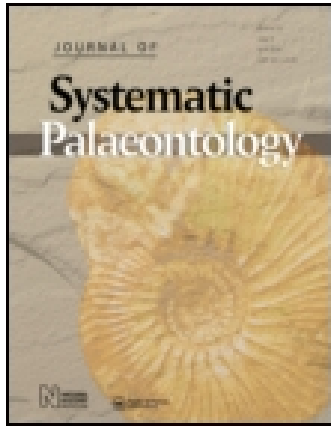


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Some palaeozoic 'protorthoptera' are 'ancestral' orthopteroids: Major wing braces as clues to a new split among the 'protorthoptera' (Insecta)

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SOME PALAEOZOIC ‘PROTORTHOPTERA’ ARE ‘ANCESTRAL’ ORTHOPTEROIDS: MAJOR WING BRACES AS CLUES TO A NEW SPLIT AMONG THE ‘PROTORTHOPTERA’ (INSECTA)

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SYNOPSIS The Archaeorthoptera is an apomorphy-based supra-ordinal clade of insect that mainly comprises the extant order Orthoptera and the fossil orders Caloneurodeia and Titanoptera. Our knowledge of this group is, however, incomplete because some taxa assigned to the paraphyletic group ‘Protorthoptera’ have not been accurately described. Here we describe or re-describe Carboniferous material assigned to *Omalia macroptera* Van Beneden & Coemans, 1867, *Coselia palmiformis* Bolton, 1922, *Palaeomastax carbonis* Handlirsch, 1904, *Omalietta ramosa* n. gen. & n. sp., *Eoblatta robusta* (Brongniart, 1885), *Ctenoptilus elongatus* (Brongniart, 1893) n. comb., *Ischnoptera diaphanes* n. gen. & n. sp., *Protodiamphipnoa gaudryi* (Brongniart, 1885), *Cnemidolestes woodwardi* (Brongniart, 1893), *Ischnoneura oustaleti* (Brongniart, 1885), *Narkeminopsis eddi* Whalley, 1979 and *Bouleites latipennis* Lameere, 1917. These taxa are all assigned to the Archaeorthoptera, based on the presence of characteristic features in their wing venation. A new system of homologies of the median system is proposed, which implies the loss of vein MP has occurred in some of these taxa. Our new data demonstrate the weakness of the previous specific, generic, familial and ordinal taxonomies.

KEY WORDS Insecta, Pterygota, Archaeorthoptera, Orthoptera, Carboniferous

Contents

Introduction	286
Material and methods	286
Systematic palaeontology	287
Super-order ARCHAEORTHOPTERA Béthoux & Nel, 2002	287
Genus <i>Omalia</i> Van Beneden & Coemans, 1867	287
<i>Omalia macroptera</i> Van Beneden & Coemans, 1867	287
Genus <i>Coselia</i> Bolton, 1922	288
<i>Coselia palmiformis</i> Bolton, 1922	288
Genus <i>Palaeomastax</i> Handlirsch, 1904 (stat. rest.)	289
<i>Palaeomastax carbonis</i> Handlirsch, 1904 (stat. rest.)	289
Genus <i>Omalietta</i> gen. nov.	289
<i>Omalietta ramosa</i> gen. et sp. nov.	290
Genus <i>Eoblatta</i> Handlirsch, 1906	290
<i>Eoblatta robusta</i> (Brongniart, 1893)	290
Genus <i>Ctenoptilus</i> Lameere, 1917 (= <i>Eoblattina</i> Bolton, 1925 syn. nov.)	291
<i>Ctenoptilus elongatus</i> (Brongniart, 1893) comb. nov.	293
Genus <i>Ischnoptera</i> gen. nov.	293
<i>Ischnoptera diaphanes</i> gen. et sp. nov.	293
Genus <i>Protodiamphipnoa</i> Brongniart, 1885	296
<i>Protodiamphipnoa gaudryi</i> (Brongniart, 1885)	296
Genus <i>Cnemidolestes</i> Handlirsch, 1906 stat. rest.	302

<i>Cnemidolestes woodwardi</i> (Brongniart, 1893) stat. rest.	303
Genus <i>Ischnoneura</i> Brongniart, 1893	304
<i>Ischnoneura oustaleti</i> (Brongniart, 1885)	304
Genus <i>Narkeminopsis</i> Whalley, 1979	305
<i>Narkeminopsis eddi</i> Whalley, 1979	305
Genus <i>Bouleites</i> Lameere, 1917	306
<i>Bouleites latipennis</i> Lameere, 1917	306
Conclusions	308
Acknowledgments	308
References	308

INTRODUCTION

Carpenter (1992) has provided the most recent assessment of the insect ordinal group 'Protorthoptera' Handlirsch, 1906*a, b*. He emended the concept of this group by including the former Protorthoptera, Protoblattodea and Paraplecoptera (see Carpenter, 1992 for a complete history of the usage of these taxa). His opinion on what Protorthoptera represent is very clear: 'a diverse assemblage of Palaeozoic species with presumed orthopteroid affinities'. Carpenter's Protorthoptera has since been accepted in several modern evolutionary studies (Labandeira & Sepkoski 1993; Jarzembowski & Ross 1996).

Since Carpenter's publication, most researchers have attempted to distribute 'protorthopterous' representatives into other recognised taxa. Kukulová-Peck & Brauckmann (1992) proposed 'hemipteroid' affinities for certain protopterans, mainly based on an assumed fusion of MA with R near the wing base. Béthoux & Nel (2002) reviewed the available data and rejected this hypothesis, showing that at least some of the presumed 'protorthopterous hemipteroids' have 'orthopteroid' affinities.

In the collegial synthesis of the 'Russian school' (Belayeva *et al.* 2002), the 'Protorthoptera' is broken up and its constituents assigned to the orders Blattinopseida Bolton, 1925, Paoliida Handlirsch, 1906*b*, Eoblattida Handlirsch, 1906*b* and Grylloblattida Walker, 1914. However, the definition of these last three orders is not clear since the order Paoliida has no proposed apomorphy (Rasnitsyn 2002*a*), the order Eoblattida is considered to be a 'mixture of stem and insufficiently known Carboniferous fossils' (Rasnitsyn 2002*b*), no apomorphy supports the order Grylloblattida (Storozhenko 2002), and the superorder Perlidea including the Grylloblattida 'might take an ancestral state in respect to Gryllidea and so might have no synapomorphies of their own' (Rasnitsyn 2002*c*). Furthermore, the order Blattinopseida (which includes only one family) is considered under this hypothesis to be a sister-group to the Caloneurodea Handlirsch, 1937. Béthoux & Nel (2002) and Béthoux *et al.* (2004) rejected this hypothesis and included the Caloneurodea in the Panorthoptera, e.g. as closely related to Orthoptera. Thus, the order Blattinopseida has no clear supra-ordinal assignment. Finally, the 'Russian school' proposals do not resolve the 'Protorthoptera' problem.

Béthoux & Nel (2002) proposed an alternative hypothesis concerning the position of some 'Protorthoptera'. They recognised the supra-ordinal Archaeorthoptera, a clade that includes the orders Orthoptera, Titanoptera, Caloneurodea and a part of the 'Protorthoptera'. The relationships of the

Palaeozoic to Mesozoic Phasmatodea and the Cenozoic to Recent Phasmida with these taxa are currently under debate (Tilgner 2001; Gorochov & Rasnitsyn 2002). Despite the clear apomorphies defining the Archaeorthoptera (complex fusions in the medio-cubital area), the composition and phylogenetic relationships of groups within this clade need further clarification because some older descriptions do not satisfy the requirements of modern cladistic methodology. Here, we redescribe some poorly known taxa assigned by Carpenter (1992) to the paraphyletic group 'Protorthoptera' that are here include in the Archaeorthoptera.

MATERIAL AND METHODS

The venation patterns and vein widths were drawn using a stereomicroscope and camera lucida direct from the fossil, dry and under alcohol. Both print and counter-print were used when available. Thus, in some cases, drawings show information not visible in the photographs. The final drawings were readjusted on photographs using image-editing software.

Some specimens were photographed under alcohol in order to make the original colouration of the wings more clearly visible. Only a very thin layer of alcohol was used to cover the specimens so that the relief to the wing veins remained visible. For some specimens, we have combined two photographs (termed 'combined' in figure captions), one under alcohol and one without, using image-editing software. When possible (depending on the relief of the rock containing the fossils), the relief of the wing veins is restored as if viewed dorsally, using a light-mirroring technique, usually lighting from the bottom right. Members of the Photographic Unit of the National History Museum (London) are responsible for photographs of specimens stored at that institution.

The specimens referred to as 'RBINS' are stored in the Department of Invertebrate Palaeontology of the Royal Belgian Institute of Natural Sciences, Brussels. Specimens referred to as 'MNHN-DHT-R' are stored in the Laboratory of Palaeontology of the Muséum National d'Histoire Naturelle, Paris. Specimens referred to as 'NHM' are stored in the Department of Invertebrate Palaeontology of the National History Museum, London. Specimens referred to as 'PIN' are stored in the Paleontological Institute of the Russian Academy of Russian Sciences, Moscow. Specimens referred to as 'MGL' are stored in the 'Musée Géologique de Lille', Lille (France). The material referred to as 'MCZ' is stored in the Museum of Comparative Zoology, Cambridge (MA, USA).

We have followed the nomenclature of insect wing venation elaborated for Archaeorthoptera (Béthoux & Nel

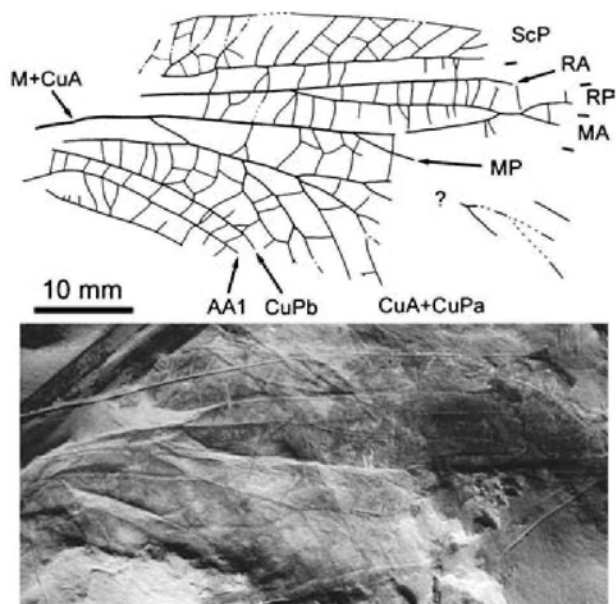


Figure 1 *Omalia macroptera* Van Beneden & Coemans, 1867 (RBINS a7687 holotype; Belgium; Upper Carboniferous): reconstruction and photograph (counter-print, light-mirrored, combined, reversed) of the right fore-wing. Abbreviations for wing venation: ScP, anterior subcosta; RA, anterior radius; RP, posterior radius; MA, anterior media; MP, posterior media; CuA, anterior cubitus; CuPa, anterior branch of posterior cubitus; CuPb, posterior branch of posterior cubitus; AA1, first anterior anal; M, media.

2002: ScA, anterior subcosta; ScP, posterior subcosta; R, radius; RA, anterior radius; RP, posterior radius; M, media; MA, anterior media; MP, posterior media; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; CuPa, anterior branch of CuP; CuPb, posterior branch of CuP; AA1: first anterior anal; AA2: second anterior anal). In the following descriptions the relief of veins is described as if viewed from a print, dorsal side.

The literature relating to the definition and composition of the relevant families is confused, thus we have decided to avoid any familial attributions here. A new familial taxonomy will require a cladistic analysis of the whole Archaeorthoptera.

SYSTEMATIC PALAEOONTOLOGY

Super-order **ARCHAEORTHOPTERA**

Béthoux & Nel, 2002

Genus **OMALIA** Van Beneden & Coemans, 1867

TYPE SPECIES. *Omalia macroptera* Van Beneden & Coemans, 1867.

DIAGNOSIS. Fore-wings: RP and MA very long before fusion; CuA + CuPa without clear pattern of branching.

REMARKS. Several fossils have been assigned to this genus, but we propose to restrict it to the species *Omalia macroptera* (Fig. 1) and to keep as distinct the genera *Coselia* and *Palaemastax* (see below). Some other assignments must be discussed.

The specimen assigned by Brauckmann *et al.* (2001) to *Omalia anae* Brauckmann *et al.*, 2001 is probably a hind-wing. This generic assignment is debatable. In the reconstruction of wing venation proposed by these authors, the specimen has branches CuPb and CuPa β (with a very short visible part of the branch CuPa α) typical of the Panorthoptera. Thus it cannot belong to the genus *Omalia*, since this genus lacks the typical feature of the Panorthoptera, i.e. the occurrence of a fork of CuPa basal of its fusion with CuA (in both fore- and hind-wings). Its position within the Panorthoptera will be discussed elsewhere.

Specimen MGL 4217 (Fig. 2: France, Pas-de-Calais basin; Upper Carboniferous, Westphalian A), was assigned by Laurentiaux (1949: fig. 2) to *Omalia macroptera*, but is here reassessed as *Omalia* sp. indet. It can be assigned to this genus because of the irregular branching pattern of CuA + CuPa. Its only distinctive character is the more basal location of the origin of RP, but this character is of unknown taxonomic significance given our poor knowledge of these insects.

Omalia macroptera Van Beneden & Coemans, 1867 (Fig. 1)

1867 *Omalia macroptera* Van Beneden & Coemans: 309 (with unnumbered figure).

1904 *Omalia macroptera* Handlirsch: 13, pl. V, fig. 21.

1919 *Omalia macroptera* Handlirsch: 552.

1922 *Omalia macroptera* Handlirsch: 89.

1930 *Omalia macroptera* Pruvost: 158, pl. VI, fig. 2, 2a.

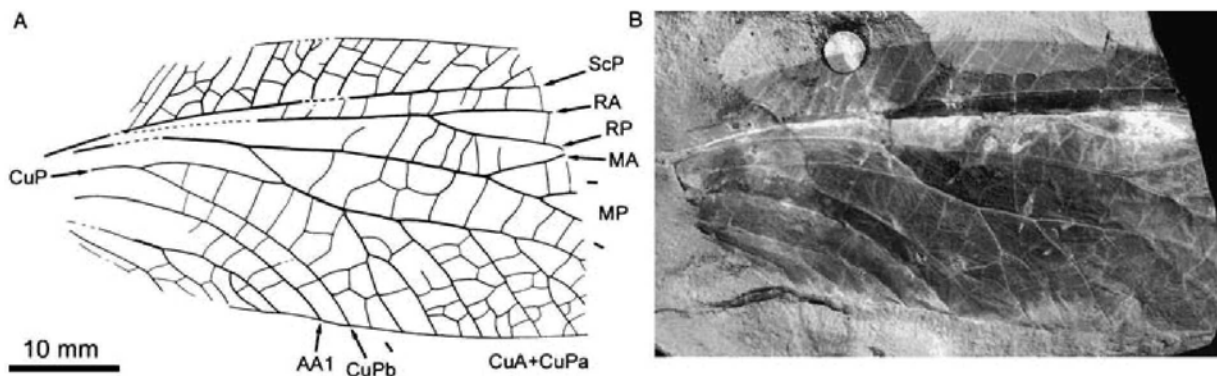


Figure 2 *Omalia* sp. ind. (MGL 4217: France; Upper Carboniferous). (A) Reconstruction and (B) photograph (counter-print, light-mirrored, combined) of the left fore-wing. For abbreviations see legend to Figure 1.

DIAGNOSIS. By monotypy, that of the genus.

MATERIAL. Holotype: Royal Belgian Institute of Natural Sciences a7687.

OCCURRENCE. Sars-Lonchamps, Mons Basin, Belgium (Van Beneden & Coemans 1867); Westphalian A, Upper Carboniferous (Pruvost 1930).

DESCRIPTION. Holotype is a counter-print of an incomplete right fore-wing, with wing base, posterior wing margin and most of distal half missing; wing surface with numerous small folds; preserved length about 54.5 mm, estimated width about 28.1 mm; area between anterior wing margin and ScP broad; RP very long (21.1 mm) basal of its connection with MA; connection of RP with MA 2.3 mm long; M 14.7 mm long basal to divergence of MA and MP; MA 20.8 mm long basal to its connection with RP, simple in its preserved part; distal parts of RA, RP, MA and MP not preserved; free part of CuA (from M + CuA) and CuA + CuPa distinctly convex; CuA + CuPa with a first posterior branch (itself branched), then trifurcate; distal part of CuA + CuPa folded, but it cannot be re-constructed with certainty; at the very least branches of CuA + CuPa distally branched; CuPa and CuPb concave, AA1 and AA2 convex; cross-veins without regular organisation, reticulated and sigmoidal in broad areas.

