guan, Zhaoying, Prokop, Jakub, Roques, Patrick, Lapeyrie, Jean, and Nel, André

Source: Acta Palaeontologica Polonica, 61(1) : 71-87

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.00051.2014

Revision of the enigmatic insect family Anthracoptilidae enlightens the evolution of Palaeozoic stem-dictyopterans

ZHAOYING GUAN, JAKUB PROKOP, PATRICK ROQUES, JEAN LAPEYRIE, and ANDRÉ NEL

Guan, Z., Prokop, J., Roques, P., Lapeyrie, J., and Nel, A. 2016. Revision of the enigmatic family Anthracoptilidae enlightens the evolution of Palaeozoic stem-dictyopterans. *Acta Palaeontologica Polonica* 61 (1): 71–87.

The position of the Palaeozoic Anthracoptilidae has been a major problem of insect systematics for over a century. The previous hypotheses suggested affinities of Anthracoptilidae with the Palaeodictyopteroida, Protorthoptera, Hypoperlida, stem-Mantodea, Paraneoptera, Holometabola, or Eoblattida. Herein we put forward a new hypothesis based mainly on a comprehensive re-evaluation of the wing venation characters and re-examination of the type material of *Anthracoptilus perrieri* and *Mesoptilus dolloi*. The Anthracoptilidae are considered as belonging to the paoliid lineage, sister group of the Dictyoptera. In particular this result refutes the presence of Mantodea in the Paleozoic fossil record. The two families Strephocladidae and Strephoneuridae, are considered as junior synonyms of the Anthracoptilidae, while the previous synonymy of the Anthracoptilidae with the Ischnoneuridae is rejected. We consider the Permarrhaphidae, previously considered as synonym of the Anthracoptilidae, (and *Permarrhaphus*) as Insecta incertae sedis. The following new taxa are proposed: *Mesoptilus carpenteri* sp. nov. from the early Permian of Wellington Formation in Oklahoma (USA) which extends the range and distribution of the genus; *Pseudomesoptilus* gen. nov. is designated to include *Mesoptilus sellardsi*; *Strephocladus permianus* sp. nov. from the middle Permian of South of France; *Westphaloptilus gallicus* gen. et sp. nov. from the Bashkirian of the North of France.

Key words: Insecta, Neoptera, Paoliida, systematics, Carboniferous, Permian, France, USA.

Zhaoying Guan [guanzy300@aliyun.com], Institute of Hydrobiology, Jinan University, 510632 Guanzhou City, China.
Jakub Prokop [jprokop@natur.cuni.cz] (corresponding author), Charles University in Prague, Faculty of Science, Department of Zoology, Viničná 7, CZ-128 44, Praha 2, Czech Republic.
Jean Lapeyrie [jean.lapeyrie@orange.fr], Corniche de Fontbonne, F-34700, Lodève, France.
Patrick Roques [patrick.roques93@wanadoo.fr] and André Nel [anel@mnhn.fr], CNRS UMR 7205, CP 50, Entomologie, Muséum National d'Histoire Naturelle, 45 rue Buffon, F-75005 Paris, France.

Received 11 January 2014, accepted 13 January 2015, available online 19 January 2015.

Introduction

Paucity of pterygote fossils in early Carboniferous (Mississippian) deposits encompassing so called Romer's gap (Ward et al. 2006) is a mystery of insect evolution possibly associated with low atmospheric oxygen levels or lack of fossils due to scarcity of worldwide terrestrial deposits (Engel et al. 2013). Sudden flourishing of insects in the earliest Pennsylvanian (Namurian to Langsettian) deposits show particularly dominance of Paoliida as sister group of Dictyoptera, documented in some European localities (Ruhr Basin and Upper Silesian Coal Basin). Palaeozoic roach-like insects superficially resembling the Recent cockroaches represent the stem groups of Dictyoptera with marked abundance in ecosystems since Bolsovian (Westphalian B). However, their systematic affinities are unclear due to record based on tegmina (forewing) venation known for large intraspecific variability and scarcity of complete body fossils (Nel and Prokop 2009). The Anthracoptilidae Handlirsch, 1922 is a group of enigmatic Palaeozoic Pterygota that has been considered for long time as member of polyphyletic Protorthoptera known also as wastebasket of polyneopteran insects without clear relationships. Carpenter (1992) proposed close relationships to Ischnoneuridae which seems to be erroneous as *Ischnoneura* belongs to the orthopteroid lineage Cnemidolestodea (Béthoux 2005a). The Anthracoptilidae (= Strephocladidae) group is important for the phylogeny of the Polyneoptera because Béthoux and Wieland (2009) and Béthoux et al. (2010) considered the "Strephocladidae" as stem-mantodean Dictyoptera, while this opinion was strongly criticized by Kukalová-Peck and Beutel (2012) and Gorochov (2013). Also *Adiphlebia* Scudder, 1885 considered as a possible representative of stem beetles (Béthoux 2009) shows a similar pattern of wing venation and the Adiphlebiidae Handlirsch, 1906

Acta Palaeontol. Pol. 61 (1): 71–87, 2016 http://dx.doi.org/10.4202/app.00051.2014

have been considered as a synonym of the Anthracoptilidae too. The present discovery of a more complete wing from the middle Permian of France, attributable to *Strephocladus* Scudder, 1885 (type genus of Strephocladidae), together with the revision of *Anthracoptilus* and some other fossils, allow us to discuss about the diagnosis, limits, and affinities of this family.

Institutional abbreviations.—Ld LAP, Musée Fleury, coll. Jean Lapeyrie, Lodève, France; MCZ, Museum of Comparative Zoology at Harvard University, Cambridge, USA; MNHN, Palaeontology Department, Muséum national d'Histoire naturelle Paris, France.

Other abbreviations.—A1/A2, first/second anal vein; CuA/CuP, cubitus anterior/posterior; M, indistinguishable polarity of median vein; MA/MP, media anterior/posterior; RA/RP, radius anterior/posterior; ScA/ScP, subcosta anterior/posterior.

Material and methods

The fossil specimens were observed in dry state and under a film layer of ethyl alcohol using Olympus SZX-9 and Nikon SMZ 1500 stereomicroscopes. The venation patterns were drawn using a stereomicroscope with camera lucida and finally overlaid to the photograph. Photographs were taken by a Nikon D7100 digital camera equipped with macro lens Nikon AF-S VR Micro-Nikkor 105 mm, and a Canon D550 digital camera equipped with macro lens EF-S 50 mm. Original photographs were processed using the image-editing software Adobe Photoshop 8.0.

The wing venation nomenclature generally follows the concept of Kukalová-Peck (1991) and flexion lines terminology sensu Wootton (1979).

Systematic palaeontology

Order Paoliida Handlirsch, 1906 (sensu Prokop et al. 2014a)

Family Anthracoptilidae Handlirsch, 1922

2002 Strephocladidae Martynov, 1938; Rasnitsyn 2002: 112.
2002 Strephoneuridae Martynov, 1940; Rasnitsyn 2002: 112, 114.

Type genus: *Anthracoptilus* Lameere, 1917 for *Anthracoptilus perrieri* (Meunier, 1909); Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian), Commentry Basin, Allier department, France.

Emended diagnosis.—Area between C and ScP with a series of veinlets and crossveins (but probably not preserved in *Strephocladus permianus*); RA with one or two posterior branches (an apomorphic character, but not shared by all taxa in Anthracoptilidae) or simple; median vein strongly approximate or shortly fused with RP near base of RP (synapomorphy); branches of RP, median vein and CuA strongly parallel at least in their basal halves (the presence of branches all simple is not shared by all taxa in Anthracoptilidae); median vein braced to CuA by a short convex cross-vein mp-cua (a character present in Holometabola, Paoliida and Dictyoptera, but very useful to separate the Anthracoptilidae from the archaeorthopteran taxa); CuA and CuP emerging from a long common stem; main stem of CuA strongly convex, but anteriorly pectinate with at least a series of parallel branches, all less convex than main stem of CuA (synapomorphy).

Remarks.—The family Strephocladidae Martynov, 1938 (type genus *Strephocladus* Scudder, 1885) is currently considered as a junior synonym of the family Anthracoptilidae Handlirsch, 1922, also synonymized with the Permarrhaphidae Martynov, 1931 (late Permian, monotypic genus *Permarrhaphus* Martynov, 1931) and the Strephoneuridae Martynov, 1940 (early Permian, monotypic genus *Strephoneura* Martynov, 1940) (Rasnitsyn 2002; Novokshonov and Aristov 2004; Rasnitsyn and Aristov 2004; Rasnitsyn et al. 2004). Lastly Rasnitsyn and Aristov (2013) proposed again a synonymy of the Permarrhaphidae with the Anthracoptilidae, Strephoneuridae, Strephocladidae, but also with the Ischnoneuridae Handlirsch, 1906 and the Adiphlebiidae Handlirsch, 1906 (see below).

Comparison of type genera *Strephoneura*, *Strephocladus*, *Permarrhaphus*, and *Anthracoptilus* leads to the following conclusions. *Strephoneura* shares with *Strephocladus* the following potential apomorphies: ScP and radius strongly approximate; RA with two apical posterior branches; RP and median vein strongly approximate or touching near base of RP; CuA with several pectinate anterior branches; branches of RP, median vein, and CuA all simple and closely parallel; CuP and first anal vein simple. *Permarrhaphus venosus* Martynov, 1931 is based on a wing fragment that was originally interpreted as a beetle elytron. It cannot correspond to any part of a strephocladid wing, except, maybe the anal area, as supposed by Rasnitsyn and Aristov (2004: 160). Nothing looking like a radius, median or CuA vein can be seen on the original photograph (Martynov 1931: fig. 28). It remains that nothing supports the attribution of this wing to the same clade with *Strephoneura* or *Strephocladus*. Therefore, we remove the first synonymy of the Strephoneuridae with the Permarrhaphidae proposed by Rasnitsyn (2002: 112–114), but we confirm the synonymies of the Strephoneuridae and Strephocladidae with the Anthracoptilidae. We consider the Permarrhaphidae (and *Permarrhaphus*) as Insecta incertae sedis status novus.

Anthracoptilus perrieri (Meunier, 1909) (Gzhelian of Commentry, see redescription below), type species of the Anthracoptilidae, shares with *Strephoneura* and *Strephocladus*: the CuA and CuP emerging from a common stem; a distinct brace between CuA and median vein; median vein and RP approximating near base of RP; an anteriorly pectinate CuA with branches less convex than main stem of CuA; ScP ending on RA; branches of main veins parallel between them but less clearly than in *Strephoneura* and *Strephocladus*. *Anthracoptilus* differs from them in the presence of several branches of RP, median vein and CuA forked distally; presence of a net of very irregular sigmoidal crossveins, instead of being straight and defining rectangular cells between main veins; RA ending on anterior wing margin in a distinctly more basal position; RA without any posterior branches in its apical part (difference with *Strephocladus*, character unknown in *Strephoneura*).

An anteriorly pectinate CuA is convergently present in the Archaeorthoptera of the subclade Cnemidolestodea Handlirsch, 1937 (sensu Béthoux 2005a), but the patterns of venation of these orthopteroid insects are completely different from those of the Anthracoptilidae, due to presence of basal fusion of CuA with M in the former and to a common stem Cu from which CuA and CuP emerge in the latter. Furthermore, the anterior branches of CuA (+CuPa) are clearly concave in the Cnemidolestodea, while the same branches are relatively more convex in the Anthracoptilidae. Rasnitsyn and Aristov (2013), refusing the argument of convexity of the different veins, proposed to synonymize the Anthracoptilidae with the Ischnoneuridae (type genus *Ischnoneura* Brongniart, 1893 (Gzhelian of Commentry), without giving any argument against the attribution of *Ischnoneura* to the archaeorthopteran lineage (and more precisely to the Cnemidolestodea; see Béthoux 2005a), as proposed by Béthoux and Nel (2005: fig. 19), on the basis of the pattern of forewing venation typical of those of the Archaeorthoptera, especially in the presence of a concave anterior branch of CuP reaching the convex CuA, itself emerging from a common stem with M. We reject this synonymy and restore the Anthracoptilidae as a separate family, in a different clade that does not belong to the Archaeorthoptera, unlike the Ischnoneuridae. More recently, Aristov (2014) synonymized the Ischnoneuridae (at least its type genus *Ischnoneura*) with the Cnemidolestidae Handlirsch, 1906, type family of the Cnemidolestodea, but without speaking again his previous proposal of synonymy of the Anthracoptilidae with the Ischnoneuridae.