REMARKS. The assignment of *Omalia macroptera*, type-species of the family Omalidae, to the clade Archaeorthoptera, was first proposed by Béthoux & Nel (2002: 15) and is supported by our new observations, specifically by the characteristic reversal of relief of the main veins near the origin of the distal free part of CuA. Unfortunately, because *Omalia* is based on just one incomplete fore-wing, it is clearly insufficiently known to establish its phylogenetic relationships within the Archaeorthoptera with confidence. Only the branching pattern of CuA + CuPa is informative and suggests close relationships with the Protophasmatidae (for a revision of this family, see Béthoux 2003).

Genus *COSELIA* Bolton, 1922

1922 *Coselia* Bolton: 81.

1930 *Omalia* in part Pruvost: 157.

1949 *Omalia* in part Laurentiaux: 56.

1992 *Coselia* Carpenter: 122 (stat. rest.).

2002b *Coselia* Rasnitsyn: 259.

TYPE SPECIES. *Coselia palmiformis* Bolton, 1922.

DIAGNOSIS. Fore-wings: RP at least connected with MA; base of RP in a distal position, probably near mid-length of wing; RP moderately long basal to its connection with MA; CuA + CuPa posteriorly pectinate.

REMARKS. Bolton (1922: 82) noted that 'about 21 mm from the base the median [M + CuA in present interpretation] gives off a strong inward branch [CuA] passing obliquely to the cubitus [CuPa] and fused with it [into CuA + CuPa]'. Nevertheless, the drawing he provided is inaccurate concerning the relative widths of these veins. This 'branch' [CuA] is stronger than illustrated by Bolton and there is a reversal of the relief of the veins connected to it. Thus, this 'branch' is the free part of CuA emerging from M + CuA, typical of the archaeorthopterid pattern of venation.

Pruvost (1930), Laurentiaux (1949), Schmidt (1962) and Brauckmann & Hahn (1980) synonymised *Coselia* with

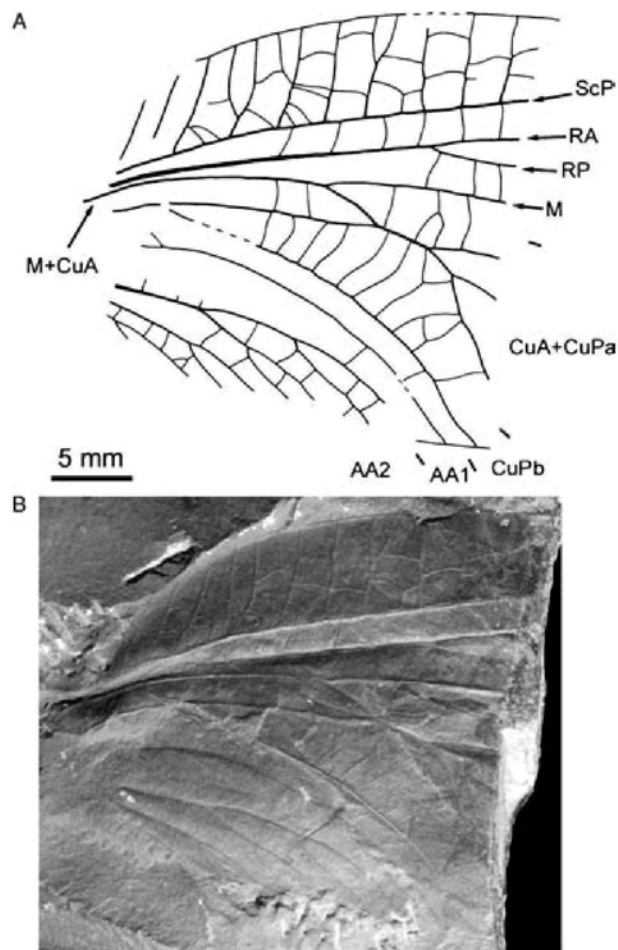


Figure 3 *Coselia palmiformis* Bolton, 1922 (NHM I.15893 holotype; United-Kingdom; Upper Carboniferous). (A) Reconstruction and (B) photograph (counter-print reversed and print under alcohol, combined) of the right fore-wing. AA2, second anterior anal. For all other abbreviations see legend to Figure 1.

Omalia. Nevertheless, the branching patterns of CuA + CuPa are very different in those taxa: it is not clearly organised in *Omalia* while it is regularly posteriorly pectinate in *Coselia*. The connection of MA with RP, which could be a potential synapomorphy of the two genera, is present in many other archaeorthopterid families. This connection differs markedly in the two genera: MA and RP are long basal to their connection in *Omalia* but shorter in *Coselia*.

The specimen assigned by Laurentiaux (1949: fig. 1) to *Omalia palmiformis* is assigned to the new genus and species *Omalietta ramosa* (see below).

Coselia palmiformis Bolton, 1922 (Fig. 3)

1922 *Coselia palmiformis* Bolton: 81, text-fig. 25, pl. 5, figs 3a–b.

1930 *Omalia (Coselia) palmiformis* Pruvost: 158.

1992 *Coselia palmiformis* Carpenter: 122.

DIAGNOSIS. By monotypy, that of the genus.

MATERIAL. Holotype: Natural History Museum, London I.15893.

OCCURRENCE. Coseley, Staffordshire, United Kingdom, Middle Coal Measures; Upper Carboniferous, Westphalian B-C (Belayeva *et al.* 2002).

DESCRIPTION. Holotype is a print and counter-print of an incomplete right fore-wing, with nearly half distal wing missing; preserved length 48.4 mm, width 26.4 mm; ScP hidden by R in basal part, due to preservation; ScP concave, anteriorly pectinate, with numerous simple branches; R and RA strongly convex; base of RP about 34.9 mm distal of wing base; RP basally sigmoidal, very probably fused with MA; RP 13.0 mm long before assumed point of fusion with MA; M + CuA, CuA and CuA + CuPa convex; origin of CuA from M + CuA about 18.4 mm distal of wing base; MA and MP diverging 21.9 mm distal of origin of CuA (from M + CuA); MA oblique, directed towards RP; MP forked 5.3 mm distal of its origin; CuA 4.7 mm long before fusion with CuPa; CuA + CuPa posteriorly pectinate, with five main branches in preserved part, first, fourth and fifth branches forked; concave CuPa long (13.3 mm) before fusion with CuA; concave CuPb and convex AA1 simple; AA2 branched; cross-veins in all areas of wing from straight to strongly sigmoidal, reticulated or not, without clear organisation.

Genus *PALAEOMASTAX* Handlirsch, 1904 (stat. rest.)

1904 *Palaeomastax* Handlirsch: 16.

1930 *Omalia* in part Pruvost: 157.

TYPE SPECIES. *Palaeomastax carbonis* Handlirsch, 1904.

DIAGNOSIS. Fore-wings: M simple at length; absence of cross-veins between branches of ScP; divergence of RA and RP in a distal position; CuA + CuPa posteriorly pectinate.

Palaeomastax carbonis Handlirsch, 1904 (stat. rest.) (Fig. 4)

1904 *Palaeomastax carbonis* Handlirsch: 16, pl. VII, figs 27–28.

1919 *Palaeomastax carbonis* Handlirsch: 552.

1922 *Palaeomastax carbonis* Handlirsch: 89.

1930 *Omalia carbonis* Pruvost: 159, pl. VI, figs 3, 3a–b.

1992 *Omalia carbonis* Carpenter: 121.

DIAGNOSIS. By monotypy, that of the genus.

MATERIAL. Holotype: Royal Belgian Institute of Natural Sciences a7700.

OCCURRENCE. Frameries, Belgium; Westphalian C, Upper Carboniferous (Pruvost 1930).

DESCRIPTION. Holotype is a print and counter-print of an incomplete left fore-wing, with wing base, nearly all distal half and posterior wing margin missing; preserved length about 31.2 mm, estimated width about 16.0 mm; area between anterior wing margin and ScP broad (3.2 mm); no cross-veins between branches of ScP; M simple at length (for 18.0 mm in preserved part); M + CuA, CuA and CuA + CuPa distinctly convex; CuA + CuPa posteriorly pectinate, with at least five posterior branches, themselves simple, branched or reticulated; CuPa and CuPb concave, AA1 and AA2 convex; most cross-veins sigmoidal.

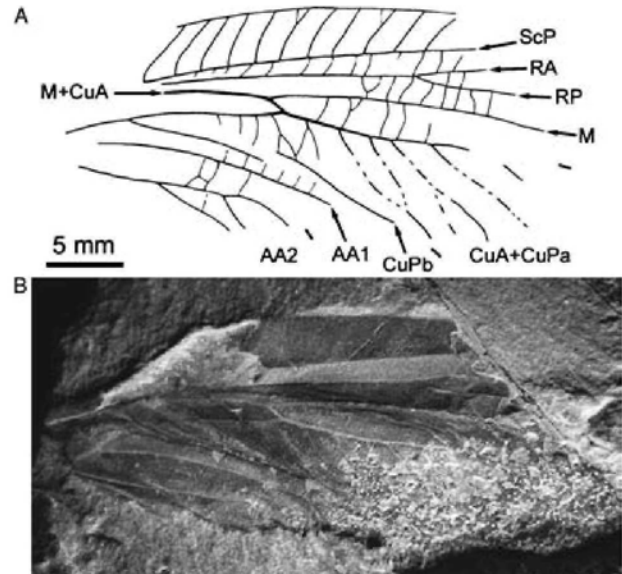


Figure 4 *Palaeomastax carbonis* Handlirsch, 1904 (RBINS a7700 holotype: Belgium; Upper Carboniferous). (A) Reconstruction and (B) photograph (counter-print, light-mirrored) of the left fore-wing. AA2, second anterior anal. For all other abbreviations see legend to Figure 1.

REMARKS. Several authors have synonymised *Palaeomastax* with *Omalia* (Pruvost 1930; Carpenter 1992). However, preparation of the specimen (O.B., March 2003) revealed additional information on the branching pattern of CuA + CuPa and the long simple basal part of M. This revealed that *Palaeomastax* has a very distal branching of M (if branched) and a CuA + CuPa that is posteriorly pectinate, all features in contradiction with placement in *Omalia*.

Pruvost (1930) also synonymised *Palaeomastax* with the genus *Coselia*. The two genera are probably closely related, but the more distal branching of M (if branched) as well as the absence of cross-veins between branches of ScP in *Palaeomastax* support generic separation.

Genus *OMALIELLA* gen. nov.

1949 *Omalia* in part Laurentiaux: 56, fig. 1.

TYPE SPECIES. *OmalIELla ramosa* sp. nov.

DIAGNOSIS. Fore-wings: RP long before its fusion with MA1; RP fused with MA1; CuA + CuPa posteriorly pectinate with numerous branches (at least 10 reaching the posterior wing margin).

REMARKS. Laurentiaux (1949) assigned specimen MGL 4247 (the holotype of *OmalIELla ramosa*; Fig. 5) to *Omalia palmiformis* (see Fig. 3). Nevertheless, the specimen differs from *Omalia* as follows: RP is fused with MA1 instead of with MA, RP is longer before its fusion with MA1 and after the more numerous branches of CuA + CuPa. In fact, the genus *OmalIELla* differs from all other Archaeorthoptera minus Panorthoptera because of this original combination of characters.

The assignment of *OmalIELla* to the Archaeorthoptera is based on indirect arguments. Since the wing base is unknown, the diagnostic medio-cubital structure of Archaeorthoptera

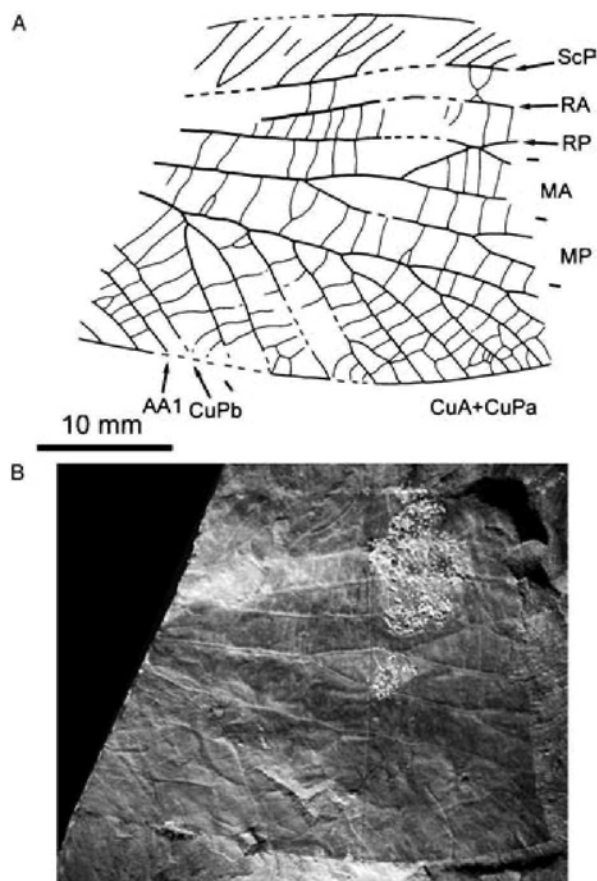


Figure 5 *Omaliella ramosa* gen. et sp. nov. (MGL 4247 holotype: France; Upper Carboniferous). (A) Reconstruction and (B) photograph (counter-print, reversed) of the right fore-wing. For abbreviations see legend to Figure 1.

cannot be demonstrated. *Omaliella* differs from the Blattodea and most Grylloblattodea because of the occurrence of a connection of RP with a branch of MA, something that is frequently seen in Archaeorthoptera. Moreover, *Omaliella* can be excluded from the Grylloblattodea because these insects have MP distinctly concave and a differentiation of CuA into CuA1 and CuA2, which is not the case in *Omaliella*. In most Blattodea, M is much more branched. Moreover, the pattern of cross-veins in *Omaliella* is very close to that of *Omalia* and *Coselia*. Consequently, *Omaliella* can probably be assigned to the Archaeorthoptera.

The closest known taxon is probably *Aenigmatella* Sharov, 1961. However, our knowledge of this last genus is very incomplete and its ordinal assignment is uncertain (Carpenter 1992; Rasnitsyn 2002b: 259). *Omaliella* differs from *Aenigmatella* by its more basal origin of MA1 and less oblique branches of CuA + CuPa (if *Aenigmatella* really has such a composite vein).

Omaliella ramosa gen. et sp. nov. (Fig. 5)

1949 *Omalia palmiformis* Laurentiaux: 56, fig. 1.

DIAGNOSIS. By monotypy, that of the genus.

TYPES. Holotype and only known specimen: Musée Géologique de Lille 4247.

OCCURRENCE. Pas-de-Calais Basin, France; Westphalien B, Upper Carboniferous (Laurentiaux 1949).

DESCRIPTION. Counter-print of an incomplete right fore-wing (apex and wing base missing); preserved length about 31 mm, width 27.4; RP long (21.5 mm in preserved part) before connection with MA1; origin of MA1 oblique (= MA and MA2 aligned); MA1 shortly fused with RP (0.8 mm); MP branched 13.1 mm after its origin; CuA + CuPa posteriorly pectinate, with at least 10 branches reaching posterior wing margin; branches of CuA + CuPa simple or forked; CuPb and AA1 simple.

Genus *EOBLATTA* Handlirsch, 1906

1885 *Leptoneura* in part, Brongniart: 62.

1893 *Stenoneura* in part, Brongniart: 429.

1906b *Eoblatta*, Handlirsch: 155, pl. 15, fig. 19.

TYPE SPECIES. *Eoblatta robusta* (Brongniart, 1893).

OTHER SPECIES. *Eoblatta zeilleri* Langiaux & Parriat, 1974. The holotype of *E. brongniarti* Lameere, 1917, figured by Brongniart (1893: pl. XLVIII(32), fig. 8), is too incomplete for reliable assignment. We consider it as Neoptera order uncertain.

DIAGNOSIS. Fore-wings: area between RA and RP very long and narrow; MA approximating RP or its first posterior branch; area between MP and the most anterior branch of CuA + CuPa narrow; CuA + CuPa without clear pattern of branching, with numerous branches covering a large area, distinctly larger than that of M.

REMARKS. Brongniart (1893) originally included *E. robusta* in the genus *Stenoneura*. Later, Handlirsch (1906b) transferred this species to the new genus *Eoblatta*. Carpenter (1992), followed by Béthoux & Nel (2002), assigned both genera to the family Stenoneuridae Handlirsch, 1906b. Béthoux & Nel (2002) restudied *Stenoneura fayoli* Brongniart, 1893, type species of the family Stenoneuridae Brongniart, 1893 and concluded that the Stenoneuridae are probably Panorthoptera, with the occurrence of a fork of CuPa into CuPa α and CuPa β . However, here we demonstrate that this fork is absent in *E. robusta* and, consequently, *Eoblatta* is not a Panorthoptera. We therefore exclude it from the Stenoneuridae.

The hind-wing morphology of *Eoblatta* is known based on the incomplete right hind-wing of *Eoblatta zeilleri* Langiaux & Parriat 1974 (see Langiaux & Parriat, 1974: illustration of exemplar 1).

Because Rasnitsyn (2002b) based his 'group' Eoblattida of ordinal rank on this genus, a formal re-description of the type species is provided.

Eoblatta robusta (Brongniart, 1893) (Figs 6–7)

1885 *Leptoneura robusta* Brongniart: 62 (*nomen nudum*).

1893 *Stenoneura robusta* in part Brongniart: 431, pl. XLVIII(32), figs 9, 10.

1906b *Eoblatta robusta* Handlirsch: 155, pl. 15, fig. 19.

1917 *Eoblatta robusta* Lameere: 172.

1919 *Eoblatta robusta* Handlirsch: 560.

1922 *Eoblatta robusta* Handlirsch: 99.

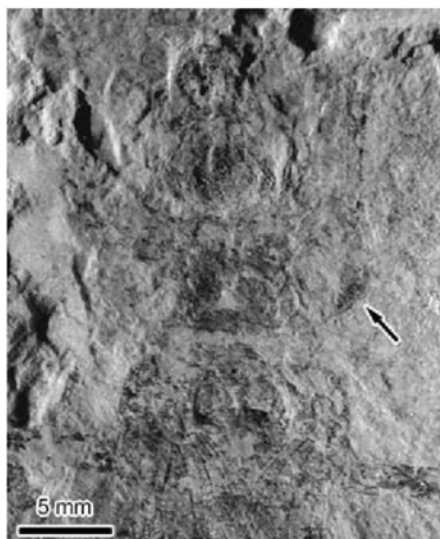


Figure 6 *Eoblatta robusta* (Brongniart, 1885) (MNHN-DHT-R51344 holotype; France; Upper Carboniferous). Photograph (combined) of the head, prothorax and mesothorax; arrows indicate the lateral expansion of the prothorax.

1992 *Eoblatta robusta* Carpenter: 129, fig. 74.7.
2002b *Eoblatta robusta* Rasnitsyn: 257, fig. 353.

DIAGNOSIS. In fore-wings, first fork of CuA + CuPa distant from point of fusion of CuA with CuPa.

TYPES. Holotype: Muséum National d'Histoire Naturelle, Paris DHT-R51344.

OTHER MATERIAL. MNHN-DHT-R11466. Another specimen, NHM I.7278, which was assigned to *E. robusta* by Bolton (1925), is too poorly preserved to be identifiable. It is considered to be a Neoptera, order uncertain.

OCCURRENCE. Commentry Basin, Allier, France; Stephanian B-C, Upper Carboniferous (Doubinger & Vetter 1985).

DESCRIPTION. Holotype is a print and counter-print of an almost complete insect, with distal parts of legs, apical part of fore-wings and most of hind-wings missing or hidden by other remains; prothorax with lateral expansions (winglets?).

Fore-wings (description mainly based on right one): estimated length about 65.5 mm, width 19.0 mm; ScP long, probably reaching RA; ScP with numerous strong, oblique anterior veins, more or less reticulated; divergence of RA and RP about 12.6 mm distal to wing base; RA simple in preserved part; first fork of RP 20.2 mm distal to its origin; RA and RP closely parallel; RP posteriorly pectinate, with six main branches; most branches of RP forked at mid-length; origin of CuA from M + CuA about 10.7 mm distal of wing base; divergence of MA and MP 16.9 mm distal to origin of CuA; MA oblique at its origin, anteriorly directed, approximating RP and distally arched towards posterior wing margin; preserved part of MA simple; MP distally branched; some branches of MP connected with anterior branch of CuA + CuPa and probably with MA; CuA + CuPa branched 3.8 mm distal to its origin; CuA + CuPa with two main basal stems but without a clear pattern of ramification, with 19 distal branches, reaching CuPb, posterior wing margin,

or MP; CuPb simple; numerous anal veins, branched, not clearly discernable.

REMARKS. *Eoblatta robusta* differs from *E. zeilleri* in having its stem CuA + CuPa simple at length. Langiaux & Parriat (1974) advocated the wing shape as a specific relevant character (rounded in *E. robusta* versus, margins parallel at length in *E. zeilleri*), but the wings of *E. zeilleri* are incompletely preserved. Thus, this character must be used with care.

Genus **CTENOPTILUS** Lameere, 1917 (= *Eoblattina* Bolton, 1925 syn. nov.)

- 1917 *Ctenoptilus* Lameere: 180.
1919 *Ischnoneurula* Handlirsch: 541.
1919 *Ischnoneurilla* Handlirsch: 556.
1922 *Ctenoptilus* Handlirsch: 76.
1922 *Ischnoneurilla* Handlirsch: 95 (*Ischnoneurula* considered as a junior synonym of *Ctenoptilus*).
1925 *Eoblattina* Bolton: 19.
1992 *Ischnoneura* in part Carpenter: 130.
1992 *Ctenoptilus* Carpenter: 130.
1992 *Eoblattina* Carpenter: 132.
2002b *Ctenoptilus* Rasnitsyn: 258.

NOTE ON SYNONYMY LIST. The holotype of *Ctenoptilus elongatus* (Brongniart, 1893) comb. nov. (MNHN-DHT-R51216) was assigned by Brongniart (1893) to the genus *Ischnoneura*, but it differs from *I. oustaleti*, the type species of this genus, mainly by the pattern of ramification of CuA + CuPa (internally pectinate in *Ischnoneura*, with one main anterior branch in *Ctenoptilus*). This justifies generic separation.

Meunier (1911) assigned the holotype of *Ctenoptilus trouessarti* (Meunier, 1911), MNHN-DHT-R51392, to the genus *Homalophlebia* Brongniart, 1893. However, this specimen differs strongly from *Homalophlebia* and *Parahomalophlebia* (*Homalophlebiidae* Handlirsch 1906b; see Carpenter 1992: fig. 74.3 and Rasnitsyn 2002b: fig. 361) in having a fewer number of branches of MA and MP and more numerous branches of CuA + CuPa. Thus, we follow Lameere (1917) who created the genus *Ctenoptilus* to encompass this specimen.

The specimens MNHN-DHT-R51216 and MNHN-DHT-R51392 are here assigned to the same species based on the occurrence of a long and posteriorly pectinate anterior branch of CuA + CuPa. Also, the distal bifurcations of branches from CuA + CuPa, the very basal origin of RA and RP, the numerous and dense veins in the anal area and the cross-vein organisation, although shared by very different Archaeorthoptera, support their assignment to the same genus and species. *Ctenoptilus trouessarti* (Meunier, 1911) must therefore be considered as a junior synonym of *Ctenoptilus elongatus*.

Handlirsch (1919) created the genus *Ischnoneurilla* on the basis of the figures provided by Brongniart (1893) of the holotype of *Ctenoptilus elongatus* (MNHN-DHT-R51216). This genus is then a junior synonym of *Ctenoptilus*.

Bolton (1925) created the genus *Eoblattina* on the basis of specimen NHM I.7279 (from the same locality as previously cited specimens). Nevertheless, the diagnostic characters provided by this author all agree with those known in *Ctenoptilus*. Our new observations support this attribution.

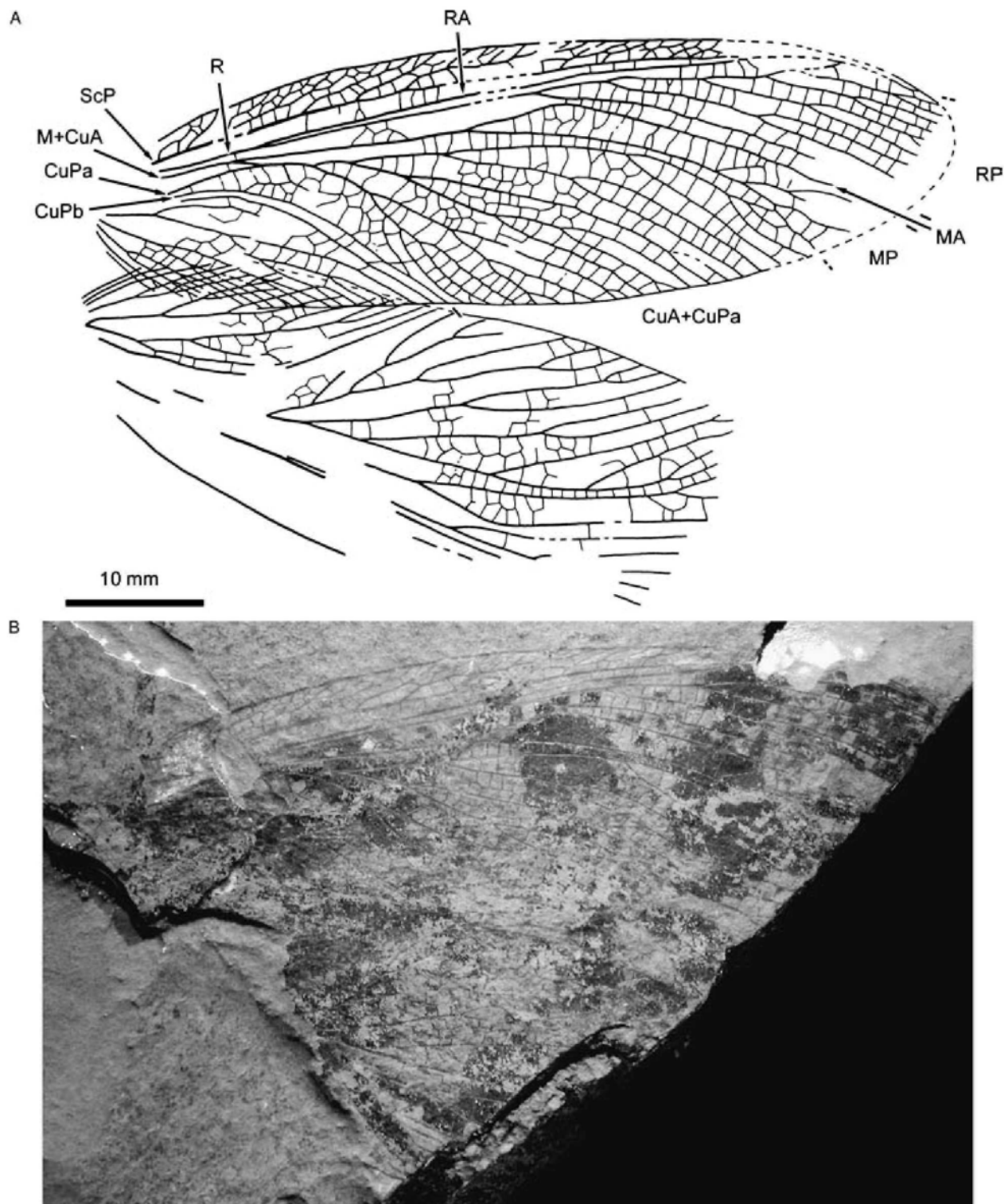


Figure 7 *Eoblatta robusta* (Brongniart, 1885) (MNHN-DHT-R51344 holotype; France; Upper Carboniferous). (A) Reconstruction (after print and counter-print) and (B) photograph (counter-print, reversed) of the fore-wings. R, radius. For other abbreviations see the legend to Figure 1.

TYPE SPECIES. *Ctenoptilus elongatus* (Brongniart, 1893) comb. nov.

DIAGNOSIS. Fore-wings: CuA + CuPa with one main anterior branch posteriorly pectinate and with more than 20 branches reaching posterior wing margin; CuA + CuPa covering about

the distal two-thirds of posterior wing margin; MP strongly concave; ScA long and well defined.

REMARKS. The genus *Ctenoptilus* can be assigned to the Archaeorthoptera because of the occurrence of medio-cubital fusions typical of this supra-ordinal clade (see Fig. 10).

Ctenoptilus elongatus (Brongniart, 1893) comb. nov. (Figs 8–11)

- 1885 *Leptoneura* (sp.?) Brongniart: pl. V, fig. 4 (specimen MNHN-DHT-R51071).
- 1893 *Ischnoneura elongata* Brongniart: 433, pl. XLVIII(32), fig. 12 (specimen MNHN-DHT-R51216).
- 1893 *Ischnoneura oustaleti*, in part Brongniart: in part, 433, pl. LII(36), figs 1–2 (specimen MNHN-DHT-R51071).
- 1911 *Homalophlebia trouessarti* Meunier: 126, fig. 11 (specimen MNHN-DHT-R51392).
- 1917 *Ctenoptilus trouessarti* Lameere: 180.
- 1917 *Ischnoneura elongata* Lameere: 174.
- 1919 *Ischnoneurula trouessarti* Handlirsch: 541.
- 1919 *Ischnoneurilla elongata* Handlirsch: 556.
- 1922 *Ctenoptilus trouessarti* Handlirsch: 76.
- 1922 *Ischnoneurilla elongata* Handlirsch: 95.
- 1925 *Eoblattina complexa* Bolton: 19, pl. II, fig. 6 (specimen NHM I.7279).
- 1992 *Ctenoptilus trouessarti* Carpenter: 130, fig. 12.
- 1992 *Eoblattina complexa* Carpenter: 132.
- 2002b *Eoblattina complexa* Rasnitsyn: 258, fig. 355.

DIAGNOSIS. By monotypy, that of the genus.

MATERIAL. Holotype: Muséum National d'Histoire Naturelle DHT-R51216. Other specimens: MNHN-DHT-R51392, MNHN-DHT-R51071, MNHN-DHT-R11197, NHM I.7279.

OCCURRENCE. Commentry Basin, Allier, France; Stephanian B-C, Upper Carboniferous (Doubinger & Vetter 1985).

DESCRIPTION. Holotype (Fig. 8), is a print of a complete individual, wings folded as in resting position; preservation of moderate quality; wing structures hardly identifiable.

Fore-wings: length about 50.0 mm; divergence of RA and RP opposite first quarter of wing length; CuA + CuPa with an anterior main stem, posteriorly pectinate; some branches of CuA + CuPa distally branched; CuPb not discernible; AA1 simple; AA2 with numerous and dense branches; cross-veins in area between first branches of CuA + CuPa sigmoidal (only visible in left fore-wing); presence of pigmented zones along R and most anterior branches of RP, along anterior stem of CuA + CuPa and its distal branches and along the more basal branches of CuA + CuPa.

Hind-wings: origin of RP near wing base; RA and RP simple and parallel at length; RP with numerous branches; main stem of CuA + CuPa very strong, convex; CuA + CuPa branched; cross-veins dense, straight and parallel.

Specimen MNHN-DHT-R51392 (Figs 9–10). Print of an almost complete individual (left hind-wing missing). Fore-wings: area between RA and RP very narrow in basal half of wing; preserved part of RA simple; RP without clear pattern of ramification, with 11 branches in preserved part; MP not clearly discernible in basal half of wing but its course can be inferred from the corresponding strongly concave fold; divergence of MA and MP at least basal of first third of wing; CuA + CuPa clearly convex, posteriorly pectinate, with numerous branches, with at least 20 branches reaching posterior wing margin, with the most basal ones reaching CuPb; first branches of CuA + CuPa reaching posterior

wing margin are branched basally; more distal branches of CuA + CuPa branched distally or simple; AA1 and AA2 convex; AA1 simple; cross-veins in area between first branches of CuA + CuPa sigmoidal, dense; in other areas, cross-veins straight, parallel, dense. Right fore-wing: width (at mid-length) 10.3 mm; ScP reaching RA just distal of first branch of RP; MA and MP very distally forked; CuPb weak, concave. Left fore-wing: width (at mid-length) 10.4 mm; fork of MA very basal; anterior branch of MA fused with first posterior branch of RP; AA2 with numerous branches. Right hind-wing: RA strongly convex, simple in preserved part; divergence of RA and RP at least basal of branching of M into MA and MP; RP posteriorly pectinate, with five branches in preserved part; origin of MA and MP not preserved but near origin of M from M + CuA; in preserved part, MA simple, MP forked, CuA + CuPa with five branches; CuA + CuPa convex.