Note that some holometabolous Permochoristidae (*Protopanorpa* spp.) also have a similar pattern of a curved vein in mid part of wing with a series of anteriorly pectinate and parallel branches, separating basally from a simple vein, but the concerned veins are completely different, the anteriorly pectinate vein being MP while the simple posterior vein is CuA (see Bashkuev 2010: fig. 1). Also the Plecoptera penturoperlid *Penturoperla* have a median vein with a series of parallel anterior branches (Illies 1960), even in some of them could be in fact interpreted as branches of CuA captured by median vein following Béthoux (2005b). These similarities support the hypothesis of a convergent evolution between the Archaeorthoptera Cnemidolestodea and the Paoliida Anthracoptilidae, due to flight ability.

Stratigraphic and geographic range.—Bashkirian (Lower Pennsylvanian)–Lopingian (upper Permian), Australia, Europe, North America, and Russia.

Genus *Anthracoptilus* Lameere, 1917

Type species: *Anthracoptilus perrieri* (Meunier, 1909); Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian), Commentry Basin, Allier department, France.

Anthracoptilus perrieri (Meunier, 1909)

Fig. 1.

Holotype: MNHN R51112, imprint of imago with head, prothorax, forewings and fragmentary legs.

Type locality: Commentry Basin, Allier department, France.

Type horizon: Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian).

Material.—Type material only.

Description.—An imprint of the head with antenna and the prothorax, nearly complete right wing and base of left wing, and fore legs attached.

Head triangular in shape, 3.2 mm long, 2.5 mm wide, with large eyes on the sides, and apparently prognathous but non suctorial mouthparts, 1.5 mm long; long and thin antennae, not completely visible, with bases 1.0 mm apart; a distinct short neck, 1.0 mm long, 1.7 mm wide; pronotum trapezoidal, 3.0 mm long, 1.0 wide anteriorly and 3.3 mm wide posteriorly; fore femur 4.3 mm long, 1.5 mm wide; tibia 4.5 mm long, 1.0 mm wide, with three faint traces of spines along inner margin.

Forewing with basal part of posterior and anterior margins partly missing, wing 31.0 mm long, 9.9 mm wide; simple, straight, convex ScP closely parallel to radius, 0.9 mm apart, ending on RA 19.3 mm from wing base; area between ScP and costal margin with numerous crossveins and veinlets, 1.8 mm wide; radial stem straight, with RP separating from RA 13.7 mm from wing base; strongly convex RA, straight but without posterior branches apically; apex of RA 6.2 mm from wing apex; slightly concave RP with two main branches, each subdivided, resulting into 14 branches ending on wing margin; RP and median vein separated but strongly approximate with a short crossvein between them 15.4 mm from wing base; median vein more convex than RP but less than RA, divided into four main branches, the first branch meeting with the second at 10.5 mm from wing base, with all branches simple except two having a short fork near posterior wing margin; median vein separated from RP and CuA at wing base, but strongly approximating CuA with a brace between them; convex CuA anteriorly pectinate with five main branches all less convex than main stem of CuA, the first branch of CuA being divided into three secondary branches distally, second main branch forked near wing margin; CuA separating from CuP 2.3 mm from wing base; concave CuP simple, weakly curved with a rather narrow area between it and CuA, 1.1 mm wide; weak crossveins between CuP and CuA; area between CuP and posterior wing margin 3.9 mm wide; at least three visible anal veins, convex and weakly curved; posterior part of anal area certainly missing; a dense net of sigmoidal crossveins between branches of all main veins.

Fig. 1. Forewing of anthracoptilid insect *Anthracoptilus perrieri* (Meunier, 1909) from Stephanian of Commentry Basin, France, holotype R51112, photograph (**A**), line drawing (**B**).

Stratigraphic and geographic range.—Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian), France.

Genus *Strephocladus* Scudder, 1885

Type species: *Strephocladus subtilis* (Kliver, 1883); Schiffweiler, Saar-Nahe Basin, Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian), Saarland, Germany.

Species included: The type species and *Strephocladus permianus* sp. nov.

Strephocladus permianus sp. nov.

Fig. 2.

Etymology: Named after the Permian period.

Holotype: Ld LAP 310A, B (imprint and counterimprint).

Type locality: Lodève Basin, Languedoc, France.

Type horizon: Salagou Formation, Mérifons Member, Guadalupian (middle Permian).

Material.—Type material only.

Diagnosis.—Forewing characters only. Three branches of RP; three branches of median vein; median vein and RP strongly approximate but not touching; costal margin straight.

Description.—Single wing with extreme base missing and basal part of posterior margin strongly curved, 28.6 mm long, 7.4 mm wide; simple, straight, concave ScP closely parallel to Radius, 0.28 mm apart, ending on RA 16.7 mm from wing base; area between ScP and costal margin 0.9 mm wide, apparently without crossveins or veinlets, even if some faint traces are weakly visible, that could correspond to veinlets between ScP and C; radial stem straight, with RP separating from RA 9.3 mm from wing base; RA straight, but with two curved posterior branches near wing apex; apex of main branch of RA 4.1 mm from wing apex; slightly concave RP with three posterior simple branches; RP strongly approximating median vein near its bases, with a cell between them; slightly concave median vein touching CuA in one point 5.6 mm from wing base; 1.2 mm distally, median stem divided into a first simple posterior branch, second branch of M divided into two simple branches 4.0 mm distally; convex CuA anteriorly pectinate with five parallel simple branches less convex than main stem of CuA; concave CuP simple, weakly curved with a rather narrow area between it and CuA, 0.8 mm wide; basal part of CuA appearing as a weak vein rather long, 3.0 mm long, between

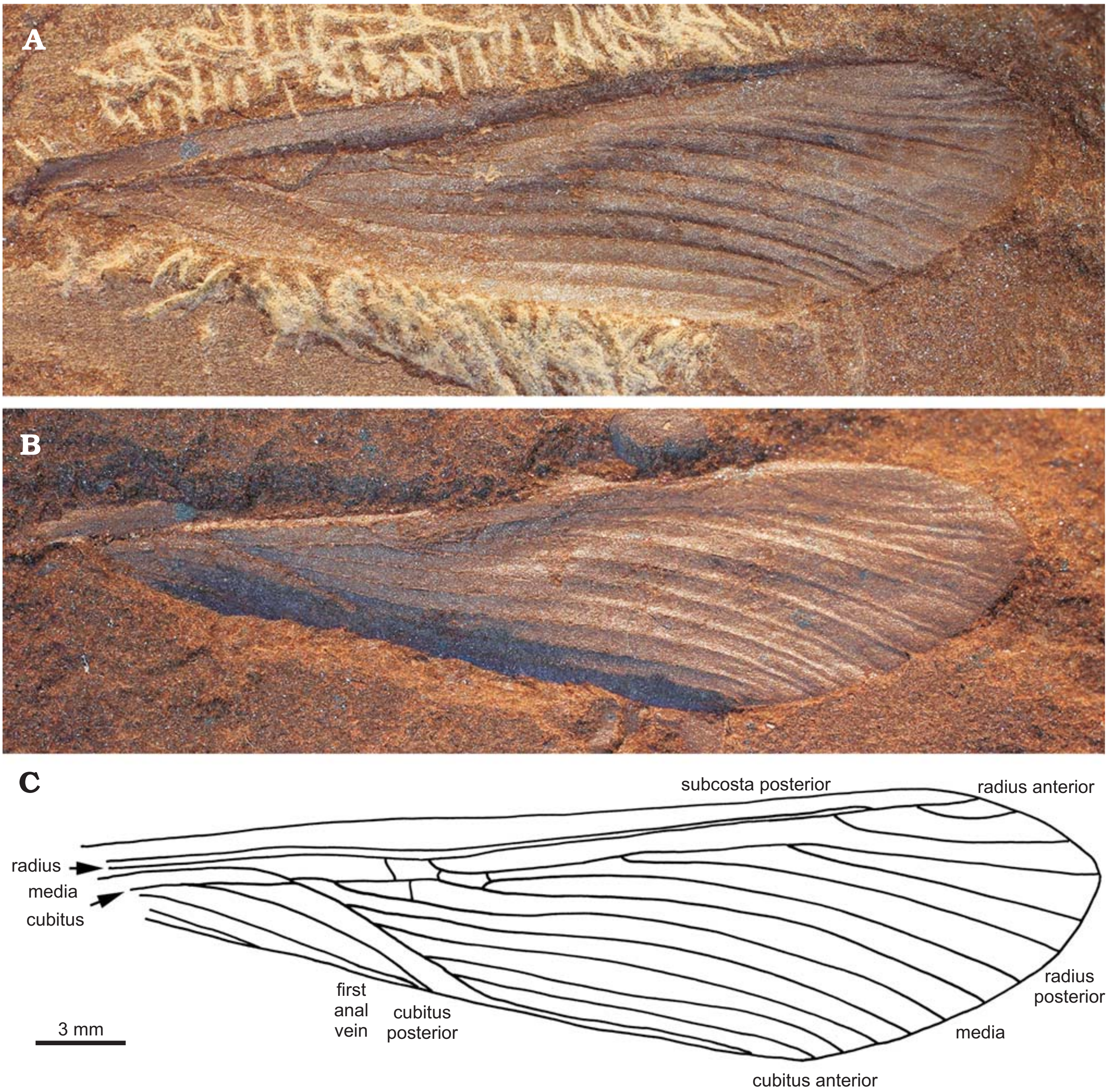

Fig. 2. Forewing of anthracoptilid insect St*rephocladus permianus* sp. nov. from Guadalupian of Lodève Basin, France, holotype Ld LAP 310A, B, photographs of imprint and couterimprint (**A**, **B**), line drawing (**C**).

its distal part and CuP, but CuA and CuP emerging from a common stem; area between CuP and posterior wing margin 1.3 mm wide; first anal vein convex, simple, nearly straight; remnants of a second anal vein visible but posterior part of anal area certainly missing; several simple crossveins are present between branches of M and RP, but generally rather poorly preserved; all branches of RP, M and CuA weakly curved and parallel.

Remarks.—The forewing of *Strephocladus permianus* sp. nov. is strongly similar to that of the Gzhelian (Late Pennsylvanian) *Strephocladus subtilis* (Kliver, 1883), revised by Carpenter (1966). They share the following potential apomorphies: branches of CuA, median vein and RP are parallel; CuA anteriorly pectinate with five branches; median vein and RP strongly approximate near base of RP; first branch of median vein close to CuA; ScP and R closely parallel with ScP ending on RA; CuP and first anal vein simple. Some differences between the two fossils are due to preservation problems, i.e., type wing of *S. subtilis* has veinlets in costal area while this zone seems to have no veins in the type specimen of *S. permianus*, apical part of wing of *S. subtilis* is missing so that it is impossible to determine if it has posterior branches of RA and the exact number of branches of median vein. More important differences are the presence of five branches of RP in *S. subtilis* instead of three in *S. permianus*; presence of only two branches of

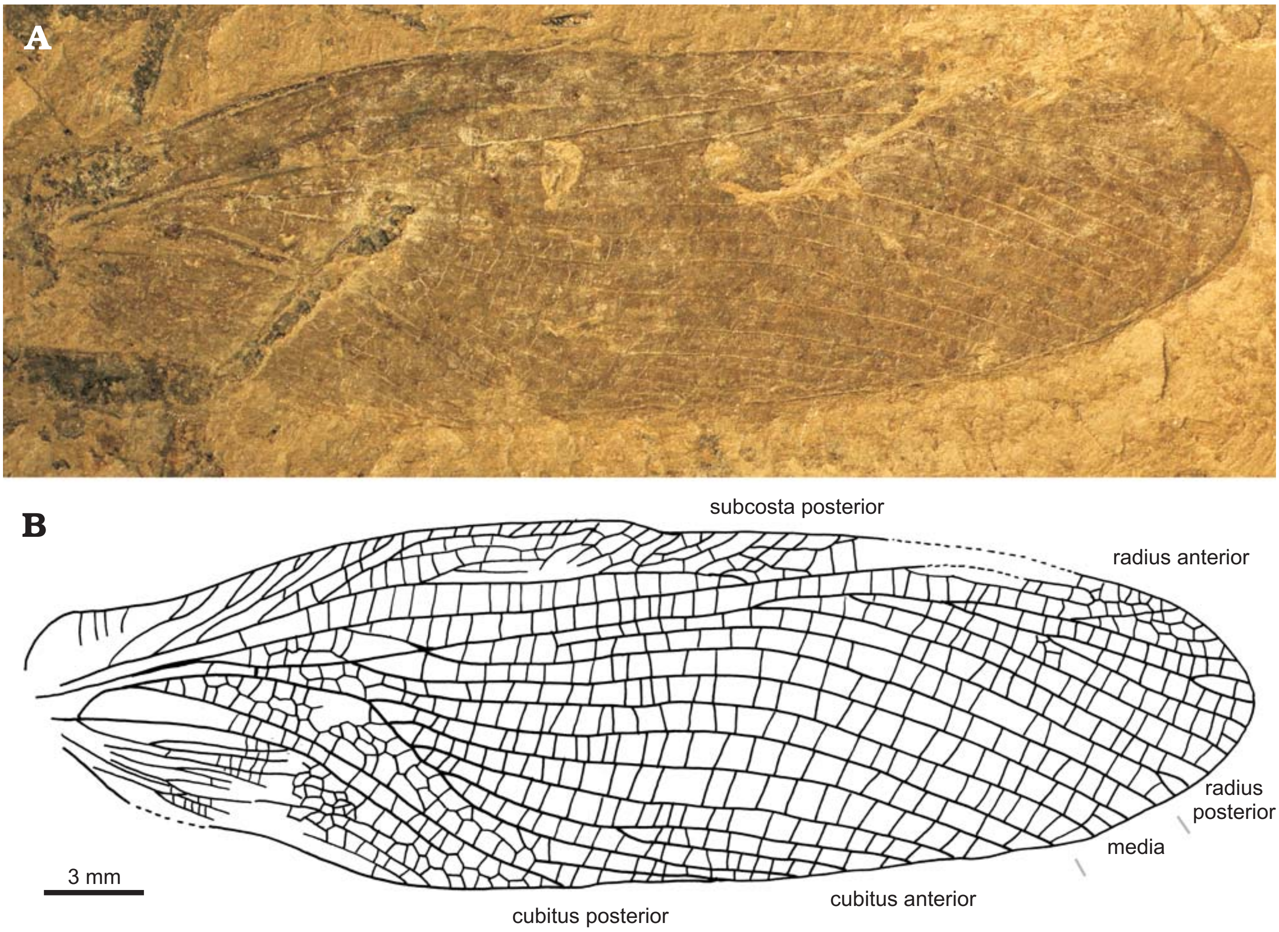

Fig. 3. Forewing of anthracoptilid insect *Mesoptilus dolloi* (Lameere, 1917) from Stephanian of Commentry Basin, France, holotype R51159, photograph (**A**), line drawing (**B**).

median vein in *S. subtilis* instead of three in *S. permianus*; median vein and RP touching in *S. subtilis* while they are only strongly approximate in *S. permianus*; and costal margin with a weak but distinct curve near the wing base in *S. subtilis* while it is straight in *S. permianus* (see Waterlot 1934: pl. 20: 5). Thus, we consider that *S. permianus* belongs to a new species of the same genus *Strephocladus*.

Stratigraphic and geographic range.—Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian)–Guadalupian, middle Permian), France and Germany.

Genus *Mesoptilus* Lameere, 1917

Type species: *Mesoptilus dolloi* Lameere, 1917; Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian, Commentry Basin, Allier department, France.

Species includes: The type species and *Mesoptilus carpenteri* sp. nov.

Emended diagnosis.—In forewing, a dense net of irregular cells in area between C and ScP; a broad area between CuA and CuP with a dense net of small irregular cells; only seven-eight main branches of RP; part of CuA basal of brace m-cua long.

Remarks.—*Mesoptilus*, already attributed to the "Strephocladidae" by Béthoux and Wieland (2009) has all the characters supporting an attribution to the Anthracoptilidae, plus the presence of a posterior branch of RA near its apex, as in *Strephocladus permianus*.

Stratigraphic and geographic range.—Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian), France.

Mesoptilus dolloi (Lameere, 1917)

Fig. 3.

Holotype: MNHN R51159, imprint of prothorax, forewings and fragmentary legs.

Type locality: Commentry Basin, Allier department, France.

Type horizon: Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian).

Material.—Type material only.

Emended diagnosis.—Forewing anterior branches of CuA strongly approximate at their bases, with first one distant from m-cua.

Description.—Some details of forewing venation have been neglected by Béthoux and Wieland (2009), so we prefer to provide a redescription of this taxon. An imprint of prothorax with nearly complete right wing and base of left wing, and some legs attached.

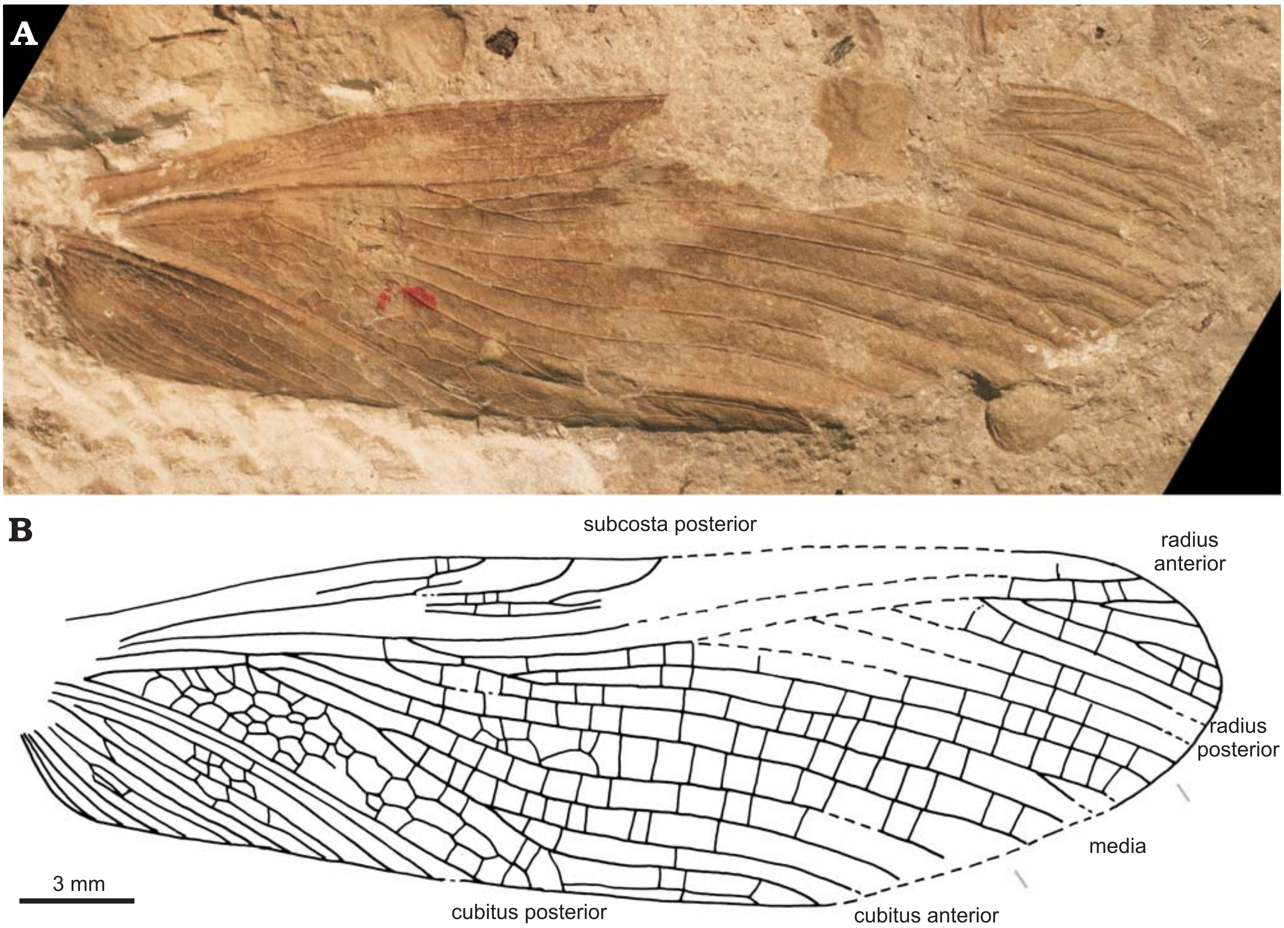

Fig. 4. Forewing of anthracoptilid insect *Mesoptilus carpenteri* sp. nov. from Artinskian of Elmo, Oklahoma, USA, holotype MCZ 11253, photograph (**A**), line drawing (**B**).

Thorax poorly preserved, 6.0 mm wide; fore femur 23 mm long, 1.7 mm wide; tibia more than 8.0 mm long, 0.9 mm wide, with a series of strong curved spines along inner margin, 0.3 mm long. Hind leg with strong femora and with tibia 1.6 mm wide, armed with an outer series of strong spines; a hind wing partly preserved; a complete forewing and basal half of the other one attached to thorax.

Forewing with anterior margin partly missing in apical part, and posterior base part missing due to covering by a leg; wing 29.6 mm long, 8.9 mm wide; straight, concave ScP with several anterior branches reaching costal margin, each subdivided; area between ScP and costal margin with numerous crossveins and veinlets, 1.5 mm wide; ScP parallel to radius, 0.7 mm apart, ending on RA 17.5 mm from wing base; radial stem straight, with RP separating from RA 7.9 mm from wing base; RA strongly convex, straight and simple, ending 3.1 mm from wing apex; slightly concave RP posteriorly pectinate, with eight main branches, resulting into 11 branches ending on wing margin; RP and median vein separated but approximate with a short crossvein between them 5.6 mm from wing base; median vein slightly more convex than RP, divided into three straight and simple branches; presence of a brace m-cua between median vein and CuA; strongly convex CuA anteriorly pectinate with four main branches distinctly less convex than main stem of CuA, resulting into seven branches ending on wing margin; CuA separating from CuP 2.3 mm from wing base; concave CuP simple, curved with numerous crossveins between it and CuA in a 1.4 mm wide area, this zone being partly covered by a leg in one wing; area between CuP and posterior wing margin 2.5 mm wide; five visible weakly curved main branches of anal veins, a net of crossveins present in between, but poorly preserved; posterior part of anal area and wing base (possible jugal area) missing; a dense net of rather straight crossveins between branches of all main veins, except in area between CuA and CuP, between C and ScP, and anal area where nets of more irregular cells are present.

Stratigraphic and geographic range.—Gzhelian (Upper Pennsylvanian), France.

Mesoptilus carpenteri sp. nov.

Fig. 4.

Etymology: In honor of Frank Morgan Carpenter, who worked particularly on Palaeozoic insect fauna in the Museum of Comparative Zoology at Harvard University, Cambridge.

Holotype: MCZ 11253, in unsorted Carpenter's collection.

Type locality: Elmo, Oklahoma, USA.

Type horizon: Wellington Formation, Artinskian (early Permian).

Material.—Type material only.

Diagnosis.—Forewing anterior branches of CuA widely separated at their bases, with first one close to m-cua.

Description.—Forewing with anterior margin partly missing, wing 35 mm long, 10.2 mm wide; straight, concave ScP with several anterior branches reaching costal margin, each subdivided; area between ScP and costal margin with numerous crossveins and veinlets, 2.3 mm wide; ScP parallel to radius, 0.5 mm apart, probably ending ca. 17 mm from wing base; radial stem straight, with RP separating from RA 11.4 mm from wing base; RA strongly convex, straight and simple, ending 2.5 mm from wing apex; concave RP posteriorly pectinate, with seven main branches, resulting into eight branches ending on wing margin; RP and median vein separated but approximate with a short crossvein between them 12.7 mm from wing base; median vein slightly more convex than RP, divided into three straight and simple branches; presence of a brace m-cua between median vein and CuA; strongly convex CuA anteriorly pectinate with four main branches distinctly less convex than main stem of CuA; CuA separating from CuP 1.9 mm from wing base; concave CuP simple, curved with numerous crossveins between it and CuA in a broad area, 2.4 mm wide; area between CuP and posterior wing margin 2.0 mm wide; five visible weakly curved main branches of anal veins, a net of secondary veinlets and crossveins present in between; a dense net of rather straight crossveins between branches of all main veins, except in area between CuA and CuP, between C and ScP, and anal area where nets of more irregular cells are present.