Specimen NHM I.7279 (Fig. 11). Print of an incomplete individual. Right fore-wing: RA without visible anterior branches; RP with 13 branches reaching apex; MA distally forked; MP simple in preserved part. Left fore-wing: ScA probably reaching anterior wing margin opposite divergence of RA and RP; divergence of RA and RP about 7.5 mm distal of wing base; MA forked opposite first branch of RP; CuPa emerging obliquely from CuP; concave CuPb and convex AA1 simple and parallel. Hind-wings: apical area with dense veins (not determinable) and cross-veins.

REMARKS. The colour pattern of the fore-wings is clearly visible in MNHN-DHT-R51216 and MNHN-DHT-R51071. It is not visible in MNHN-DHT-R51392 and NHM I.7279, probably due to preservation (the relief of the veins in specimens where colour is preserved is weak, but it is well marked in specimens without coloration; coloration can be absent in one of the prints from many fossil insects from the Commentry Basin; O.B., pers. obs., 2002). This does not justify a specific separation and we include all of the specimens assigned to the genus *Ctenoptilus* in the same species.

Genus *ISCHNOPTERA* gen. nov.

TYPE SPECIES. *Ischnoptera diaphanes* sp. nov.

ETYMOLOGY. After the name of the genus *Ischnoneura*, probably related to *Ischnoptera*.

DIAGNOSIS. Fore-wings: branches of ScP strongly oblique; divergence of RA and RP basal to first branch of CuA + CuPa; CuA + CuPa with two main branches; no clear branching pattern of main branches of CuA + CuPa; pronotum subquadrate, broader than long.

REMARKS. The specimen was part of a collection of undescribed specimens from Commentry, France. The specimen was labelled by F. Meunier as follows: 'nervation très effacée, peut-être *Sthenarocera pachytyloides*, très mauvais exemplaire 1902–14'. A new preparation (O.B., 2003) revealed that the specimen is good enough for formal description. It belongs to a new genus and species.

***Ischnoptera diaphanes* gen. et sp. nov.** (Fig. 12)

DIAGNOSIS. By monotypy, that of the genus.

ETYMOLOGY. Term 'diaphanes' (transparent in Greek) after the absence of wing coloration.

TYPES. Holotype: Muséum National d'Histoire Naturelle DHT-R11469.

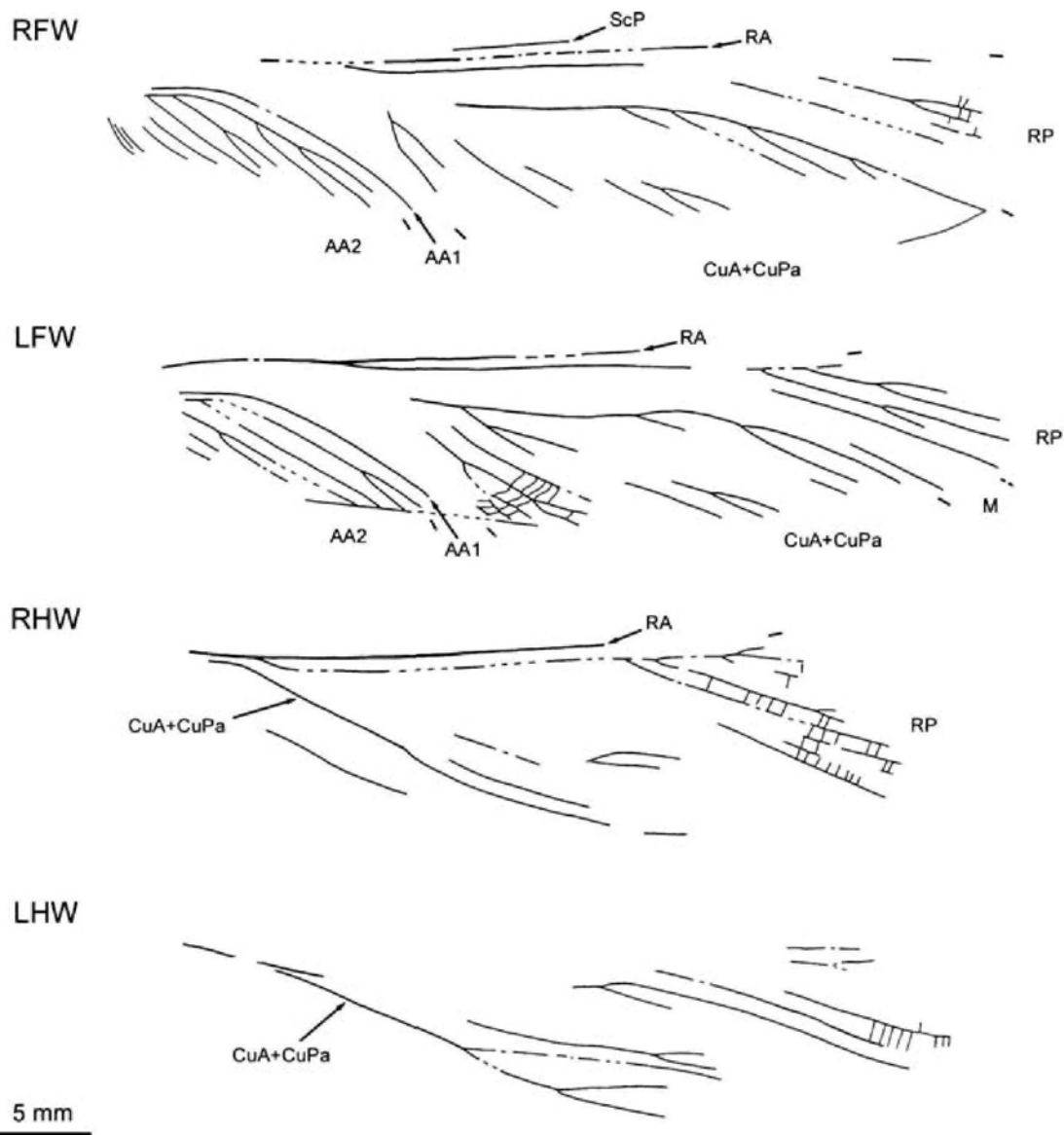


Figure 8 *Ctenoptilus elongatus* (Brongniart, 1893) comb. nov. (MNHN-DHT-R51216 holotype: France; Upper Carboniferous). Reconstructions of the right fore-wing (RFW), left fore-wing (LFW, reversed), right hind-wing (RHW), left hind-wing (LHW, reversed) and photograph of the whole specimen (under alcohol). AA2, second anterior anal. For other abbreviations see the legend to Figure 1.

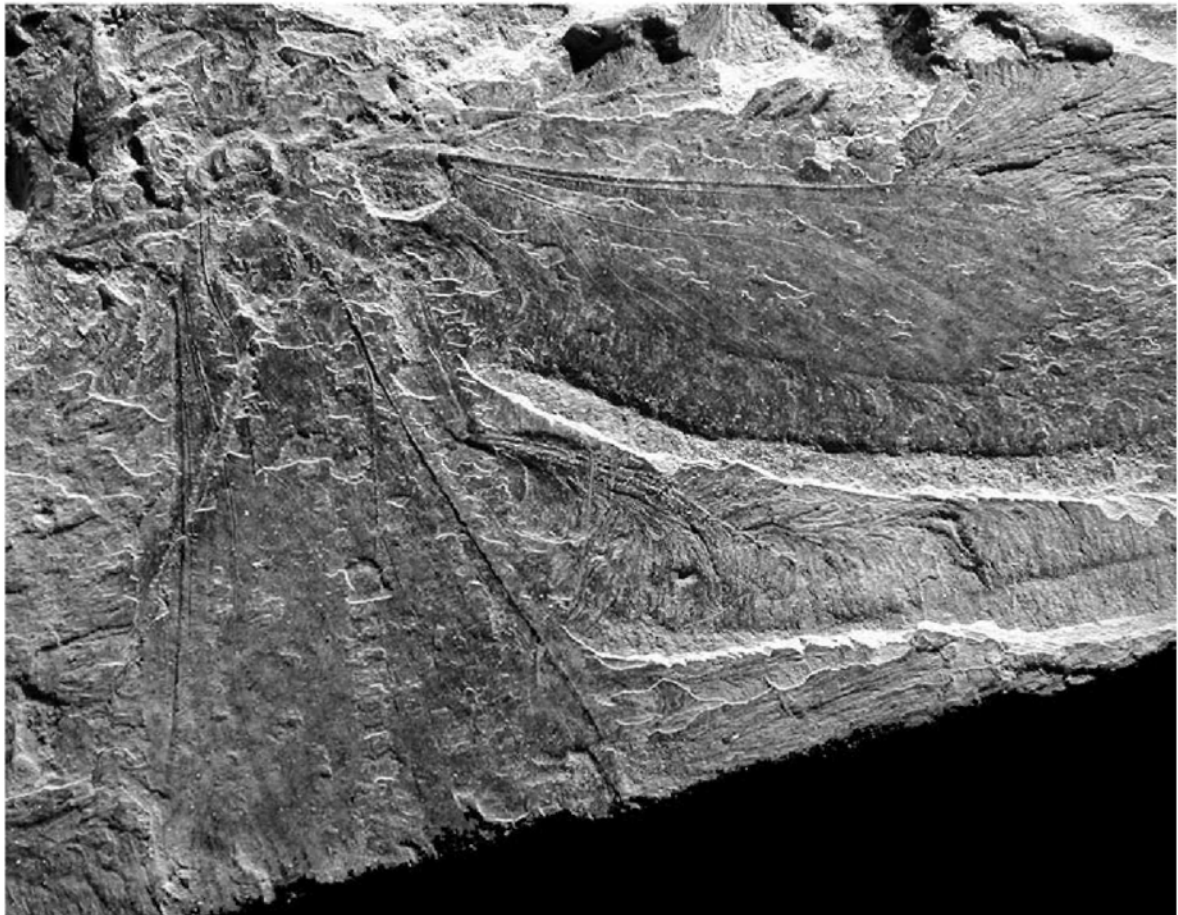
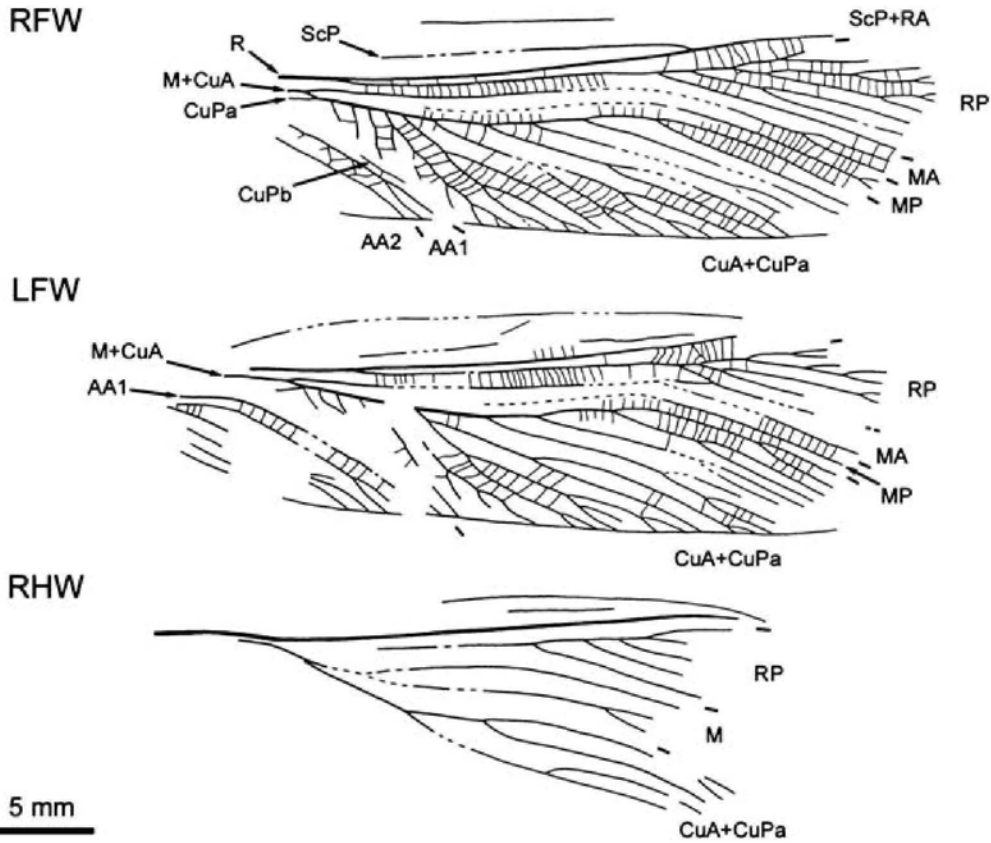


Figure 9 *Ctenoptilus elongatus* (Brongniart, 1893) comb. nov. (MNHN-DHT-R51392: France; Upper Carboniferous). Reconstructions of the right fore-wing (RFW), left fore-wing (LFW, reversed), right hind-wing (RHW) and photograph (print). R, radius; AA2, second anterior anal. For other abbreviations see the legend to Figure 10.

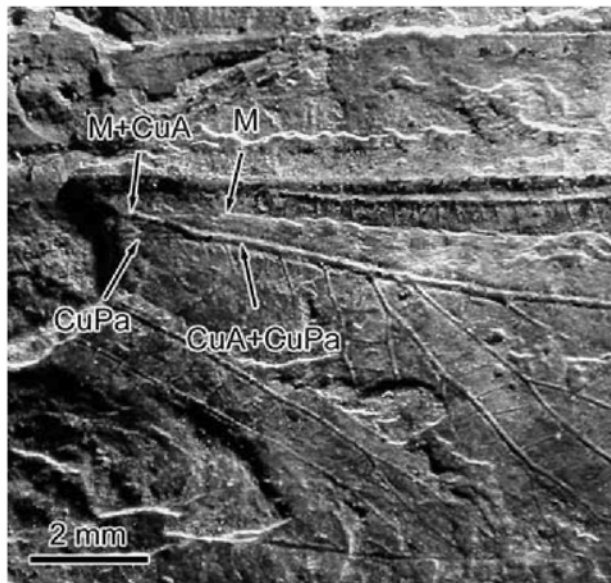


Figure 10 *Ctenoptilus elongatus* (Brongniart, 1893) comb. nov. (MNHN-DHT-R51392; France; Upper Carboniferous). Photograph of the medio-cubital area, right fore-wing (print) (same specimen as in Figure 9). For abbreviations see legend to Figure 1.

OCCURRENCE. Commeny Basin, Allier, France; Stephanian B-C, Upper Carboniferous (Doubinger & Vetter 1985).

DESCRIPTION. Print of an almost complete individual; body *c.* 57.0 mm long; pronotum subquadrate, broader than long, 5.0 mm long, 11.5 mm wide; head *c.* 7.0 mm long; relief of the wing venation altered.

Left fore-wing: length about 69.5 mm, width 17.8 mm; branches of ScP very oblique and long in preserved parts; ScP reaching RA about 43.1 mm distal of wing base; RA and RP diverging *c.* 12.6 mm distal of wing base; area between RA and RP narrow at length; RA simple; RP simple at length (38.5 mm); M 13.9 mm long before divergence of MA and MP; MA simple at length (26.4 mm), with two preserved branches; MP with three preserved branches, probably distally reticulated; distal free part of CuA (from M + CuA) 3.6 mm long before its fusion with CuPa; CuA + CuPa short (3.5 mm) before its first branching; CuA + CuPa with two main branches; anterior branch of CuA + CuPa with four branches reaching posterior margin, posterior branch with seven branches reaching posterior wing margin, parallel at length to posterior wing margin in their distal parts; a branch of CuA + CuPa probably vanishing in area between two main branches; main branches of CuA + CuPa without clear pattern of branching; area between posterior branch of CuA + CuPa and CuPb broad, with two rows of cells; CuPb weak, strongly concave, close to AA1; AA1 simple, AA2 branched.