Remarks.—This fossil can be attributed to the Anthracoptilidae on the basis of the presence of all the diagnostic characters of the family listed above. It differs from all the other representatives of the family, except *Mesoptilus dolloi*, *Spargoptilon* Kukalová, 1965, and *Homocladus* Carpenter, 1966, in the presence of a rather broad area between CuA and CuP with a dense net of small irregular cells. *Mesoptilus carpenteri*, *M. dolloi*, and *Spargoptilon* differ from *Homocladus* in the presence of much less branches of M and RP in the tegmina. *Spargoptilon* differs from *Mesoptilus* in the shorter part of CuA basal of brace m-cua, and narrower area between CuA and CuP. *M. carpenteri* differs from *M. dolloi* in the anterior branches of CuA more widely separated at their bases, with first one close to m-cua, and media ending with three terminal branches instead of four in *M. carpenteri*.

Stratigraphic and geographic range.—Artinskian (lower Permian), Oklahoma, USA.

Genus *Pseudomesoptilus* nov.

Etymology: To indicate it was originally included into the genus *Mesoptilus*.

Type species: *Mesoptilus sellardsi* Lameere, 1917; monotypic, see below.

Diagnosis.—Presence of two main veins (RP and MA?) emerging separately from radius; RP emerging distal of mid part of wing, instead of in the basal third or fourth; absence of brace or approximation between RP and median vein or between median vein and CuA.

Stratigraphic and geographic range.—Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian), France.

Pseudomesoptilus sellardsi (Lameere, 1917) comb. nov.

Fig. 5.

Type material: Holotype: MNHN R51350, imprint of fragmentary thorax with a pair of forewings.

Type locality: Commentry Basin, Allier department, France.

Type horizon: Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian).

Material.—Type material only.

Diagnosis.—Forewing ca. 30 mm long; RP distally pectinate ending with five simple branches; CuA with five main anterior branches.

Description.—Imprint of two forewings attached to thorax fragments. Forewing with apex and posterior margin partly missing, and posterior base partly missing; wing 30.7 mm long, 8.9 mm wide; straight, concave ScP with several anterior branches reaching costal margin; area between ScP and costal margin with numerous crossveins and veinlets, 1.2 mm wide; ScP parallel to radius, 0.8 mm apart, ending on RA 20.9 mm from wing base; radial stem straight; RA convex, straight and simple, ending 1.7 mm from anterior wing margin; two main veins emerging separately from radial stem, viz. basal (MA?) plus distal concave RP, first one simple and straight, emerging 9.8 mm from wing base, second main branch emerging 16.3 mm distally, posteriorly pectinate into five branches; convex median vein straight and simple, emerging from a common stem with radius, 6.2 mm from wing base, with a rather strong veinlet between it and radius just basal of most basal posterior vein (MA?) emerging from radius, this veinlet could be anterior branch of median vein reaching radius and re-emerging just distally; distal part of median vein only forked near posterior wing margin; median vein parallel with first vein (MA?) emerging distally from radius and well separated from CuA at its base; convex CuA anteriorly pectinate with five main branches less convex in distal parts, resulting into six or seven branches ending on wing margin; concave CuP simple and curved, CuA and CuP emerging from a common stem Cu; several crossveins between CuP and CuA in a 3.2 mm wide area; areas between CuA, CuP, anal and posterior margin poorly preserved and posterior wing margin partly missing in both wings; one visible anal vein, simple.

Remarks.—This taxon strongly differs from *Mesoptilus dolloi* (and all other Anthracoptilidae) in the presence of two main veins (MA? and RP) emerging separately from radius; RP emerging distal mid part of wing, instead of in the basal

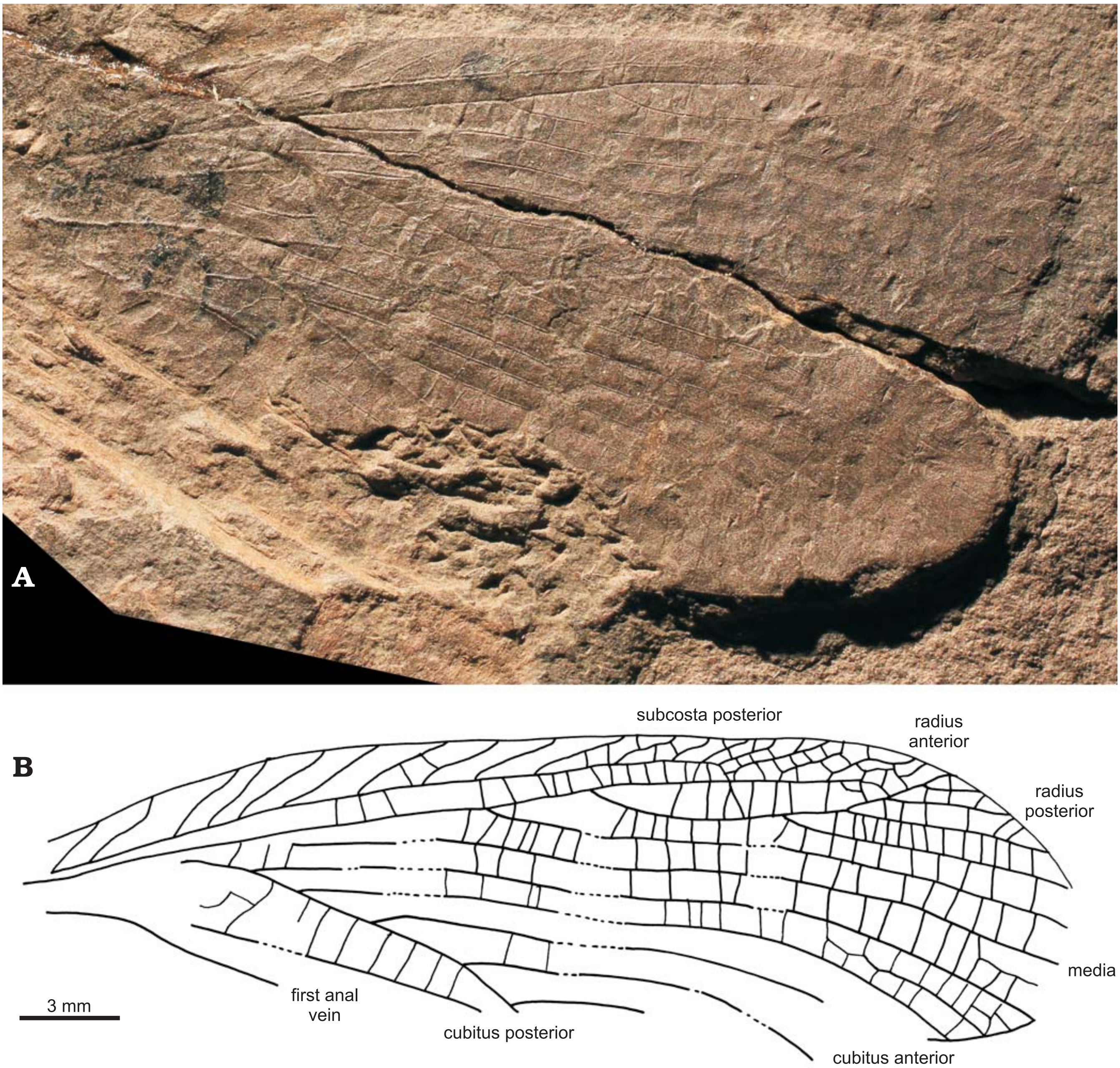

Fig. 5. Forewing of anthracoptilid insect *Pseudomesoptilus sellardsi* (Lameere, 1917) comb. nov. from Stephanian of Commentry Basin, France, holotype R51350, photograph (**A**), line drawing (**B**).

third or fourth; absence of brace or approximation between RP and median vein or between median vein and CuA. Nevertheless it shares with the Anthracoptilidae (especially *Strephocladus*) the presence of a strongly convex stem CuA from which emerge a series of five more concave anterior branches, ScP ending on RA, area between ScP and C with numerous anterior veinlets emerging from ScP, branches of main veins all parallel and generally simple, with a net of rectangular cells between them. Thus, if we provisionally maintain it in the Anthracoptilidae, it is necessary to transfer it into a new genus different from *Mesoptilus*.

Stratigraphic and geographic range.—Stephanian, Carboniferous (= Gzhelian, Upper Pennsylvanian), France.

Genus *Westphaloptilus* nov.

Etymology: Named after the Westphalian stage and *Anthracoptilus*.

Type species: *Westphaloptilus gallicus* sp. nov.; monotypic, see below

Diagnosis.—Forewing characters only. Area between C and ScP with a series of veinlets and crossveins; RP emerging from R in basal half of wing; median vein braced to CuA by a short convex mp-cua; CuA and CuP emerging from a long common stem Cu; main stem of CuA strongly convex, but anteriorly pectinate with only three parallel convex branches (apomorphy).

Stratigraphic and geographic range.—Westphalian C or D, Carboniferous (= Bashkirian, Lower Pennsylvanian), France.

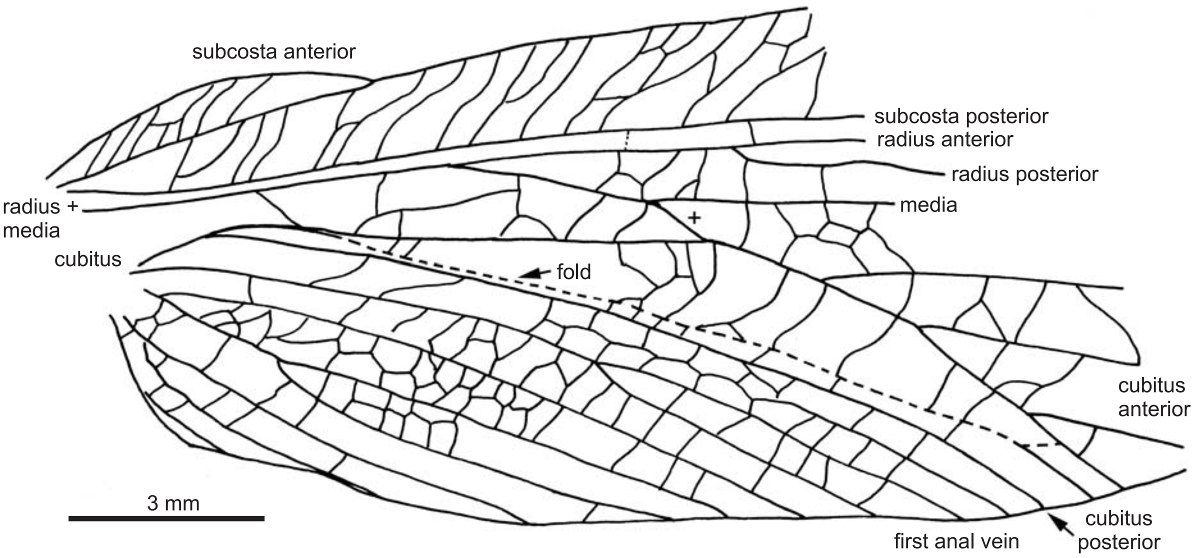

Fig. 6. Forewing of anthracoptilid insect *Westphaloptilus gallicus* sp. nov. from Westphalian of Bruay-en-Artois, Department of North, France, holotype Bruay F.5 BR27–28.

Westphaloptilus gallicus sp. nov.

Figs. 6, 7.

Etymology: Named after Gallia, Latin name for France.

Holotype: Bruay F.5 BR27–28 imprint and counterimprint of a basal third of a forewing. Collected by Patrick Roques provisionally stored in the collection of Entomological Laboratory, MNHN, Paris, France. This collection will be deposited in the Musée Géologique Pierre Vetter, Decazeville, France.

Type locality: Bruay-en-Artois, coal heap n°26, Department of North, France.

Type horizon: Westphalian C or D, Carboniferous (= Bashkirian, Lower Pennsylvanian).

Material.—Type material only.

Diagnosis.—As for the genus.