Right fore-wing: RP simple along length (about 39.0 mm), posteriorly pectinate, with at least seven branches reaching apex; M 7.5 mm long before divergence of MA and MP; MA simple along length (23.1 mm); MA with three preserved branches; branches of MP not clearly determinable; CuA (from M + CuA) 2.3 mm long before its fusion with CuPa; CuA + CuPa short (4.5 mm) before first branching; CuA + CuPa with two main branches; CuA + CuPa with 8–9 branches in preserved parts, with the most posterior ones parallel at length to posterior wing margin.

Hind-wings: ScP reaching RA; even if preserved remains cannot be reliably attributed to any of the main veins RP, MA and MP, they are very probably branched; CuA + CuPa simple along length; vannus filled with fan-shaped veins.

REMARKS. The location of the branching point of M (into MA and MP) in the fore-wings varies significantly.

Genus *PROTODIAMPHIPNOA* Brongniart, 1885

1885 *Protodiamphipnoa* Brongniart: 66.

2002b *Protodiamphipnoa* in part Rasnitsyn: 258.

TYPE SPECIES. *Protodiamphipnoa gaudryi* (Brongniart, 1885).

DIAGNOSIS. Fore-wings: ScA and anterior wing margin very closely parallel at length but distinct; anterior branch of CuA + CuPa orientated towards anterior wing margin basal to first fork of MA; first branch of RP opposite end of ScP on RA; dark pigmentation with clear spots in cells in areas between anterior wing margin and MP and a large 'eye-like' spot near middle of wing.

Protodiamphipnoa gaudryi (Brongniart, 1885) (Figs 13–16)

1885 *Protodiamphipnoa gaudryi* Brongniart: pl. II, fig. 1 (specimen lost).

1893 *Protodiamphipnoa tertrini* Brongniart: 411, pl. XL(24), figs 7, 8, 9 (specimens MNHN-DHT-R51400, R51416, R51205).

1893 *Protodiamphipnoa gaudryi* Brongniart: 427, pl. XLIX(33), figs 5, 6 (specimen lost).

1906b *Cnemidolestes gaudryi* Handlirsch: 135, pl. XIV, fig. 3.

1906b *Protodiamphipnoa tertrini* Handlirsch: 135, pl. XIII, fig. 24.

1917 *Protodiamphipnoa tertrini* Lameere: 166 (new description, probably based on MNHN-DHT-R51393).

1917 *Protodiamphipnoa (Protodiamphipnoa) gaudryi* Lameere: 171 (new generic assignment in text).

1917 *Protodiamphipnoa (Protodiamphipnoa) woodwardi* Lameere: 171 (new generic assignment in text).

1919 *Cnemidolestes gaudryi* Handlirsch: 553.

1919 *Protodiamphipnoa tertrini* Handlirsch: 553.

1992 *Protodiamphipnoa tertrini* Carpenter: 129, fig. 75 (specimen MNHN-DHT-R51393).

1992 *Protodiamphipnoa gaudryi* Carpenter: 129, fig. 76 (specimen lost).

2002b *Protodiamphipnoa tertrini* Rasnitsyn: 258, fig. 357b.

NOTE ON SYNONYMY LIST. Brongniart (1885) assigned the holotype to the genus *Protodiamphipnoa* Brongniart, 1879. Nevertheless, the type species of this genus differs from all other Archaeorthoptera in having a well-developed AP area (Béthoux 2003). Consequently, the species *Protodiamphipnoa gaudryi* must be assigned to a separate genus. In 1893, Brongniart created the new genus and species *Protodiamphipnoa tertrini* on the basis of three very incomplete specimens. Lameere (1917), who had at his disposal more complete specimens of this last species (probably including MNHN-DHT-R51393; see Figs 14–15), correctly assigned *Protodiamphipnoa gaudryi* to the genus *Protodiamphipnoa*.

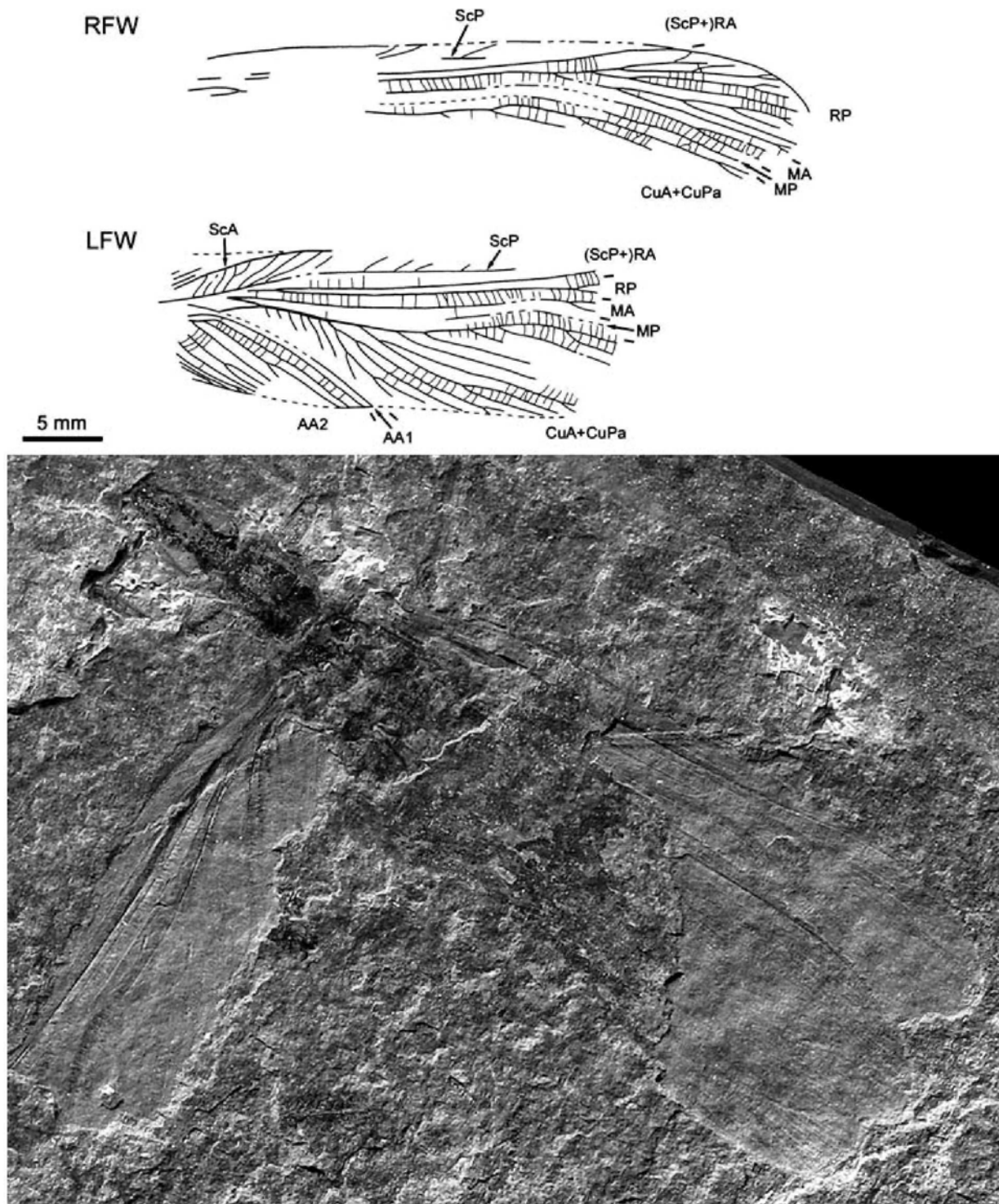


Figure 11 *Ctenoptilus elongatus* (Brongniart, 1893) comb. nov. (NHM I.7279; Upper Carboniferous, France). Reconstructions of the right fore-wing (RFW), left fore-wing (LFW, reversed) and photograph (print; light-mirrored). AA2, second anterior anal. For other abbreviations see the legend to Figure 1.

Lameere distinguished the two included species on the basis of (1) their size (*P. gaudryi* is smaller than *P. tertrini*) and (2) the robustness of the fore-legs (less robust in *P. gaudryi* than in *P. tertrini*). However, (1) a direct comparison of the specimen MNHN-DHT-51393 with photographs of the holotype provided by Brongniart (1893) and Carpenter (1992) revealed that *P. gaudryi* and *P. tertrini* do not differ signi-

ficantly in size; (2) a comparison of MNHN-DHT-R51045 (see Fig. 16, original negative labelled '*Protodiamphipnoa tertrini* apparently not a type' by F. M. Carpenter) with the photograph of the holotype of *P. gaudryi* reveals that, with respect to wings and body sizes, the robustness of the fore-legs is not significantly different. Furthermore, the coloration pattern of *P. gaudryi* and *P. tertrini* are identical in the preserved

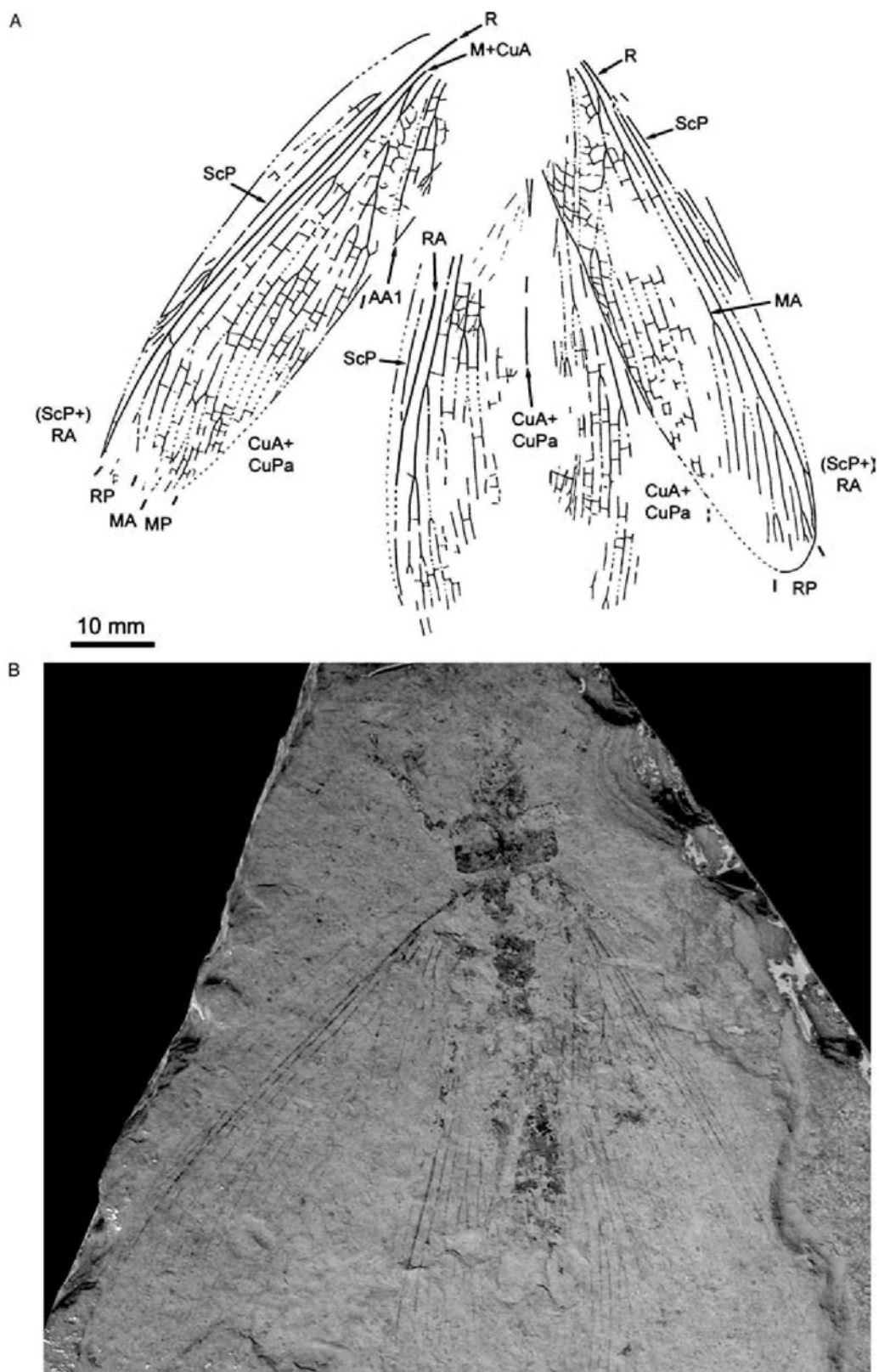


Figure 12 *Ischnoptera diaphanes* gen. et sp. nov. (MNHN-DHT-R11469 holotype: France; Upper Carboniferous). (A) Reconstruction of the left fore-wing and (B) photograph of the wings (counter-print; combined). R, radius. For other abbreviations see the legend to Figure 1.

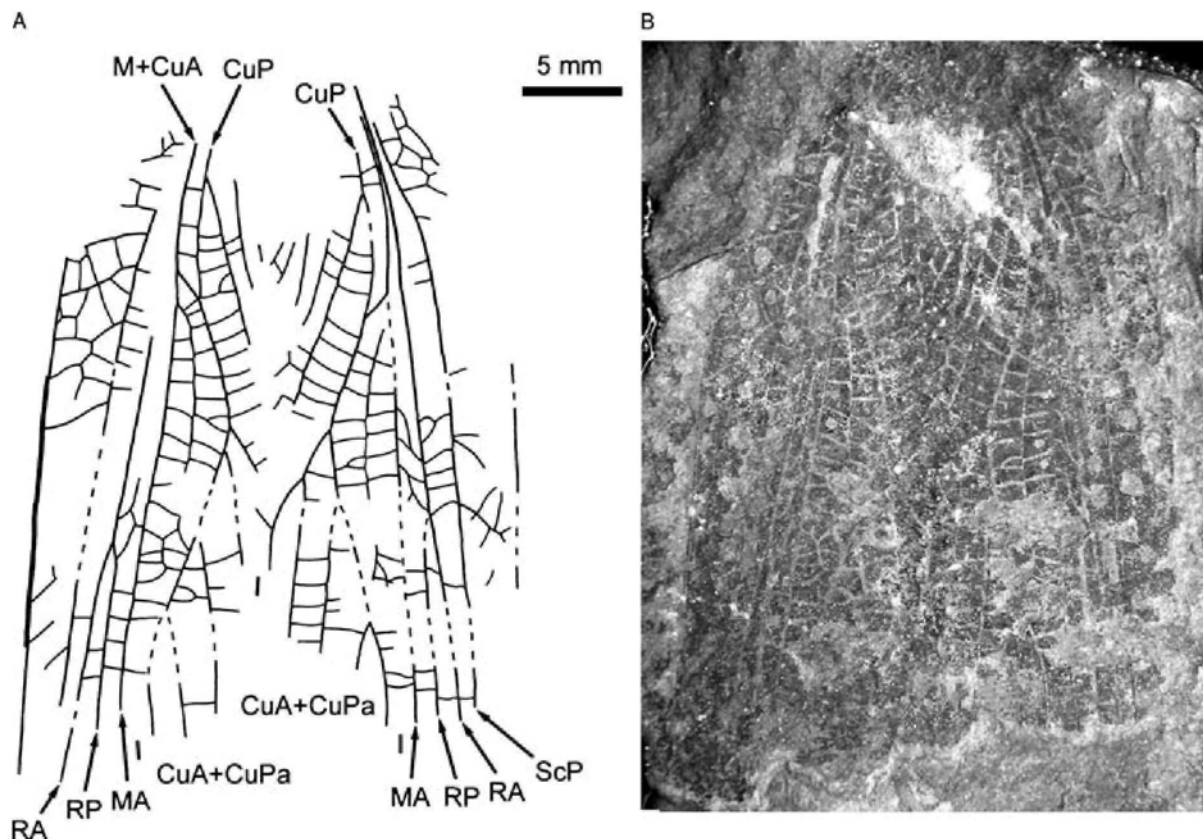


Figure 13 *Protodiamphipnoa gaudryi* (Brongniart, 1885) (MNHN-DHT-R51400 neotype; France; Upper Carboniferous). (A) Reconstruction of the wings and (B) photograph (under alcohol). For abbreviations see the legend to Figure 1.

parts: in the basal half of the wing, white spots occur between veins from ScP, while the rest of the wing is dark. Consequently, we consider *P. tertrini* to be a junior synonym of *P. gaudryi*.

DIAGNOSIS. By monotypy, that of the genus.

MATERIAL. Neotype: Muséum National d'Histoire Naturelle DHT-R51400 (syntype of *P. tertrini*); other syntype specimens of *P. tertrini*: MNHN-DHT-R51416 and MHN-DHT-R51205, other specimens: MNHN-DHT-R51393 and MNHN-DHT-R51045.

The holotype of *P. gaudryi* is presumed lost, although photographed in Carpenter (1992: fig. 76). It is missing from the collections of the MNHN where other specimens from Commentry are stored and there is no record of a loan of this specimen. It was also not amongst F. M. Carpenter's material from Commentry, which was on loan and previously stored at the MCZ and which was recently returned to the MNHN. In order to avoid any confusion we propose to designate a neotype. *Protodiamphipnoa gaudryi* was based on a unique specimen in the original publication. Consequently, we designate MNHN-DHT-R51400, the best-preserved syntype of *P. tertrini*, from the same locality as the holotype of *P. gaudryi*, as the neotype.

OCCURRENCE. Commentry Basin, Allier, France; Stephanian B-C, Upper Carboniferous (Doubinger & Vetter 1985).

DESCRIPTION. Neotype MNHN-DHT-R51400 (Fig. 13). Flat impression (it cannot be determined if it is a print or a counter-print) of the base of two fore-wings, folded as in rest-

ing position. Fore-wings: preserved length about 32.6 mm; wings dark, with small white spots centred in wing cells, mainly in area between anterior margin and ScP; ScA very close but distinct from anterior wing margin; branches of ScP zigzagged; RA and RP diverging about 24.0 mm/22.5 mm (left wing/right wing) distal to wing base; M (from M+CuA) short (1.7 mm) before divergence of MA and MP; MA simple in preserved part (for at least 1.7 mm); MP weak, vanishing in area between MA and CuA+CuPa; CuA+CuPa branched 6.6 mm/6.1 mm distal of its origin; anterior branch of CuA+CuPa directed towards anterior wing margin basal of distal vanishing of MP, then directed towards apex; branches of CuA+CuPa simple in preserved parts; CuPa 6.1 mm long before its fusion with CuA; CuPb simple in preserved parts; in area between R and MA, cross-veins strongly sigmoidal; in other preserved parts, cross-veins straight, rarely reticulated.

Specimen MNHN-DHT-R51393 (Figs 14–15). Print and counter-print of an incomplete individual, with wing apices and head missing, legs not clearly visible; the four wings can be recognised; some anal veins visible but not reliably attributable to the hind-wings. Fore-wings: dark coloration, with a 'C-shaped' light spot near middle of wing that is delimited by cross-veins, also small spots in basal part of the wing, especially in areas between ScA and ScP and between CuA+CuPa and CuPb. Right fore-wing: width (opposite first fork of MA) 14.6 mm; distal third of wing, wing base, basal part of both posterior and anterior wing margins not discernible; ScA very close but distinguishable from anterior wing margin; area between ScA and ScP broad (greatest

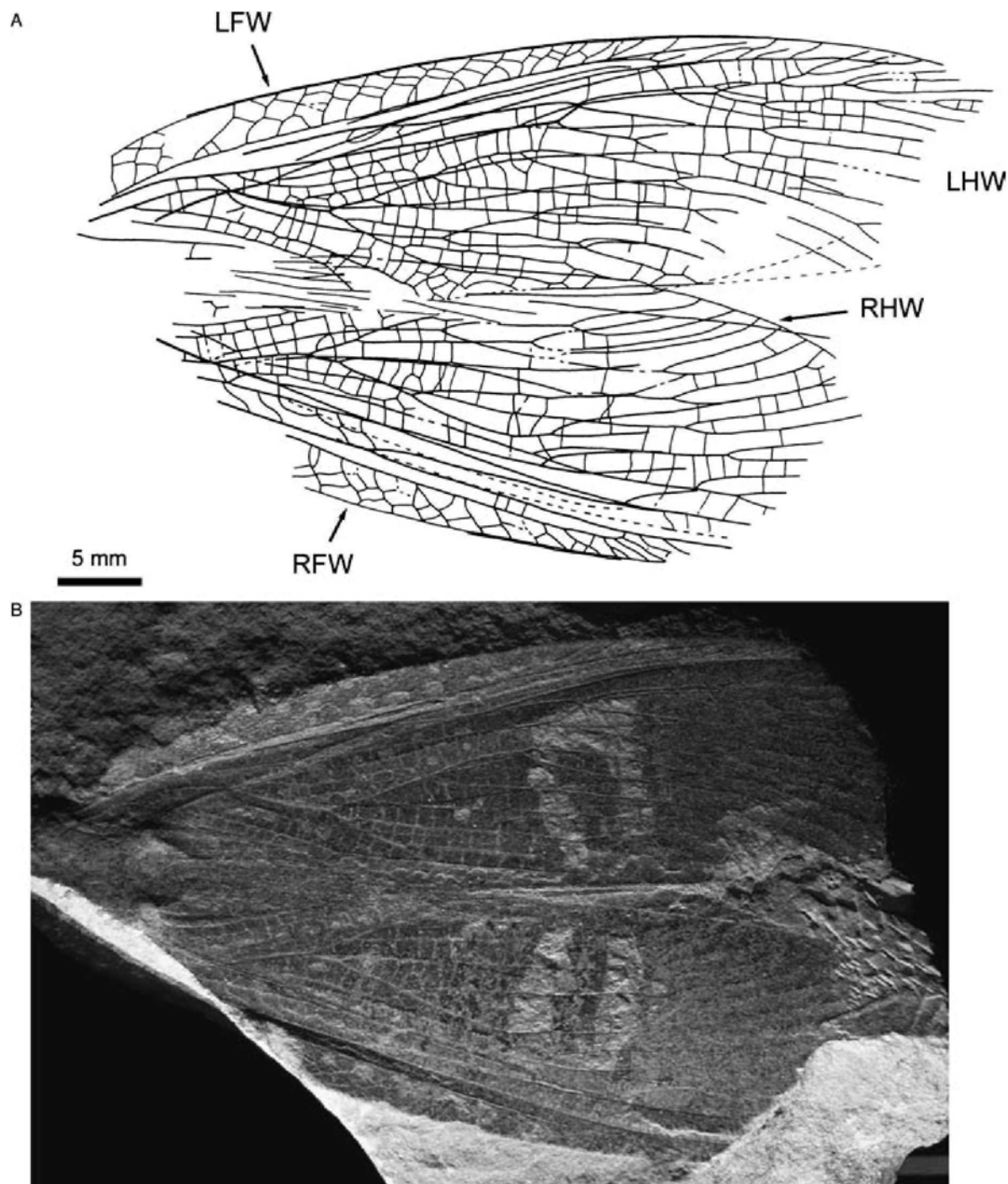


Figure 14 *Protodiamphipnoa gaudryi* (Brongniart, 1885) (MNHN-DHT-R51393; France; Upper Carboniferous). (A) Reconstruction of the wings and (B) photograph (combined). LFW, left fore-wing (reversed); LHW, left hind-wing (reversed); RFW, right fore-wing; LFW, left fore-wing.

width 2.4 mm); ScP concave, anteriorly pectinate, with 14 branches reaching ScA; almost all branches of ScP simple, more or less zigzagged and oblique; ScP ending on RA; RA convex; few anterior branches of RA visible; RP long (15.4 mm) before its first fork; cross-veins between R and M sigmoidal and reticulated; MA long (19.1 mm) before its first fork; RP concave; MA and MP neutral; anterior branch of MA without connection with R, directed towards posterior wing margin; MP emerging obliquely from M (i.e. M and MA are aligned); MP progressively weaker and zigzagged in

its distal part, probably fused with the most anterior branch of CuA + CuPa; area between MA and CuA + CuPa broad until MP vanishes; CuA + CuPa strongly convex; first fork of CuA + CuPa dichotomous, with two branches of equal width; anterior branch of CuA + CuPa directed towards anterior wing margin, posteriorly pectinate, with three simple branches in preserved part; posterior branch of CuA + CuPa with at least two branches, the anterior one being distally forked; area between CuA + CuPa and CuPb broad (1.6 mm); concave CuPb and convex AA1 slightly bowed posteriorly,

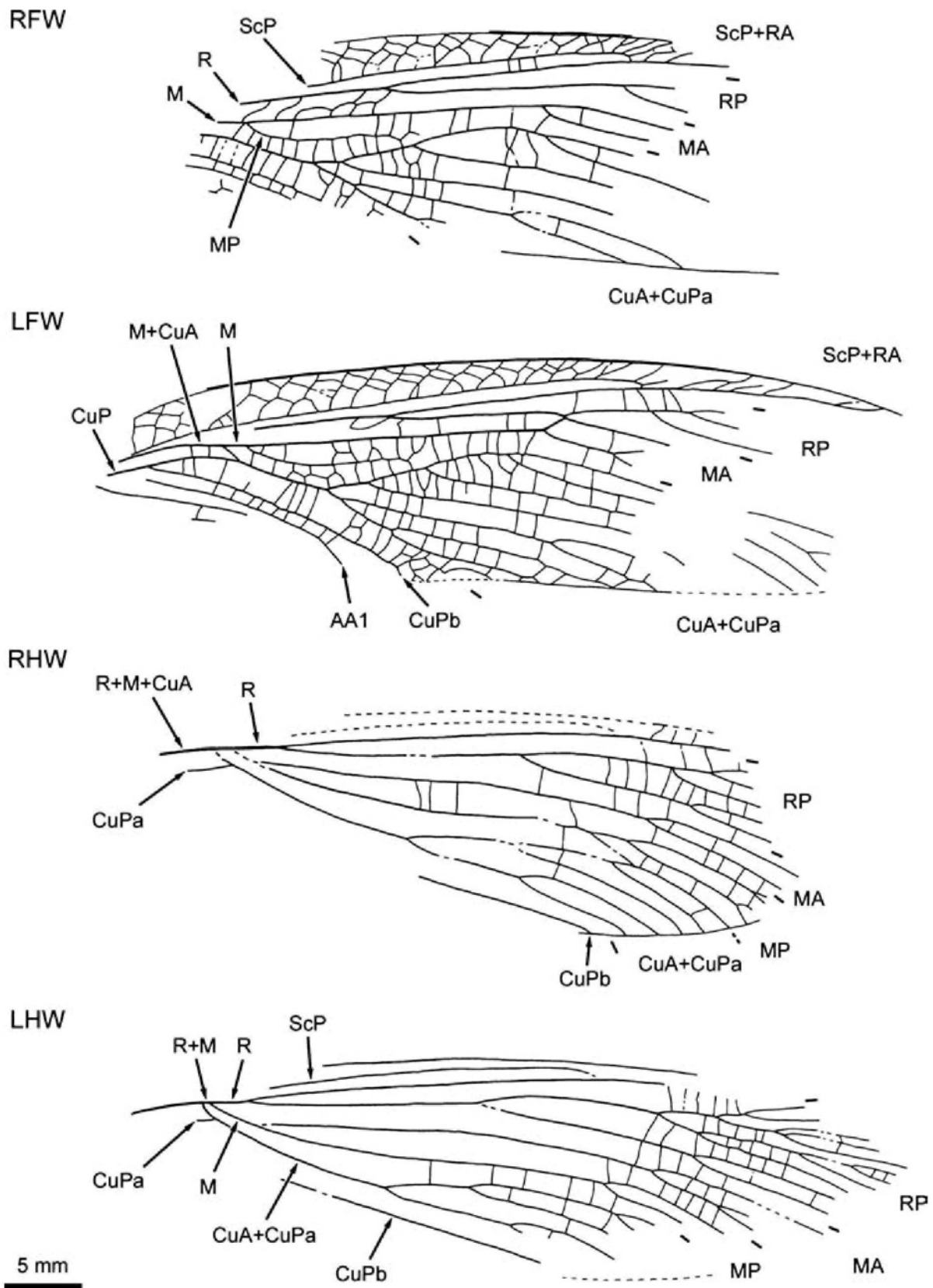


Figure 15 *Protodiamphipnoa gaudryi* (Brongniart, 1885) (MNHN-DHT-R51393; France; Upper Carboniferous). Reconstructions of the wings, separated (same specimen as in Figure 14). RFW, right fore-wing; LFW, left fore-wing (reversed); RHW, right hind-wing; LHW, left hind-wing (reversed); R, radius; M, media. For all other abbreviations, see the legend to Figure 1.

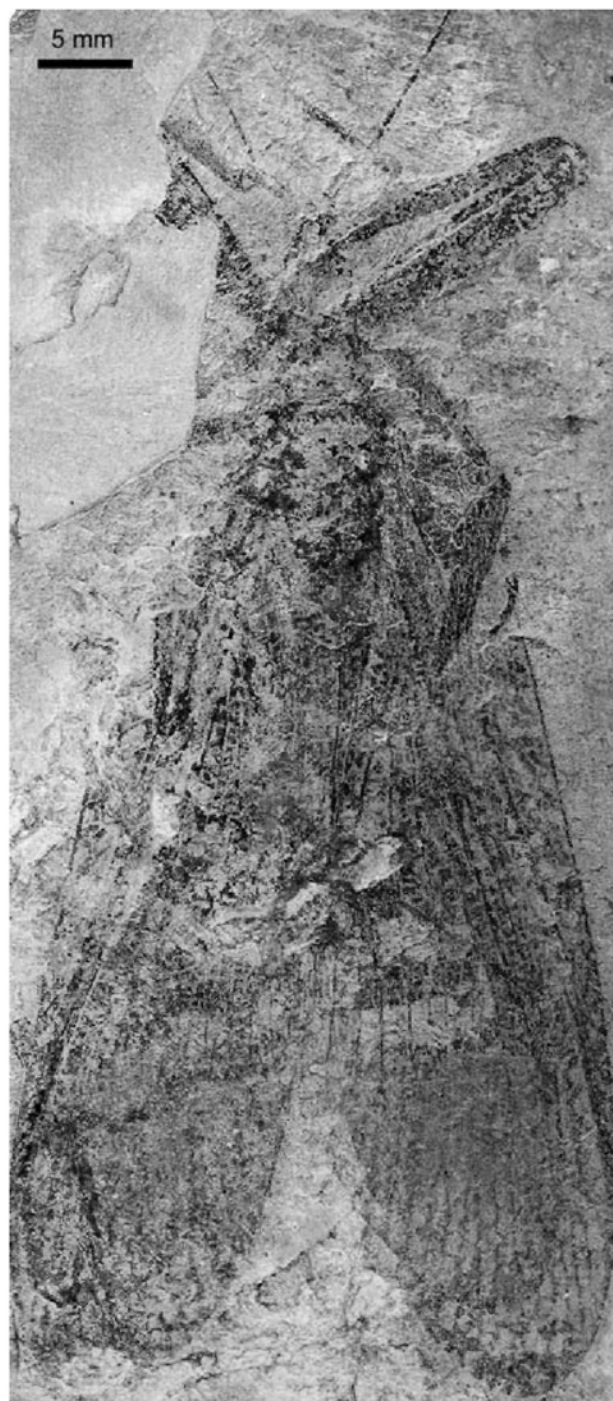


Figure 16 *Protodiamphipnoa gaudryi* (Brongniart, 1885) (MNHN-DHT-R51045; France; Upper Carboniferous). Photograph (by F. M. Carpenter).

simple in preserved part; area between CuPb and AA1 narrow (0.7 mm).