Description.—Length of fragment 9.2 mm long, wing 5.0 mm wide; bulging basal part of costal margin delimited by simple convex vein (ScA?), several oblique crossveins between this vein and costal margin; simple, straight, concave ScP closely parallel to Radius, 0.1 mm apart, with few crossveins between them; area between ScP and costal margin with numerous crossveins and veinlets; radial stem straight, with RP separating from RA 5.4 mm from wing base; strongly convex RA, straight; RP slightly concave; RP and median vein separated near their base; median vein more rather concave separated from R 3.1 mm from wing base; M strongly approximating CuA with a brace between them, convex but less than CuA; convex CuA anteriorly pectinate with three main convex branches; convex CuA separating from concave CuP 2.3 mm from wing base; CuP simple, straight with a rather wide area between it and CuA, 0.6 mm wide; weak sigmoidal crossveins between CuP and CuA; area between CuP and posterior wing margin 1.9 mm wide; seven visible anal veins, convex and weakly curved; a dense net of sigmoidal crossveins between branches of all main veins.

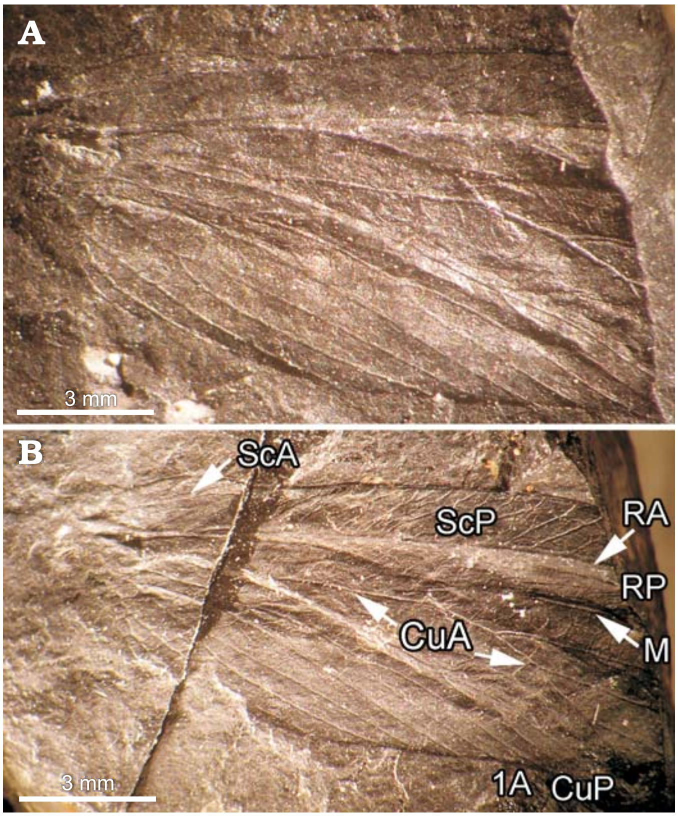

Fig. 7. Anthracoptilid insect *Westphaloptilus gallicus* sp. nov. from Bashkirian of Bruay-en-Artois, Department of North, France, holotype Bruay F.5 BR27–28, photograph of imprint (**A**), photograph of counterimprint (**B**). 1A, first anal vein; CuA/P, cubitus anterior/posterior; M, indistinguishable polarity of median vein; RA/P, radius anterior/posterior; ScA/P, subcosta anterior/posterior.

Remarks.—*Westphaloptilus* gen. nov. has the main diagnostic characters of the Anthracoptilidae: area between C and ScP with a series of veinlets and crossveins; RP emerging from R in basal half of wing; median vein braced to CuA by a short convex mp-cua; CuA and CuP emerging from a long common stem Cu; main stem of CuA strongly convex, but anteriorly pectinate with at least a series of parallel convex branches (synapomorphy); CuP concave simple; anal veins more convex than CuP.

Westphaloptilus has only three anterior branches of CuA while *Anthracoptilus*, *Mesoptilus*, *Pseudomesoptilus*, *Strephocladus*, *Graticladus*, *Homocladus*, *Spargoptilon*, *Carrizocladus*, *Adiphlebia*, and also certainly *Strephoptilus* have five such veins or more. *Jarmilacladus* and *Opisthocladus* have also more branches of CuA, but posteriorly pectinate. Even the poorly known *Rhinomaloptila* has more branches of CuA (see below for precisions on these taxa).

Stratigraphic and geographic range.—Bashkirian (Lower Pennsylvanian) Westphalian C or D, Carboniferous (= Bashkirian, Lower Pennsylvanian), France.

Further taxa currently included in Anthracoptilidae

***Graticladus* Novokshonov and Aristov, 2004**.—Monospecific (*G. severus* Novokshonov and Aristov, 2004). According to Novokshonov and Aristov (2004) this species has the following combination of wing venation characters: simple weakly curved CuP, anteriorly pectinate CuA, brace between median vein and CuA, approximate RP and median vein, branches of main veins nearly all simple and strongly parallel, ScP ending on RA, and costal area with several long veinlets emerging from ScP those are sufficient for an attribution to the Anthracoptilidae.

***Homocladus* Carpenter, 1966**.—Carpenter (1966) described two species *H. grandis* Carpenter, 1966 and *H. ornatus* Carpenter, 1966 in this genus. Béthoux et al. (2010) synonymized them together with *Paracladus retardatus* Carpenter, 1966 under the name *H. grandis*. Nevertheless, Rasnitsyn and Aristov (2004) considered *Paracladus* as a valid genus, while they synonymized *Homocladus* with *Spargoptilon*. The type specimen of *Paracladus* is incompletely preserved, so that it is not possible to determine its exact number of branches of RP. Only the discovery of further specimen attributable to *Paracladus retardatus* will allow solving the problem. The same arguments as for *Graticladus* allow an attribution of *Homocladus* (and *Paracladus*) to the Anthracoptilidae.

***Spargoptilon* Kukalová, 1965**.—Kukalová (1965) described two species *S. latericius* Kukalová, 1965 (type species) and *S. confertus* Kukalová, 1965 in this genus. The main difference with *Homocladus* is the distinctly less numerous branches of RP (five main in *Spargoptilon* contra ca. 10 in *Homocladus*), and the ScP ending on costal margin instead on RA in *Homocladus*. Rasnitsyn and Aristov (2004: 160) proposed a synonymy of *Homocladus* with *Spargoptilon*, considering that the main difference between the two would be the narrower wing of *Homocladus*. The differences indicated above are sufficient for a generic separation, thus we restore *Homocladus* as a different genus status restored.

***Mycteroptila* Rasnitsyn, 1977**.—Rasnitsyn and Aristov (2004: 160) suggested that *Mycteroptila* Rasnitsyn, 1977 (type species *M. dina* Rasnitsyn, 1977) may be a synonym of *Spargoptilon*, after a new examination of the type species, but without more precise argument. The same authors also suggest that the second species *M. armipotens* Novokshonov, 1998 could be “more similar to representatives of *Strephoneura*” and “may represent another species of the same genus”. A comparison of the original figures of Novokshonov (1998) with Martynov (1940) does not show many structures that could be really compared in these fossils. The problem remains open.

***Jarmilacladus* Rasnitsyn and Aristov, 2004**.—Type species *J. variabilis* Rasnitsyn and Aristov, 2004, differ from the other taxa in Anthracoptilidae by the ScP terminating on costal margin. The other anthracoptilid characters (brace between median vein and CuA and median vein approximating RP, parallel branches, branches of CuA anteriorly pectinated) are present. An attribution to the Anthracoptilidae is well supported. Rasnitsyn and Aristov (2013: 686, fig. 11f, but neither fig. 11d nor 11e) described “?*Jarmilacladus patiens*” on the basis on an incomplete clavus, which is a rather weakly informative area. In particular nothing is known on the structure of the cubital veins, diagnostic of the Anthracoptilidae.

***Rhinomaloptila* Rasnitsyn, 1977**.—Type species *R. polyneura* Rasnitsyn, 1977, is based on a very incomplete wing, showing several parallel veins in radial to cubital areas, but even their exact origins (RP, media, CuA?) cannot be determined. It has also a ScP ending on costal margin. Nevertheless the head of *Rhinomaloptila* and *Anthracoptilus* seem to have a similar shape of head, elongate and triangular. *Rhinomaloptila* could well be an Anthracoptilidae, but the very incomplete state of preservation forbids an accurate attribution.

***Carrizocladus* Rasnitsyn in Rasnitsyn et al., 2004)**.—Type species *Carrizocladus arroyo* Rasnitsyn, 2004, based on a nearly complete forewing; other species “?*Carrizocladus*” *deter* Rasnitsyn, 2004, based on a very incomplete forewing. *Carrizocladus arroyo* shares with the Anthracoptilidae the presence of numerous simple parallel branches of RP, M, and CuA. Rasnitsyn (in Rasnitsyn et al. 2004: 9) considered in his drawing that about five anteriorly pectinate branches are emerging from M while he wrote that M has only two branches, which would be quite abnormal for an attribution to the Anthracoptilidae. After the original photograph of the type specimen, it is more likely that these veins are emerging anteriorly from CuA, while M has two branches only. The second species “?*Carrizocladus*” *deter* shares few characters with the type species and its attribution to this genus (or even to the Anthracoptilidae) is weakly supported (maybe by the presence of some anterior branches of CuA).

***Strephoptilus* Rasnitsyn and Aristov, 2013**.—Type species *Strephoptilus borealis* Rasnitsyn and Aristov, 2013. Other species *S. longus* Rasnitsyn and Aristov, 2013, both based on nearly complete forewings, clearly shows the basal common stem of Cu from which the convex CuA and the concave CuP emerge, plus the presence of a series of anterior branches of CuA that are less convex than the main stem of this vein (see Rasnitsyn and Aristov 2013: fig. 12e, f). As these characters are diagnostic for the Anthracoptilidae, the attribution of *Strephoptilus* to this family remains well supported.

***Pruvostia* Bolton, 1921**.—Type species *Pruvostia spectabilis* Bolton, 1921 has a venation typical of the Anthracoptilidae, with convex CuA having three anterior branches clearly concave, and CuA and CuP with a common stem (see photograph of the type in Bolton 1921: pl. 3: 2).

***Adiphlebia* Scudder, 1885**.—Monospecific (*A. lacoana* Scudder, 1885). Béthoux (2009) considered this taxon as a representative of stem beetles but Kukalová-Peck and Beutel (2012) transferred it into the "Strephocladidae", ignoring the synonymies proposed by Rasnitsyn and Aristov (2004), and considered this family as belonging to the Holometabola but not related to Coleoptera. Rasnitsyn and Aristov (2013) confirmed the synonymy of the Adiphlebiidae with the Ischnoneuridae (and consequently with the Anthracoptilidae), but without new arguments. The attribution of *Adiphlebia* to the Anthracoptilidae would be supported by the anteriorly pectinate CuA, median vein approximating RP, ScP ending in RA, presence of numerous parallel and simple branches of main veins, Cu apparently divided into CuA and CuP, presence of numerous veinlets in costal area, numerous simple crossveins between main veins defining small rectangular cells. Nevertheless some uncertainty remains because the relative convexity of CuA and its branches is difficult to establish because of the poor preservation of this vein in all specimens studied by Béthoux or Kukalová-Peck and Beutel (2012). A crucial difference with the Anthracoptilidae (and especially *Anthracoptila*) is the presence of curious lateral extensions of prothorax in *Adiphlebia*, which would be sufficient for a family separation at least.

Definition and relationships of the Anthracoptilidae

Protorthoptera hypothesis.—Carpenter (1992) included the Anthracoptilidae, Strephocladidae, and Strephoneuridae in the polyphyletic "Protorthoptera", while considering the Permarrhaphidae as Neoptera incertae sedis.

Hypoperlida hypothesis.—Rasnitsyn (2002), and more recently Rasnitsyn and Aristov (2013) included these insects in the order Hypoperlida that these authors considered as paraphyletic relatively to the Palaeodictyoptera (= Dictyoneuridea), and Paraneoptera (Psocidea and Cimicidea). It is currently admitted that the Palaeodictyoptera are palaeopteran insects related to Ephemeroptera and that the Paraneoptera are the sister group of the neopteran Holometabola. Thus the Hypoperlida cannot be "ancestors" relatively to these two very distant groups and cannot be considered in a phylogenetic analysis under the sense proposed by these authors.