Left fore-wing: width 14.7 mm, estimated length about 58 mm; apex poorly preserved, wing base missing; ScA parallel to anterior wing margin, not discernible from wing margin distal to end of ScP; 18 branches of ScP visible, zig-zagging, oblique, most of them simple; ScP ending on RA or fused with first anterior branch of RA, about 36.4 mm from wing base; RA and RP separating 20.0 mm distal to wing base; distal to end of ScP, RA with sigmoidal anterior branches reaching anterior wing margin; RP connected with

the anterior branch of MA 11.3 mm distal to origin of RP, with inflexion at this point; first fork of RP 16.8 mm distal to its origin; RP with at least three branches; origin of CuA from M + CuA about 8.9 mm distal to wing base; M short (1.5 mm) before origin of MA and MP; MA long (19.2 mm) before first fork; anterior branch of MA directed towards anterior wing margin, shortly connected to RP and distally directed towards posterior wing margin; posterior branch of MA forked; MP emerging obliquely from M, progressively weaker and zigzagged in its distal part, vanishing in area between MA and CuA + CuPa; CuP branched into CuPa and CuPb about 4.2 mm distal to wing base; CuPa long (5.8 mm) before fusion with free part of CuA; CuA + CuPa branched 6.0 mm distal to its origin; first fork of CuA + CuPa dichotomous; anterior branch of CuA + CuPa posteriorly pectinate, with at least four branches; posterior branch of CuA + CuPa anteriorly pectinate, with three branches, with first one distally forked; concave CuPb and convex AA1 slightly posteriorly bowed, simple; area between R (basal to divergence of RA and RP) and MA with strongly sigmoidal cross-veins; in all other areas, cross-veins straight, rarely sigmoidal, moderately reticulated.

Right hind-wing: anterior wing margin and apical part missing; width about 14.2 mm; R branched into RA and RP basally; RA simple in preserved part; first branch of RP 15.6 mm distal to its origin, about opposite mid-length of wing; branches of RP long (anterior branch = 9.8 mm, posterior branch = 11.4 mm) before their first fork; first forks of MA and MP in a very distal position (about 25.5 mm and 22.0 mm distal to their origins, respectively); MA with two branches in preserved part; MP with three main branches, the first posterior one fused with anterior branch of CuA + CuPa; CuA + CuPa branched 12.3 mm distal to its origin; anterior branch of CuA + CuPa posteriorly pectinate, with three simple branches; posterior branch of CuA + CuPa with one fork; few cross-veins discernable, straight, not reticulated.

Left hind-wing: apical and posterior wing margins, wing base and anal area not discernable; ScP probably distally fused with RA; R, M and CuA fused into a basal common stem; CuA emerging first from this common stem; R and M separate 0.5 mm distal to origin of CuA; RA and RP diverging 2.5 mm distal to origin of R; RA simple in preserved part; first fork of RP 14.7 mm distal to its origin; branches of RP long before their first fork; RP with at least 11 branches, close together; MA and MP branched very distally; MA with at least three branches, MP with at least two branches; CuA + CuPa with at least five branches; CuPb simple in preserved part, straight.

REMARKS. In Neoptera preserved as compressions, where wings are frequently superimposed or found in isolation, it is not often that both fore- and hind-wings can be reliably assigned to the same species. Fortunately, the preservation of the specimen MNHN-DHT-R51393 is so good that most of the wing parts can be isolated. It allows assignment of other isolated hind-wings to the *Archaeorthoptera*.

Genus *CNEMIDOLESTES* Handlirsch, 1906 stat. rest.

- 1906b *Cnemidolestes* Handlirsch: 135.
1917 *Cnemidolestes* Lameere: 171 (in text, synonymised with *Protodiamphipnoa*).
1919 *Cnemidolestes* in part Handlirsch: 553.



Figure 17 *Cnemidolestes woodwardi* (Brongniart, 1893) (MNHN-DHT-R51272 holotype: France; Upper Carboniferous). Photograph (counter-print, combined) of the whole specimen.

1992 *Protodiamphipnoa* Carpenter: 129.

2002b *Protodiamphipnoa* in part Rasnitsyn: 258, fig. 357a (erroneous attribution of type specimen of *C. woodwardi* to *P. gaudryi*).

TYPE SPECIES. *Cnemidolestes woodwardi* (Brongniart, 1893).

DIAGNOSIS. Fore-wings: first branching of RP distal to end of ScP on RA; alternation of dark and clear strips crossing wing from anterior to posterior wing margins.

REMARKS. Rasnitsyn (2002a: 80) referred 'an isolated wing of unknown affinity' to *Cnemidolestes* but, in the same account (Rasnitsyn 2002b: fig. 357a) assigned the holotype of the type species *C. woodwardi* to the genus *Protodiamphipnoa*. This is probably due to a mistake occurring in the legend of the corresponding original plate from Brongniart (1893: pl. XLIX(33)): the three last legends correspond, respectively, to the true figures 4, 5 and 6 of the plate, instead of 3, 4, 5.

Each of the genera *Protodiamphipnoa* and *Cnemidolestes* are represented by a single species. Following the opinion of Lameere (1917), Carpenter (1992) and Rasnitsyn (2002b) synonymised these genera (see above). The characters 'anterior stem of CuA + CuPa strongly orientated towards anterior wing margin basal to first fork of MA' (diagnostic of *Protodiamphipnoa*) and 'first branching of RP distal to end of ScP on RA' (diagnostic of *Protodiamphipneura*) are of generic relevance.

Cnemidolestes woodwardi (Brongniart, 1893)
stat. rest. (Figs 17–18)

1893 *Protophasma woodwardi* Brongniart: 427, pl. XLIX(33), fig. 4.

1906b *Cnemidolestes woodwardi* Handlirsch: 135, pl. XIV, fig. 4.

1917 *Protodiamphipnoa* (*Protophasma*) *woodwardi* Lameere: 171.

1919 *Cnemidolestes woodwardi* Handlirsch: 553.

2002b *Protodiamphipnoa gaudryi* Rasnitsyn: 258, fig. 357a.

DIAGNOSIS. By monotypy, that of the genus.

MATERIAL. Holotype: Muséum National d'Histoire Naturelle DHT-R51272.

OCCURRENCE. Commentry Basin, Allier, France; Stephanian B-C, Upper Carboniferous (Doubinger & Vetter 1985).

DESCRIPTION. Counter-print of a nearly complete individual; prothoracic legs with broadened femora; only the venation of the right fore-wing is discernable. Right fore-wing: preserved length about 58.7 mm; venation poorly preserved in clear strips; near wing base, anterior wing margin with four preserved spines, located opposite probable ends of branches of ScP; cross-veins between branches of ScP; ScP reaching RA; divergence of RA and RP distal to first fork of CuA + CuPa; RP simple in preserved part; MP weak, reaching anterior branch of CuA + CuPa distal to its first fork; MA long (about 29.0 mm) basal to its first branching; MA with four branches

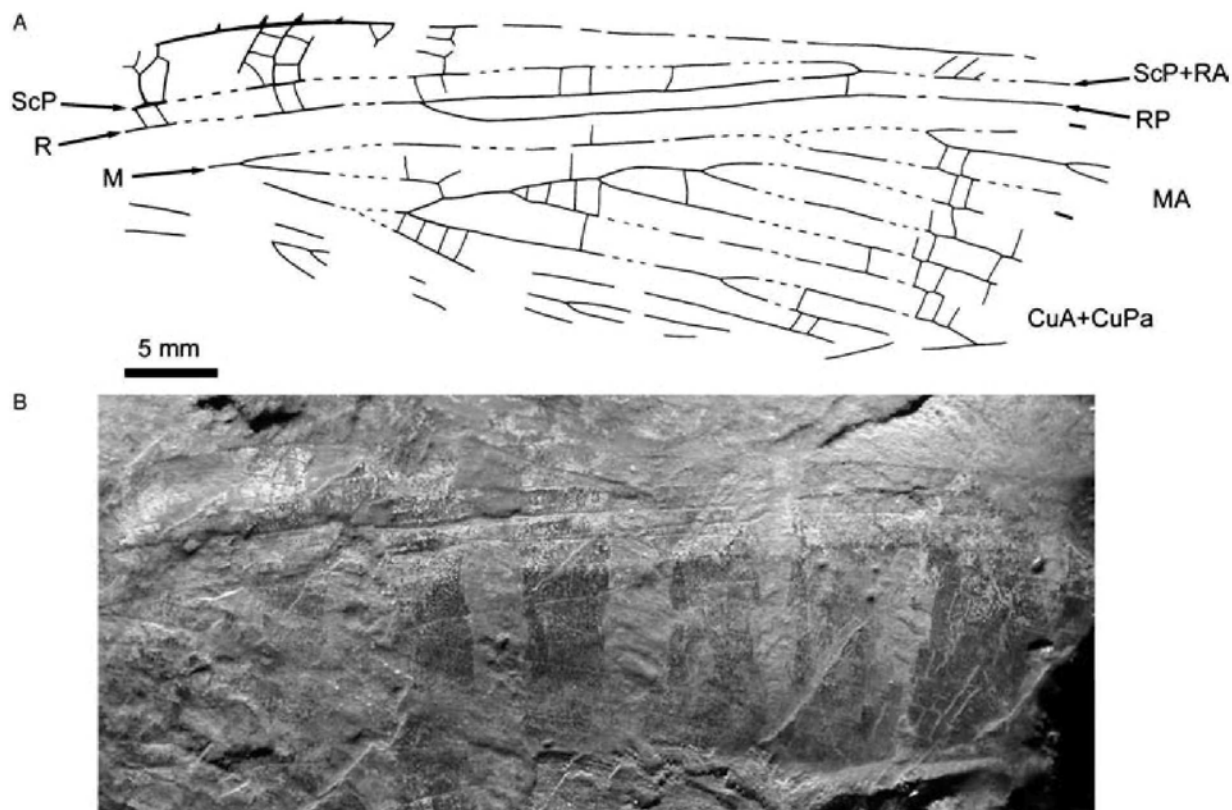


Figure 18 *Cnemidolestes woodwardi* (Brongniart, 1893) (MNHN-DHT-R51272 holotype: France; Upper Carboniferous). (A) Reconstruction and (B) photograph (under alcohol) of the right fore-wing (reversed). For abbreviations see the legend to Figure 1.

in preserved part; CuA + CuPa internally pectinate, anterior main branch of CuA + CuPa with more branches than posterior one; anterior branch of CuA + CuPa with five branches, the first one being distally branched; preserved cross-veins not reticulated; coloration pattern with at least seven parallel dark strips.

Genus *ISCHNONEURA* Brongniart, 1893

- 1885b *Leptoneura* in part Brongniart: 62.
 1893 *Ischnoneura* in part Brongniart: 433.
 1906b *Ischnoneura* in part Handlirsch: 134.
 1922 *Ischnoneura* in part Handlirsch: 75.
 1992 *Ischnoneura* in part Carpenter: 130.

DIAGNOSIS. Fore-wings: absence of cross-veins between branches (veinlets?) of ScP and RA; RP posteriorly arched at mid-course, just basal of end of ScP on RA; branches of RP simple; MP fused with anterior stem of CuA + CuPa; CuA + CuPa internally pectinate; branches of CuA + CuPa simple.

TYPE SPECIES. *Ischnoneura oustaleti* Brongniart, 1893, type designation in Carpenter (1992: 130).

REMARKS. Other specimens assigned by previous authors to this genus are here assigned to different genera. *Ischnoneura delicatula* (Brongniart, 1893), type species of *Ischnoneurona* Handlirsch, 1919, is based on a very poorly preserved specimen and is herein considered as a Neoptera *incertae sedis*.

Ischnoneura oustaleti (Brongniart, 1885) (Fig. 19)

- 1885 *Leptoneura oustaleti* Brongniart: 62, pl. V, fig. 4.
 1893 *Ischnoneura oustaleti* in part Brongniart: 433, pl. LII(36), fig. 3.
 1906b *Ischnoneura oustaleti* in part Handlirsch: 134.
 1922 *Ischnoneura oustaleti* in part Handlirsch: 76.
 1992 *Ischnoneura oustaleti* Carpenter: 130, fig. 74.8.

DIAGNOSIS. By monotypy, that of the genus.

MATERIAL. Holotype: Muséum National d'Histoire Naturelle DHT-R51077.

OCCURRENCE. Commeny Basin, Allier, France; Stephanian B-C, Upper Carboniferous (Doubinger & Vetter 1985).

DESCRIPTION. Incomplete individual, with parts of head, legs, thorax, complete left fore-wing, a part of a left hind-wing and a folded part of an undetermined wing. Left fore-wing: length about 58.3 mm, width (opposite mid-length) 14.1 mm; branches (veinlets) of ScP and RA simple and short, without cross-veins between them; ScP reaching RA about 35.0 mm distal to wing base; divergence of RA and RP very basal, about 13.6 mm from wing base; RP with a slight posterior arch opposite its mid-course, just basal to the end of ScP on RA; first branch of RP just distal to this arch; RP posteriorly pectinate with six simple branches; divergence of MA and MP 4.4 mm distal to origin of M (from M + CuA); MP sigmoidal, fused with main anterior branch of CuA + CuPa basal to its first branching; MA branched distal to its

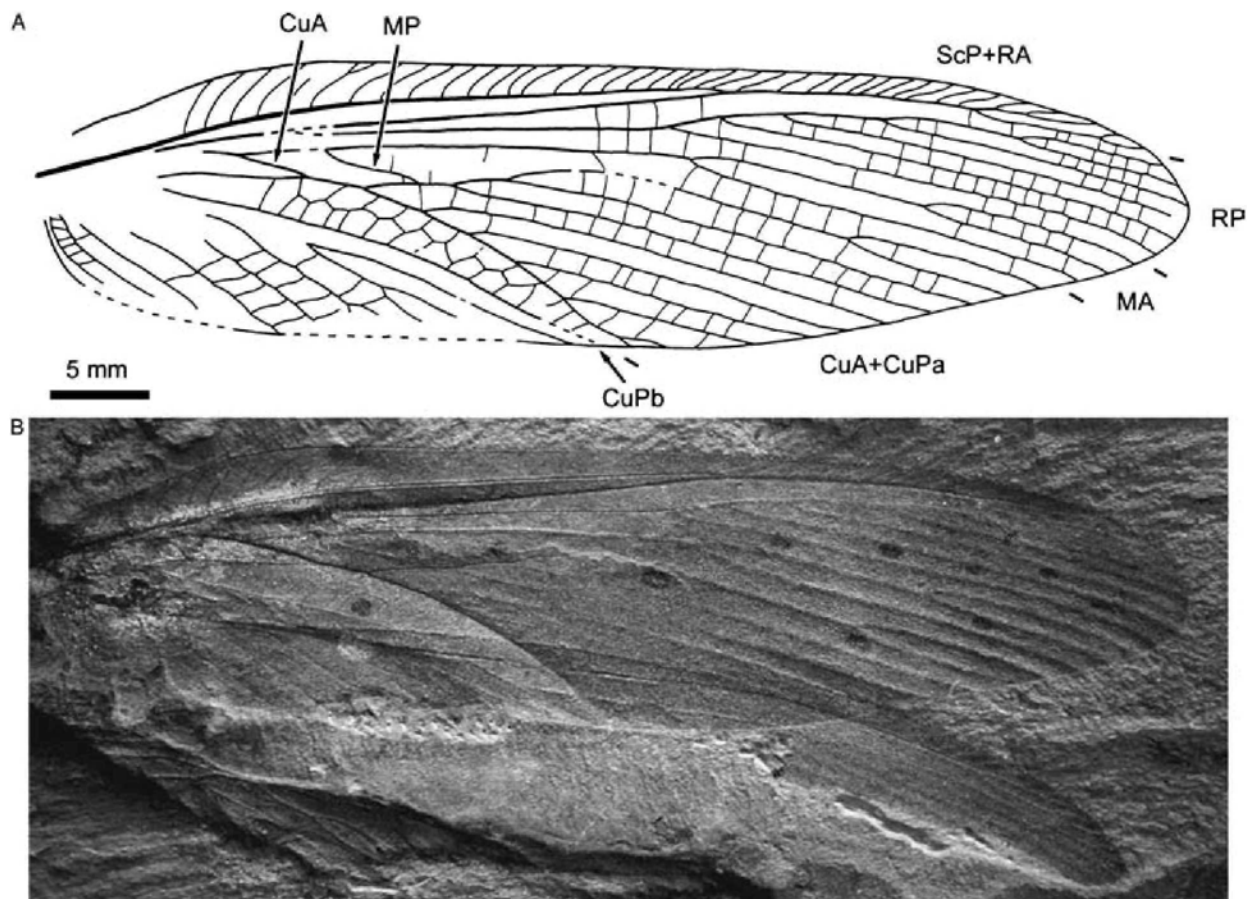


Figure 19 *Ischnoneura oustaleti* (Brongniart, 1885) (MNHN-DHT-R51077 holotype: France; Upper Carboniferous). (A) Reconstruction and (B) photograph (combined, counter-print) of the left fore-wing. For abbreviations see the legend to Figure 1.

mid-length, with three branches reaching posterior wing margin; CuA (from M+CuA) long (3.4 mm) before its fusion with CuPa; CuA + CuPa internally pectinate, anterior branch [= (CuA + CuPa) + MP] with four simple branches, main posterior branch of CuA + CuPa with six simple branches; area between posterior stem of CuA + CuPa and CuPb broad, with two rows of cross-veins; CuPb simple; anal area very long, covering basal 45% of posterior wing margin; with sigmoidal cross-veins; in distal two-thirds of wing, cross-veins straight, parallel, spaced out and not reticulated.