Palaeodictyopteroida hypothesis.—Affinities of the Anthracoptilidae with the palaeodictyopteroid orders are unlikely because, even if some Palaeodictyoptera have a branched CuA (viz. the Homoiopteridae), they do not have a cubito-anal area so well defined by a distinctly concave CuP as in the Anthracoptilidae (see Prokop and Nel 2004); a free convex vein MA is present in the palaeodictyopteroid orders, which is not the case in the Anthracoptilidae; Kukalová-Peck and Beutel (2012) also proposed the following synapomorphy of Anthracoptilidae with the Neoptera, absent in palaeodictyopteroid insects: "AA2+3 and AP basally fused with several parallel forks".

Paraneoptera hypothesis.—Affinities of the Anthracoptilidae with the Paraneoptera are also unlikely because in the latter clade, CuA is basally fused with M (and R) and re-emerging distally as demonstrated by Nel et al. (2012), which is not the case in the Anthracoptilidae.

Stem-mantodean hypothesis.—Béthoux and Wieland (2009) and Béthoux et al. (2010) considered the "Strephocladidae" as stem-mantodean Dictyoptera. Kukalová-Peck and Beutel (2012) strongly criticized Béthoux et al.'s (2010) opinion and considered that the "Strephocladidae" are not related to the Dictyoptera, on the basis of the following arguments, that we propose to comment on: (i) the area occupied by the RP branches is large as in Neuroptera and Mecoptera, whereas it is supposed to be small in Dictyoptera. This is a weak argument because the width of an area can greatly vary within an order, for instance the Namurian Dictyoptera *Qilianiblatta namurensis* Zhang, Schneider, and Hong, 2013 has a RP area as broad as those of the "Strephocladidae" (Zhang et al. 2013); (ii) a medio-medial brace (m) (one or several) is present as in Neuroptera, but is absent in Dictyoptera. If this brace is present in some Neuroptera, it is not the case for all Holometabola; furthermore this brace between median vein and RP is due to these strongly approximate veins and occurs convergently in very different clades (Dictyoptera, Plecoptera, even in the palaeodictyopteroid family Permothemistidae); (iii) MP± and CuA± would be perfectly levelled as in most Holometabola, not slightly concave (MP-) and convex (CuA+) or vertically undulated as in Mantodea. This point is erroneous as the main stem of CuA is much more convex than the median vein in the Anthracoptilidae; (iv) a flight-important brace/short fusion mp-cua so called arculus is always present in both wing pairs as in Holometabola, whereas it is only very rarely present in the forewings and sometimes missing in the hind wings of Dictyoptera. The rarity of a character in a clade is not an argument to exclude a taxon from it; this brace is present in Paoliida and in the most basal and the oldest dictyopteran lineages (Prokop et al.

2014a); (v) CuP- is supposed to be weakly concave and running in parallel to a weakly concave claval flexion line as in Holometabola, and not running through the bottom of a deep claval line ("vena dividens") as in Dictyoptera. True Dictyoptera have their CuP more strongly concave than in the Anthracoptilidae, but this character is not sufficient for an inclusion into the Holometabola because CuP is also weakly concave in different clades, viz. the neopteran Plecoptera. The presence of strongly concave CuP is likely to be a synapomorphy of the Dictyoptera and a CuP with a less pronounced concavity is a plesiomorphy; (vi) AA1+2 in the forewing is supposed to be very distinct and strongly protruding, especially close to the base as in Endoneoptera, and not weak and irregular (or absent) as in Mantodea. The first anal vein in the Anthracoptilidae is nearly as high as in Mantodea; (vi) the jugal area is supposed to be small as in Holometabola, not enlarged and conspicuous as in Mantodea. This argument is very uncertain because it is impossible to be sure of the presence versus absence of a jugal area in the Anthracoptilidae due to the broken extreme bases of the isolated fossil wings or to bad preservation in fossils with wings attached to body. In contrast, anal loops and pseudo-veins are equally frequent in Endoneoptera and Mantodea; (vii) the hind wing has MA± diverging from RP. The arguments favoring a capture of MA by RP are very weak, even those given by Kukalová-Peck and Beutel (2012) appears to be erroneous; (viii) a concave CuP- followed by a parallel concave claval line, with both grooves running close together as in Holometabola, but not merging into one claval line as in Mantodea. The presence of a claval line is quite difficult to observe in these fossils; (ix) the veins are supposed to bear prominent setae as in many Holometabola, but not in Mantodea. The presence of prominent setae on the wings of Anthracoptilidae is far from being accurate, we could not find any of them in the observed material.

In conclusion, only one argument remains favoring an exclusion of the Anthracoptilidae from the Mantodea and the Dictyoptera, i.e., their fore- and hindwing CuP are less concave than in the Dictyoptera. This character state is likely to be a plesiomorphy, sufficient for an exclusion from the Dictyoptera sensu stricto, but not sufficient for an exclusion from the stem-Dictyoptera.

Holometabola hypothesis.—Kukalová-Peck and Beutel (2012: 642–643) proposed a list of characters "typical" for the "Strephocladidae" (= Anthracoptilidae), supposedly supporting their attribution to the Holometabola. We also comment on these characters below: (i) forewing coriaceous. If *Strephocladus* seems to have a rather coriaceous forewing, it is not the case for *Anthracoptilus*; (ii) hind wings shorter than forewing; precosto-costal strip prominent and relatively broad. This is a plesiomorphy in Neoptera; (iii) convex ScA reduced, expressed as ScA bulge. No bulge is visible in *Strephocladus* or *Anthracoptilus*; (iv) concave ScP shortened, ending on RA close to 2/3 of the wing length. The same character is present in Blattoneoptera; (v) ScP sending out a series of long, branched, conspicuously slanted twigs. This character is also present in many Dictyoptera; (vi) stem of radius present, short; branches of radius, media and cubitus very long, sinuous, parallel and neutral in fluting (a tentative synapomorphy: a similar condition occurs in modern Neuroptera and Mecoptera). This conclusion is unlikely as more or less neutral RP, median and branches of CuA are also present in Dictyoptera; (vii) MA likely fused basally to R and separating as the first branch from RP (as in Blattoneoptera and Endoneoptera, and based on indirect evidence; the alternative, MA separating from the stem of M occurs only in Orthoneoptera and Pleconeoptera, while associated with a very different veinal pattern; Kukalová-Peck 2008). No evidence supports this hypothesis of fusion of MA with radial stem, even if Kukalová-Peck and Beutel (2012: 644, loc. cit.) also indicated that "MA+ in some modern mantodeans (e.g., *Tenodera angustipennis* Saussure, 1869) still retained MA+ visibly joining RP at the wing base (an important synapomorphy shared by Blattoneoptera, Hemineoptera and Endoneoptera)". A direct examination of specimens of this mantid show no basal free MA between median and radius; (viii) MP braced to RP and MA with cross-vein/short fusion brace (m) (Figs. 1, 6) (as in modern Neuropterida). Not all modern Neuropterida have such brace between Median vein and RP, this character is not sufficient for an attribution of the "Strephocladidae" to the Holometabola; (ix) MP braced to CuA by a short important cross-vein brace mp-cua, a supposed fore- and hind wing synapomorphy of (Holometabola + Paraneoptera). As demonstrated by Nel et al. (2012), the Paraneoptera have not such a brace but a fusion of CuA with median vein, thus this brace cannot be a synapomorphy of the clade (Holometabola + Paraneoptera), furthermore, such a brace is also present in Paoliida and Dictyoptera, see Prokop et al. (2014a); (x) stem of Cu very short. This character is erroneous, as the stem of Cu is long in "Strephocladidae"; (xi) CuA branches long, apically oriented. This important character is better and more precisely formulated as the presence of an anteriorly pectinate CuA; (xii) CuP weakened and leveled near posterior margin. CuP in "Strephocladidae" is not especially weak and is distinctly concave; (xiii) claval flexion line shortened. Such claval line or claval furrow in forewing sensu Wootton (1979), is simply not visible in many "Strephocladidae", and not shortened in *Homocladus grandis* and *Paracladus retardus* (see Fig. 8), this point is inconclusive. The claval furrow is a flexion line present in both latter species just behind the CuP as a prominent band or groove running parallel towards the posterior wing margin. This structure with primary aerodynamic function can be used in some cases as substantial character for phylogeny and broader comparison. But the morphology of claval furrow present in *Homocladus* and *Paracladus* is usual situation for members of several insect orders (see Wootton 1979: figs. 2–7). Nevertheless, Hennig (1981: 189) considered a smoothly curved anal furrow along which the vein CuP runs forming a well-defined anterior edge to the anal lobe as significant character of Blattopteroidea (Blattodea + Mantodea); (xiv) AA1+2 strongly elevated ver-

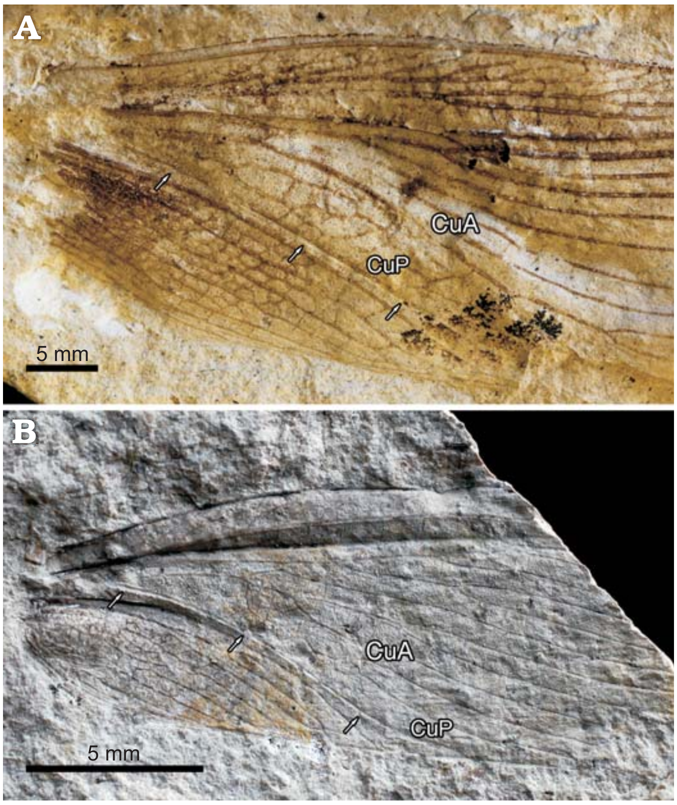

Fig. 8. Position of claval furrow on forewing (marked by arrows). **A**. *Homocladus grandis* Carpenter, 1966 from Artinskian of Elmo, Kansas, USA, paratype MCZ 5875. **B**. *Paracladus retardus* Carpenter, 1966 from Artinskian of Elmo, Kansas, USA, holotype MCZ 5877. CuA/P, cubitus anterior/posterior.

tically (as in Holometabola). The first anal vein is convex, but not especially more than in Paoliida or a Dictyoptera; (xv) AA2+3 and AP basally fused with several parallel forks. This is an autapomorphy of Neoptera; (xvi) network present as a mix of slightly irregular fine cross-veins and fine reticulum. This character is clearly not shared by all “Strephocladidae”, at least absent in the type genus of the family; (xvii) pseudo-veins present. This character is clearly not shared by all “Strephocladidae”; large macrotrichia present on veins (as in Neuroptera). This is a very doubtful character, generally not visible in all these fossils, and even not visible in the photographs of *Adiphlebia* proposed by Kukalová-Peck and Beutel (2012); (xviii) wing membrane covered with dense microtrichia (as in many lineages of Neoptera). Same remark: this is a doubtful character, generally not visible in all these fossils.

In summary, no clear synapomorphy supports the attribution of the Anthracoptilidae (= Strephocladidae = Strephoneuridae) to the Holometabola.

Eoblattida hypothesis.—Gorochov (2013) also criticized the works of Béthoux and Wieland (2009) and Béthoux et al. (2010), suggesting that “*Mesoptilus* has the same type of tegminal venation (including preservation of the distal fusion of Sc and RA stocks) as many typical representatives of the Palaeozoic order Eoblattida” (= Cnemidolestodea sensu Béthoux, 2005a). As already indicated above, the “Eoblattida” strongly differs from the Anthracoptilidae in the organisation of the cubital veins (convex CuA fused with M and re-emerging distally with a concave branch of CuP reaching distal convex part of CuA in the former group while convex CuA and concave CuP emerging from a common stem in the latter group). Gorochov (2013) ignored the work of Kukalová-Peck and Beutel (2012) and neglected the arguments based on the convexity versus concavity of the different veins. Therefore his argumentation does not stand.