Genus **NARKEMINOPSIS** Whalley, 1979

TYPE SPECIES. *Narkeminopsis eddi* Whalley, 1979.

DIAGNOSIS. Fore-wings: areas between anterior margin and ScP and between ScP and RA with equal widths (i.e. area between anterior margin and ScP not broadened); few cross-veins; five parallel dark strips crossing wing from anterior to posterior wing margins (probably of specific relevance).

REMARKS. The genus *Narkeminopsis* is related to the genera *Protodiamphipnoa*, *Cnemidolestes*, *Aetophlebia* Scudder, 1885, *Ischnoneura*, *Narkemina* Martynov, 1930, *Paranarkemina* Pinto & Pinto de Ornellas, 1980, *Bouleites* Lameere, 1917 and *Amphiboliacridites* Langiaux & Parriat, 1974, in having a CuA + CuPa internally pectinate, i.e. with the anterior main branch posteriorly pectinate, while the

posterior main branch is anteriorly pectinate. The list of genera above nearly coincides with the *Ischnoneuridae sensu* Rasnitsyn, 2002b. Despite the absence of the main diagnostic character of Archaeorthoptera, i.e. the course of CuA, this genus can be reliably assigned to that clade. Note that *Narkemina windsoriensis* Lewis, 1979 probably does not belong to the genus *Narkemina* but to *Aetophlebia*.

Narkeminopsis eddi Whalley, 1979 (Fig. 20)

DIAGNOSIS. By monotypy, that of the genus.

MATERIAL. Holotype: Natural History Museum, London, In. 64531.

OCCURRENCE. Radstock, Avon, United Kingdom; Westphalian D, Upper Carboniferous (Whalley 1979).

DESCRIPTION. Counter-print of an almost complete left fore-wing; venation hardly distinguishable outside pigmented areas; estimated length about 25.7 mm, width 8.4 mm; ScP reaching RA 14.6 mm distal to wing base; area between anterior wing margin and ScP of moderate width (1.0 mm); area between anterior wing margin and ScP/RA with spaced out and slightly oblique cross-veins, without secondary cross-veins between them; RA and RP diverging 10.2 mm distal to wing base; RA without clear branches; RP short, about

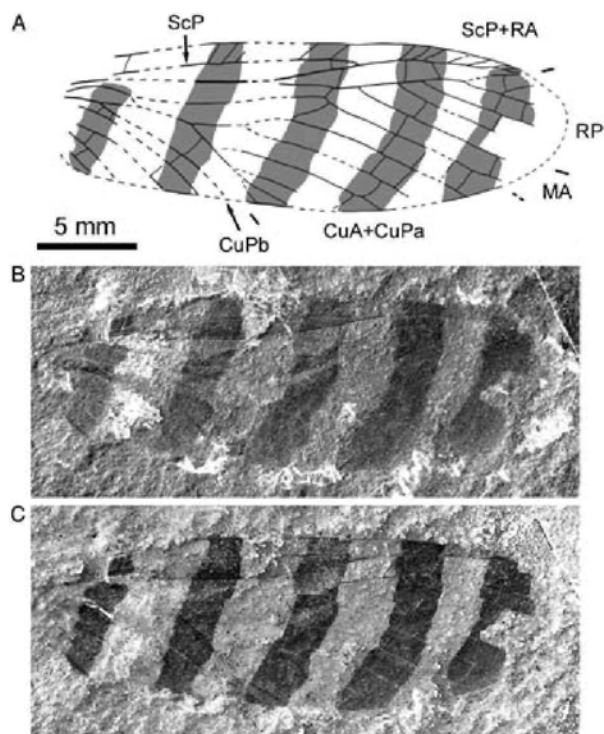


Figure 20 *Narkeminopsis eddi* Whalley, 1979 (NHM In. 64531 holotype: United Kingdom; Upper Carboniferous). (A) Reconstruction and (B, C) photographs (counter-print, (B) dry and (C) under alcohol) of the left fore-wing (reversed). For abbreviations see the legend to Figure 1.

3.1 mm long, before its fusion with anterior branch of MA; RP with five branches in preserved part; convex M+CuA arched basal of origin of CuA; origin and course of MP not discernible (see remark below); MA long before branching; anterior branch of MA very short (0.6 mm) before fusion with RP; posterior branch of MA fused with most anterior branch of CuA + CuPa into a composite simple branch; free part of CuA from M + CuA, fusion of CuA with CuPa and basal part of CuA + CuPa not preserved; CuA + CuPa internally pectinate, with three branches of the anterior main branch and four branches of the posterior one; CuPa and CuPb concave, AA1 convex; CuPb and AA1 simple; five pigmented strips crossing wing from anterior to posterior wing margins.

REMARKS. Our observation of the holotype found that the original (and only available) description of this fossil (Whalley 1979) was inaccurate and so we here provide a re-description.

The interpretation of the median vein requires further explanation. The genera *Protodiamphipnoa*, *Cnemidolestes*, *Aetophlebia* and *Ischnoneura*, together with the species *Narkemina winsdoriensis* Lewis, 1979 (probably not belonging to *Narkemina* but to *Aetophlebia*), are assumed to be related to *Narkeminopsis* because they share a pattern of branching of CuA + CuPa, in which the first branch of M occurs near the origin of CuA (from M + CuA). The posterior branch is assumed to be the true MP, even if all branches of M share the same relief in these insects. MP is either lost in a network of cross-veins between MA and the anterior branch of CuA + CuPa or distally fused with this last vein, but still discernible. MA is branched distally. In the genera *Narkemina*

(excluding *N. winsdoriensis*), *Narkeminopsis*, *Paranarkemina* and *Amphiboliacridites*, the visible first branch of M is very distal, opposite the location of the first branch of MA in the other genera listed above. Thus, it is assumed that MP is lost in the area between MA and the anterior stem of CuA + CuPa in the last genera, or fused with the free part of CuA.

The most distal anterior branch of CuA + CuPa connected with the posterior branch of MA, which is present in the genera *Aetophlebia*, *Narkemina*, *Narkeminopsis*, *Paranarkemina* and *Amphiboliacridites*, is probably not MP emerging distally because this vein is distinctly convex at its origin, at least on the specimen PIN 3315/250 belonging to *Narkemina angustata* Martynov, 1930 (see Rasnitsyn 2002b: fig. 356).

The genus *Aetophlebia* and the genera with a non-discernible MP share: (1) a fusion of the most distal anterior branch of CuA + CuPa with the posterior branch of MA; (2) a fusion of the anterior branch of MA with RP (occurring also in *Protodiamphipnoa* but variable). Also, the only visible vein corresponding to M is branched in a very distal position. In the absence of any argument about the location of MP, one can assume that a 'non-discernible MP' corresponds to a basal fusion of MP with CuA + CuPa.

Genus **BOULEITES** Lameere, 1917

TYPE SPECIES. *Bouleites latipennis* Lameere, 1917.

DIAGNOSIS. Fore-wings: branches of ScP reticulated; base of RP distal to first ramification of CuA + CuPa; anterior branch of MA connected with RP (but variability unknown); area between R and anterior branch of CuA + CuPa wide (at least a quarter of wing width).

REMARKS. This genus is very poorly known because it has never been illustrated and it is not recorded in the compilation of Carpenter (1992).

The genus *Bouleites* is very close to *Aetophlebia* but differs from it in having more irregular ramifications and reticulations of the main veins, notably in the areas between the anterior wing margin and ScP and between branches of CuA + CuPa. It is also close to *Paranarkemina* but differs from that genus by its more distal origin of RP and the broader area between R and anterior branch of CuA + CuPa.

Bouleites latipennis Lameere, 1917 (Fig. 21)

1917 *Bouleites latipennis* Lameere: 175.

1922 *Bouleites latipennis* Handlirsch: 212.

DIAGNOSIS. By monotypy, that of the genus.

MATERIAL. Holotype: Muséum National d'Histoire Naturelle DHT-R51241.

OCCURRENCE. Commentry Basin, Allier, France; Stephanian B-C, Upper Carboniferous (Doubinger & Vetter 1985).

DESCRIPTION. Print of an almost complete specimen, head, median part of left fore-wing and apical part of fore-wings missing; only apical parts of hind-wings discernible. Right fore-wing: length about 64 mm, width 17.5 mm; ScA distinct from anterior wing margin; branches of ScP strongly reticulated; ScP reaching RA 40.7 mm distal to wing base;

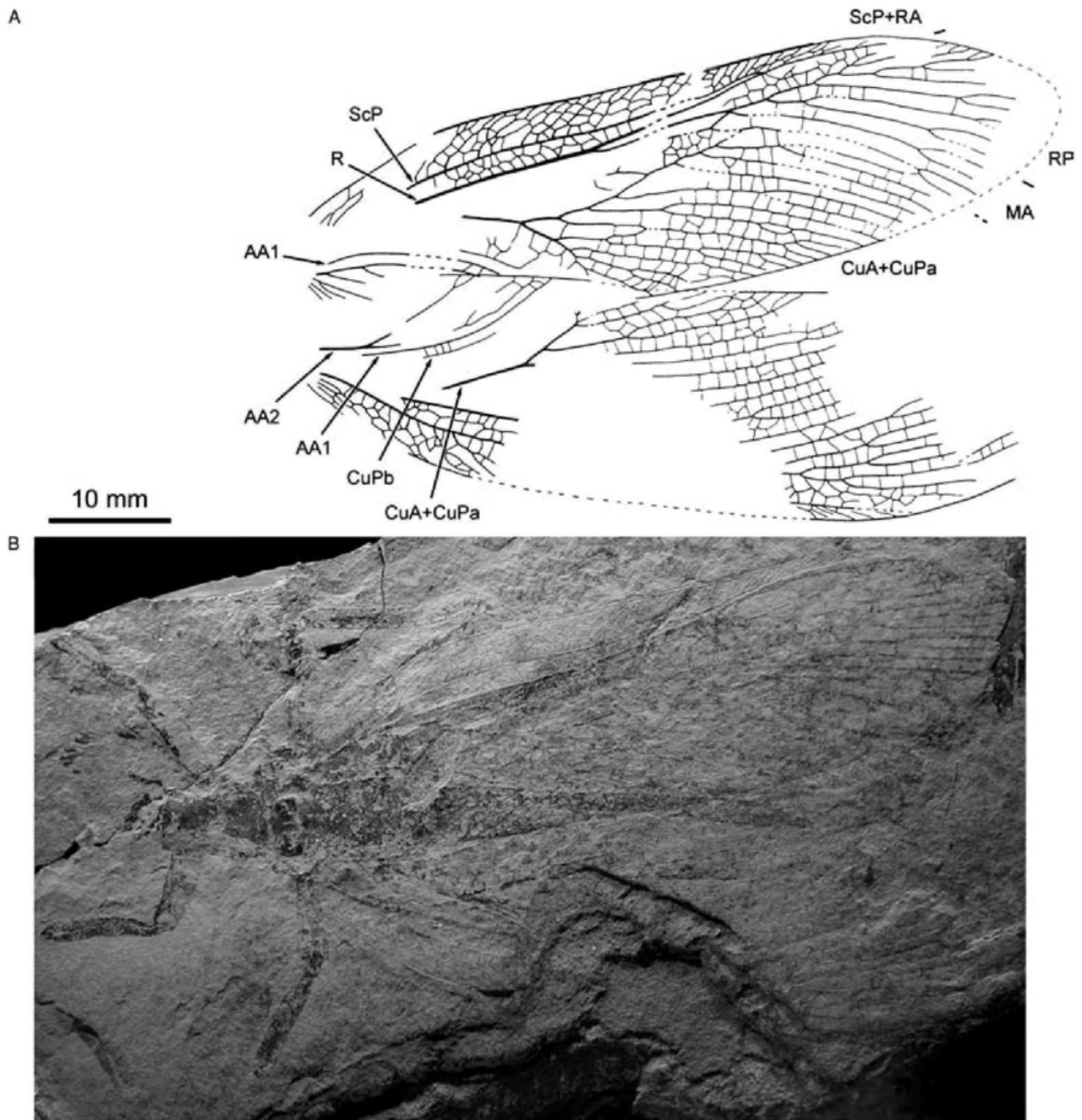


Figure 21 *Bouleites latipennis* Lameere, 1917 (MNHN-DHT-R51241 holotype: France; Upper Carboniferous). (A) Reconstruction of the forewings and (B) photograph (combined, print). R, radius; AA2, second anterior anal. For all other abbreviations see the legend to Figure 1.

RA without well defined anterior branches; origin of RP 25.6 mm distal to wing base; RP without clear pattern of ramification, with at least 10 branches; basal half of M not discernible; basal to the origin of RP, in area between R and CuA + CuPa, presence of a network of cross-veins but not clearly discernible; in this area, presence of a 'vein', maybe MP, slightly stronger than others, reaching anterior branch of CuA + CuPa, between third and fourth branches of this last vein; MA forked 9.5 mm distal to origin of RP; anterior branch of MA connected to RP; branches of MA distally forked; CuA + CuPa with two main branches, internally pectinate; anterior branch with more branches than

posterior one; branches of CuA + CuPa irregularly branched and reticulated; most anterior branch of CuA + CuPa connected with posterior branch of MA; CuPb strongly concave and weak; AA1 simple, AA2 posteriorly pectinate; numerous cross-veins, generally reticulated or sigmoidal, distinct and straight in postero-distal part of wing.

REMARKS. The vein MP is not determinable for certain, but the occurrence of a fusion of the most distal anterior branch of CuA + CuPa with the posterior branch of MA and of a fusion of the anterior branch of MA with RP both support a 'non-discernible MP' interpretation (see above).

CONCLUSIONS

This revision supports the 'archaeorthopterid' (and, consequently, 'orthopteroid') affinities of some 'protorthopterous' taxa, based on new examination of type material. These new assignments are mainly established on fore-wing venation, based on the typical course of CuA (fused with M, free, fused with a branch of CuP) and the branching pattern of CuP. These characters are highly suitable for supra-ordinal attribution because they are easy to recognise and are complex, minimising the risk of homoplasy.

The incompleteness of previous descriptions has led to erroneous generic and familial attributions. The most significant problems lie in the composition of the Ischnoneuridae *sensu* Carpenter (1992), in which the synonymies of the type genus are erroneous and the familial composition wrong: *Ischnoneura* is obviously related to the families Aetophlebiidae Handlirsch, 1906 and Narkeminidae Pinto & Pinto de Ornellas, 1991, supporting the opinion of Rasnitsyn (2002b), *Ctenoptilus* is probably more closely related to *Eoblatta*, while *Mesoptilus* is a Strephocladidae (O.B., unpublished results). Thus, one has to question the reliability of some palaeobiodiversity studies that use counts of families based mainly on Carpenter's classification (Jarzembowski & Ross 1996; Labandeira & Sepkoski 1993), at least concerning the Late Palaeozoic period.

Our work suggests that the Archaeorthoptera were highly diverse during the Late Carboniferous period. At that time, this clade comprised the orders Orthoptera, Caloneurodea and probably Titanoptera (Gorochov 2001), encompassing a set of diverse taxa, some of them highly specialised, such as those having a reduced MP and fore-legs with broadened femora. The Archaeorthoptera appears to have been a major component of the Late Carboniferous entomofauna, along with Palaeodictyopteroidea. It provides evidence of an evolutionary history longer than currently recorded.

Most taxa of the 'Protorthoptera' group *sensu* Carpenter (1992) are now confidently assigned either to the Archaeorthoptera or to the 'Grylloblattida' (Storozhenko 2002; Béthoux *et al.* 2005). These new data will serve as a basis for future work on the phylogenetic relationships in both of these groups, as well as of the whole 'Polyneoptera'.

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