New hypothesis: Anthracoptilidae belong to Paoliida, sister group of Dictyoptera.—After extensive studies on the family Paoliidae (Prokop and Nel 2007; Prokop et al. 2012), Prokop et al. (2014a) proposed a sister group relationships between Paoliida (Paoliidae + Blattinopsidae) and the Dictyoptera, based on: presence of anteriorly concave branches of CuA (synapomorphy). They noted that another shared character is the presence of a convex and short “arculus” between concave M and convex CuA, but this character is likely to belong to the ground plan of Neoptera. One of the most typical characters of the Anthracoptilidae is the presence of a convex main stem Cu with CuA emitting several less convex anterior branches. Further characters also present in Paoliida and Dictyoptera (at least in some taxa in these clades) are: presence of posterior apical branches of RA (*Silesiapteron jarmilae* Prokop, Krzeminski, Krzeminska, Hörnschemeyer, Ilger, Brauckmann, Grandcolas, and Nel 2014a), a brace between RP and median vein (*Protoblattinopsis stubblefieldi* Laurentiaux, 1953). Therefore we propose that the Anthracoptilidae could belong to a clade Paoliida (paoliidan synapomorphy: presence of a dense net of veinlets and irregular cells in subcostal area between ScP and C), sister group of Dictyoptera (dictyopteran synapomorphy: deeply concave CuP). The Anthracoptilidae would then be the sister group of the (Paoliidae + Blattinopsidae) in Paoliida, with the anthracoptilid synapomorphies “presence of brace between median vein and RP”, “numerous concave anterior branches of CuA”, while the latter two families (Paoliidae + Blattinopsidae) would be supported by the synapomorphies “no anal fan in hindwing” (an anal fan is likely to be present in Anthracoptilidae after the general shape of hindwing in some of them; viz. *Strephoneura tenebrosa* Novokshonov and Aristov, 2004), even if this structure is badly preserved in the known fossils), “a broad area between CuP and CuA with convex posterior branches of CuA”, and a “more straight CuP than in Anthracoptilidae”. A further possible synapomorphy of the Anthracoptilidae could be a shortened ScP, even if this vein can be rather long in some taxa currently attributed to this family (viz. *Pseudomesoptilus*, *Jarmilacladus*). The Paoliidae are supported by the presence of a “very broad area between CuP and CuA” and the Blattinopsidae by the presence of “a transverse median fold in mid part of fore wing”, plus the “branches of main veins parallel”, this later character being convergently present in some Anthracoptilidae, but not all.

The hindwing described under the name *Stenaropodites mistshenkoi* Storozhenko, 1992 has a series of anterior branches of CuA identical to what can be observed in the Anthracoptilidae, as can be compared between Storozhenko (1998: fig. 206) and Béthoux et al. (2010: figs. 4.1 and 4.2). Prokop et al. (2014a) proposed to transfer *Stenaropodites* into the Paoliidae, as the forewing described under the name *Stenaropodites reticulata* Martynov, 1928 or *S. sojanensis* Storozhenko, 1992 have venations typical of this family. The unique difference of *Stenaropodites mistshenkoi* with an Anthracoptilidae is the longer ScP. The presence of the pattern of CuA typical of the Anthracoptilidae in a taxon attributable to the paoliids support the hypothesis if close relationships between the two groups.

The few known heads of Paoliidae are hypognathous of triangular shape with mouthparts directed as in the Anthracoptilidae, which would also support possible affinities, but these structures are too imperfectly known to give accurate conclusions (Ilger and Brauckmann 2008; JP personal observation of specimens *Kemperala hagenensis* Brauckmann, 1984).

Prokop et al. (2014a) proposed to include the taxon *Protoblattinopsis stubblefieldi* Laurentiaux, 1953 in Paoliidae. It shares with the Anthracoptilidae the presence of a brace between median vein and RP but it has a broad area between CuP and CuA with numerous posterior branches but only one anterior branch of CuA. *Silesiapteron jarmilae* shares with the Anthracoptilidae the presence of three concave anterior branches of CuA plus three apical convex posterior branches of RA, and strongly approximate RP and median vein, but its area between CuP and CuA is very broad, with convex posterior branches of CuA. Thus the position of this taxon remains questionable in part.

Discussion

Position of *Opisthocladus*.—*Opisthocladus* Carpenter, 1976 (in family Tococladidae Carpenter, 1966, *O. arcuatus* Carpenter, 1976, and *O. strictus* Carpenter, 1976). Rasnitsyn and Aristov (2013: 686–687, figs. 11i, 12g, but not 11e) described a further species *Opisthocladus kargalensis* Rasnitsyn and Aristov, 2013. They considered that the separate status of the Tococladidae requires confirmation. The difficulty is that the other Tococladidae (type genus *Tococladus* Carpenter, 1966 and *Aviocladus* Prokop, Roques, and Nel, 2014) are archaeorthopterans with a convex CuA basally fused to R+M, and a concave branch of CuP between main CuP and CuA (Béthoux 2007; Prokop et al. 2014b). If, as indicated by Rasnitsyn and Aristov (2013), *Opisthocladus kargalensis* has a CuA independent of radial and median veins, then it would not fall in the Archaeorthoptera, and then it would not belong to the same family as *Tococladus*. *Opisthocladus* shares with the Anthracoptilidae the presence of a CuA completely separated from median vein (if the original interpretation of Carpenter 1976 is right), a m-cua brace, median vein approximating RP, ScP ending on RA, anterior branches of ScP, branches of main veins parallel (and maybe simple, although their portion near wing margin are not preserved). But the main difference is the CuA clearly posteriorly pectinate, but without anterior branches (Carpenter 1976). An attribution to the Anthracoptilidae would be weakly supported. The CuA of *Opisthocladus* is identical to that of a paoliid, associated with a broad area between CuP and CuA and a straight CuP. The only difference with paoliids is the shortened ScP. Nevertheless, the latter character is also present in genus *Katerinka* and some Camptoneuritidae (Prokop and Nel 2007; Aristov et al. 2010; Prokop et al. 2014a). *Opisthocladus* could as well belong to the Paoliidae, but its formal transfer into this last family can be decided only after the verification of the situation of the pattern of the CuA at its base (common stem with CuP as paoliidan-dictyopteran character versus basal fusion with M as archaeorthopteran character).

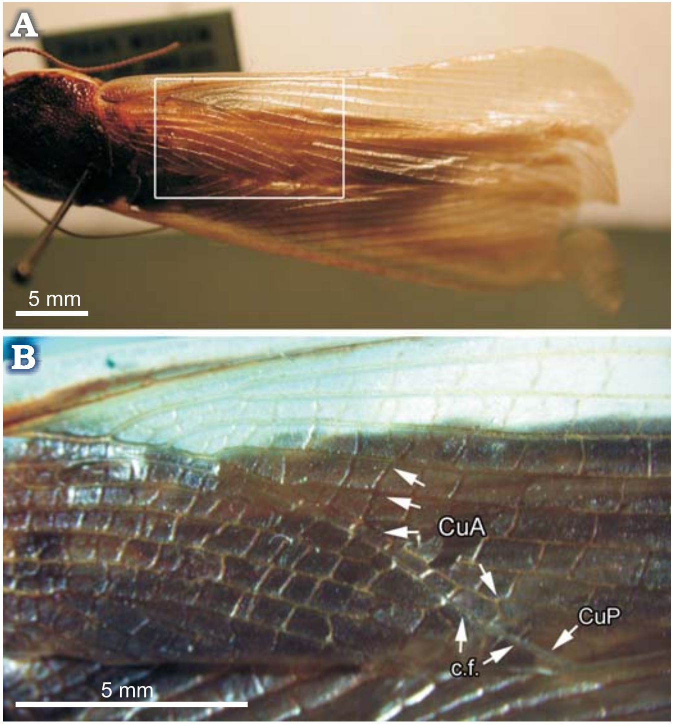

Fig. 9. Blaberid blattoid *Pilema thoracica* (Walker, 1868) Recent, specimen MNHN, Paris coll., Steynsburg, South Africa, R. Ellenberger leg, habitus (**A**), forewing basal part (**B**) with marked c.f., claval furrow; CuA/P, cubitus anterior/posterior.

Position of the Euryptilonidae Martynov, 1940.—The Euryptilonidae are currently considered as Grylloblattodea (Storozhenko 1998; Storozhenko 2002). *Euryptilon* Martynov, 1940 (type genus) and *Euryptilodes* Sharov, 1961 have an anteriorly pectinate CuA, and a CuA emerging from a common stem with CuP (see Sinitshenkova in Rasnitsyn and Quicke 2002: fig. 404), but they differ from the Anthracoptilidae in the fusion of CuA with M and re-separation of the two veins more distally (absence of a brace m-cua). Their very broad area between CuA and CuP is a synapomorphic character with the Paoliidae. Therefore the Euryptilonidae could be related to the Paoliida and the

Anthracoptilidae. Nevertheless Storozhenko (1998) included taxa in the Euryptilonidae that do not show the anterior pectination of CuA. This family needs a revision.

Convergencies between modern cockroaches and the Anthracoptilidae.—Some modern Blattodea show tegmina venation quite similar to those of the Anthracoptilidae, and especially to *Strephocladus*. It is especially the case for the blaberid genus *Pilema* Saussure, 1873 (see Fig. 9), that has a series of simple anterior branches of CuA, a M with few branches, RP with parallel and simple posterior branches, and a RA with short apical branches. The main difference between *Strephocladus* and *Pilema* is the more basal position of separation between CuA and CuP in the latter, plus the pectinate simple anterior branches of CuA being more convex than the main stem of CuA in *Pilema* instead of being in a contrary situation in *Strephocladus*. The blaberid genus *Salganea* Stål, 1877 shows also strong similarities with *Strephocladus* in the presence of a series of parallel simple branches of RP, M, and CuA, but it has not a pectinate series of anterior branches of CuA, unlike *Strephocladus* and *Pilema*. These blaberid cockroaches are either digging holes in dead wood or making tunnels in the ground. Generally the species with elongate and narrow tegmina live in dead wood. This would suggest a possible similar habitat for *Strephocladus*.

Conclusions

The systematic position of family Anthracoptilidae was unclear for nearly a century. We provide revisions of included taxa resulting in a new family definition. In addition we provide description of two new taxa from the Late Pennsylvanian and middle Permian localities in France. We consider the Anthracoptilidae as a clade belonging to paoliidan lineage (sister group of Dictyoptera) mainly due to presence of a dense net of veinlets and irregular cells in subcostal area between veins ScP and C, RA ending with several terminal branches, convex stem Cu basally separated from M, CuA with less convex anterior branches, and deeply concave CuP (dictyopteran synapomorphy). According to our concept the Anthracoptilidae ranges from Bashkirian (Early Pennsylvanian) to Lopingian (late Permian) with peak in diversity in Gzhelian (Late Pennsylvanian). Records of their members concentrated to the Euramerican sites are overestimated by rich sampling followed by taxa from Russian and Australian localities may indicate their possible cosmopolitan distribution during Palaeozoic.

Acknowledgements

We are grateful to Andrew Ross (National Museum of Scotland, Edinburgh, UK) and editorial board of APP for constructive comments and improvements. We thank the President and Fellows of Harvard College for permission to use MCZ copyrighted material. We thank to Philip Perkins (Museum of Comparative Zoology at Harvard University, Cambridge, USA) who allowed studying and provided permission to take photographs of the type specimens from Frank Morgan Carpenter's collection housed in the Museum of Comparative Zoology at Harvard University (Cambridge, USA). We sincerely thank Philippe Grandcolas (Muséum National d'Histoire Naturelle, Paris, France) for his kind help in providing information and material of modern Blattodea. JP expresses thanks for research support from the Grant Agency of the Czech Republic No. 14-03847J.

References

Aristov, D.S. 2014. Classification of the order Cnemidolestida (Insecta: Perlidea) with descriptions of new taxa. *Far Eastern Entomologist* 277: 1–46.

Aristov, D.S., Storozhenko, S.Yu., and Cui, Y.Y. 2010. Review of the Permian Camptoneuritidae Insecta: Grylloblattida). *Acta Geologica Sinica (English Edition)* 84: 756–761.

Bashkuev, A.S. 2010. New scorpionflies (Insecta: Mecoptera: Permochoristidae) from the Ufimian of Cisuralia. *Paleontological Journal* 44: 291–296.

Béthoux, O. 2005a. Cnemidolestodea (Insecta): an ancient order reinstated. *Journal of Systematic Palaeontology* 3: 403–408.

Béthoux, O. 2005b. Wing venation pattern of Plecoptera (Insecta: Neoptera). *Illiesia* 1: 52–81.

Béthoux, O. 2007. Cladotypic taxonomy applied: titanopterans are orthopterans. *Arthropod Systematics* and *Phylogeny* 65: 135–156.

Béthoux, O. 2009. The earliest beetle identified. *Journal of Paleontology* 83: 931–937.

Béthoux, O. and 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. and Wieland, F. 2009. Evidence for Carboniferous origin of the order Mantodea (Insecta: Dictyoptera) gained from forewing morphology. *Zoological Journal of the Linnean Society* 156: 79–113.

Béthoux, O., Beckemeyer, R.J., Engel, M.S., and Hall, J.D. 2010. New data on *Homocladus grandis*, a Permian stem-mantodean (Polyneoptera: Dictyoptera). *Journal of Paleontology* 84: 746–753.

Bolton, H. 1921. A monograph of the fossil insects of the British coal measures. *Palaeontological Society Monograph London* 73: 1–80.

Brongniart, C. 1893. Recherches pour servir à l'histoire des insectes fossiles des temps primaires précédées d'une étude sur la nervation des ailes des insectes. *Bulletin de la Société d'Industrie Minérale de Saint-Etienne* (3) 7: 124–615.

Brauckmann, C. 1984. Weitere neue Insekten (Palaeodictyoptera: Protorthoptera) aus dem Namurium B von Hagen-Vorhalle. *Jahresberichte des Naturwissenschaftlichen Vereins in Wuppertal* 37: 108–115.

Carpenter, F.M. 1966. The Lower Permian insects of Kansas. Part 11. The orders Protorthoptera and Orthoptera. *Psyche* 73: 46–88.

Carpenter, F.M. 1976. The Lower Permian insects of Kansas. Part 12. Protorthoptera (continued), Neuroptera, additional Palaeodictyoptera, and families of uncertain position. *Psyche* 83: 336–376.

Carpenter, F.M. 1992. Arthropoda 4, superclass Hexapoda*. In*: R.C. Moore and R.L. Kaesler (eds.), *Treatise on Invertebrate Paleontology*, 1–655. The Geological Society of America and the University of Kansas, Boulder.

Engel, M.S., Davis, S.R., and Prokop, J. 2013. Insect wings: The evolutionary development of Nature's first flyers. *In*: A. Minelli, G. Boxshall, and G. Fusco (eds.), *Arthropod Biology and Evolution—Molecules, Development, Morphology*, 269–298. Springer, Heidelberg.

Gorochov, A.V. 2013. No evidence for Paleozoic origin of mantises (Dictyoptera: Mantina). *Zoosystematica Rossica* 22: 6–14.

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

Handlirsch, A. 1922. *Animalia Insecta Palaeozoica. Fossilium Catalogus*. 230 pp. W. Junk, Berlin.

Hennig, W. 1981. *Insect Phylogeny*. 514 pp. J. Wiley and Sons, Chichester.

Ilger, J.-M. and Brauckmann, C. 2008. Evidence for prothoracic winglets in *Kochopteron hoffmannorum* from Hagen-Vorhalle ("basal Neoptera"; early Late Carboniferous; Germany). *Entomologia Generalis* 31: 279–285.

Illies, J. 1960. Penturoperlidae, eine neue Plecopteren Familie. *Zoologischer Anzeiger* 164: 26–41.

Kliver, M. 1883. Über einige neue Blattinarien, zwei Dictyoneura und zwei Arthropleura-Arten aus der Saarbrücker Steinkohlenformation. *Palaeontographica* 29: 249–269.

Kukalová, J. 1965. Permian Protelytroptera, Coleoptera and Protorthoptera (Insecta) of Moravia. *Sborník geologických věd: Paleontologie* 6: 61–95.

Kukalová-Peck, J. 1991. Fossil history and the evolution of hexapod structures. *In*: I.D. Naumann (ed.), *The Insects of Australia, a Textbook for Students and Research Workers* (2nd edition), 141–179. Melbourne University Press, Melbourne.

Kukalová-Peck, J. 2008. Phylogeny of higher taxa in Insecta: finding synapomorphies in the extant fauna and separating them from homoplasies. *Evolutionary Biology* 35: 4–51.

Kukalová-Peck, J. and Beutel, R.G. 2012. Is the Carboniferous †*Adiphlebia lacoana* really the "oldest beetle"? Critical reassessment and description of a new Permian beetle family. *European Journal of Entomology* 109: 633–645.

Lameere, A. 1917. Révision sommaire des Insectes fossiles du Stéphanien de Commentry. *Bulletin du Museum National d'Histoire Naturelle, Paris* 23: 141–200.

Laurentiaux, D. 1953. Classe des insectes (Insecta Linné, 1758). *In*: J. Piveteau (ed.), *Traité de Paléontologie*, 397–527. Masson, Paris.

Martynov, A.V. 1931. New fossil insects from Tikhie Gory. 2. Neoptera (excluding Miomoptera) [in Russian]. *Trudy Geologičeskogo Muzeâ, Akademii nauk SSSR* 8: 149–212.

Martynov, A.V. 1928. Permian fossil insects of North-East Europe. *Trudy Geologičeskogo Muzeâ, Akademii nauk SSSR* 4: 1–118.

Martynov, A.V. 1938. Etude sur l'histoire géologique et de phylogénie des ordres des insectes (Pterygota). Première partie. Palaeoptera et Neoptera—Polyneoptera [in Russian, with French summary]. *Trudy Paleontologičeskogo Instituta Akademii nauk SSSR, Moskva* 7 (4): 1–149.

Martynov, A.V. 1940. Permian fossil insects from Tshekarda [in Russian, with English summary]. *Trudy Paleontologičeskogo Instituta Akademii nauk SSSR* 11: 1–62.

Meunier, F. 1909. Nouveaux insectes du Stéphanien de Commentry. *Bulletin du Museum National d'Histoire Naturelle* 15: 37–49.

Nel, A. and Prokop, J. 2009. Go to the species in paleoentomology: illusion or necessity. *Mémoires de la Société Entomologique de France* 8: 49–55.

Nel, A., Prokop, J., Nel, P., Grandcolas, P., Huang, Di-ying, Roques, P., Guilbert, E., Dostál, O., and Szwedo, J. 2012. Traits and evolution of wing venation pattern in paraneopteran insects. *Journal of Morphology* 273: 480–506.

Novokshonov, V.G. 1998. New fossil insects (Grylloblattida; Caloneurida; Hypoperlida?; *ordinis incertis*) from the Kungurian beds of the Middle Urals. *Paleontological Journal* 32: 362–368.

Novokshonov, V.G. and Aristov, D.S. 2004. New taxa of hypoperlids (Insecta: Hypoperlida) from the Upper Permian of the Arkhangelsk Region. *Paleontological Journal* 38: 60–66.

Prokop, J. and Nel, A. 2004: A new genus and species of Homoiopteridae from the Upper Carboniferous of the Intra-Sudetic Basin, Czech Republic (Insecta: Palaeodictyoptera). *European Journal of Entomology* 101: 583–589.

Prokop, J. and Nel, A. 2007. An enigmatic Palaeozoic stem-group: Paoliida, designation of new taxa from the Upper Carboniferous of the Czech Republic (Insecta: Paoliidae, Katerinkidae fam. n.). *African Invertebrates* 48: 77–86.

Prokop, J., Krzemiński, W., Krzemińska, E., and Wojciechowski, D. 2012. Paoliida, a putative stem-group of winged insects: morphology of new taxa from the Upper Carboniferous of Poland. *Acta Palaeontologica Polonica* 57: 161–173.

Prokop, J., Krzeminski, W., Krzeminska, E., Hörnschemeyer, T., Ilger, J.-M., Brauckmann, C., Grandcolas, P., and Nel, A. 2014a. Late Palaeozoic Paoliida is the sister group of Dictyoptera (Insecta: Neoptera). *Journal of Systematic Palaeontology* 12: 601–622.

Prokop, J., Roques, P., and Nel, A. 2014b. New non-holometabolous insects from Pennsylvanian of Avion locality in Pas-de-Calais, France (Insecta: "Exopterygota"). *Alcheringa* 38: 155–169.

Rasnitsyn, A.P. 1977. New Paleozoic and Mesozoic Insecta. *Paleontological Journal* 11 (for 1978): 60–72.

Rasnitsyn, A.P. 2002. Superorder Hypoperlidea Martynov, 1928. Order Hypoperlida Martynov, 1928. *In*: A.P. Rasnitsyn and D.L.J. Quicke (eds.), *History of Insects*, 111–115. Kluwer Academic Publishers, Dordrecht.

Rasnitsyn, A.P. and Aristov, D.S. 2004. Two new insects from the Upper Permian (Tatarian) of Belmont (NSW, Australia) (Insecta: Hypoperlida: Anthracoptilidae = Strephocladidae; Grylloblattidae: Phenopteridae). *Paleontological Journal* 38: 158–163.

Rasnitsyn, A.P. and Aristov, D.S. 2013. New fossil insects (Insecta: Caloneurida, Hypoperlida, Palaeomanteida, Jurinida) from the Middle and Upper Permian of European Russia. *In*: D.S. Aristov, A.S. Bashkuev, V.K. Golubev, A.V. Gorochov, E.V. Karasev, D.S. Kopylov, A.G. Ponomarenko, A.P. Rasnitsyn, D.A. Rasnitsyn, N.D. Sinitshenkova, I.D. Sukatsheva, and D.V. Vassilenko (eds.), Fossil Insects of the Middle and Upper Permian of European Russia. *Paleontological Journal* 47: 678–703.

Rasnitsyn, A.P. and Quicke, D.L.J. 2002. *History of Insects*. xi + 517 pp. Kluwer Academic Publishers, Dordrecht.

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

Saussure, H. de 1873. Études sur les Myriapodes et les insectes. Famille des Mantides. *In*: H. de Saussure (ed.), *Recherches Zoologiques pour servir à l'histoire de la Faune de l'Amerique Centrale et du Mexique, Vol. 6*, 202–295. Imprimerie Impériale, Paris.

Scudder, S.H. 1885. Systematische Übersicht der fossilen Myriapoden, Arachnoiden und Insekten. *In*: K.A. Zittel (ed.), *Handbuch der Paläontologie, 1 Abtheilung, Paläozoologie* 2, 721–831. Oldenbourg, München.

Stål, C. 1877. Orthoptera nova ex Insulis Philippinis descripsit. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* 34: 33–37.

Storozhenko, S.Yu. 1992. Permian fossil insects of North-East Europe—new and little-known Ideliidae (Insecta, Plecopteroidea, Grylloblattida). *Entomologica Fennica* 3: 21–39.

Storozhenko, S.Yu. [Storoženko, S.Û.] 1998. *Systematika, filogeniâ i evolûtsiâ grilloblattidovyh nasekomyh (Insecta: Grylloblattida)*. 207 pp. Dal'nauka, Vladivostok.

Waterlot, G. 1934. *Études des gîtes minéraux de la France. Bassin houiller de la Sarre et de la Lorraine. Vol. 2. Faune fossile, Étude de la faune continentale du terrain houiller Sarro-lorrain*. 320 pp. Imprimerie L. Danel, Lille.

Wootton, R.J. 1979. Function, homology and terminology in insect wing. *Systematic Entomology* 4: 81–93.

Ward, P., Labandeira, C., Laurin, M., and Berner, R.A. 2006. Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization. *Proceedings of the National Academy of Sciences* 103: 16818–16822.

Zhang, Z.-J., Schneider, J.W., and Hong, Y.-C. 2013. The most ancient roach (Blattodea): a new genus and species from the earliest Late Carboniferous (Namurian) of China, with a discussion of the phylomorphogeny of early blattids. *Journal of Systematic Palaeontology* 11: 27–40.