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Source: Journal of Orthoptera Research, 12(1) : 57-62

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/1082-6467(2003)012[0057:PDBALB]2.0.CO;2

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Protophasma dumasii Brongniart 1879, a link between Orthoptera and the 'dictyopterid' orders?

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Abstract

In the perspective of the general review of the 'archaeorthopterid' insects (including Orthoptera and the extinct orders Caloneurodea and Titanoptera), a redescription of *Protophasma dumasii* Brongniart 1879, type species of the Protophasmatidae Brongniart 1885, is provided. The forewing morphology allows the assignment of this taxon to the Archaeorthoptera, but the hindwing morphology is very similar to that of Blattodea, with some particular features. *Protophasma dumasii* shares several symplesiomorphies with the Blattodea and Neoptera. Thus, this species is a good candidate to be the absolute outgroup for the future phylogenetic analysis of the Archaeorthoptera.

Key words

Archaeorthoptera, Protophasmatidae, Orthoptera, Blattodea, Carboniferous, Commentry, wing venation pattern

Introduction

The Commentry Basin (Allier, France; Upper Carboniferous) is famous for the numerous and well-preserved fossil insects discovered in this locality. Because this collection is one of the longest studied, it includes numerous type taxa, some being type species of orders. This deposit is 20My younger than the oldest deposit providing winged insects (Brauckmann *et al.* 1994), which ensures a strong significance of the fossils in the phylogenetic analyses of high rank in Pterygota.

Here I redescribe the first taxon described from this locality, *Protophasma dumasii* Brongniart 1879, type species of the Protophasmatidae Brongniart 1885. Despite its historical significance, this taxon has escaped a correct interpretation since its discovery, mainly because of the poor state of preservation of the material. Thanks to the definition of the Archaeorthoptera Béthoux & Nel, 2002 (including Orthoptera and extinct taxa such as the orders Titanoptera and Caloneurodea), a new homologization of the venation pattern of the Protophasmatidae is proposed. This family turns out to be of unexpected importance in the resolution of the relationships of the Orthoptera with the 'dictyopterid' orders.

Systematic paleontology

I follow the nomenclature of wing venation of the 'archaeorthopterid' insects proposed by Béthoux & Nel (2001, 2002). These authors did not specify the nomenclature of the anal veins. Thus, I use the nomenclature of the anal area proposed by Haas & Kukalová-Peck (2001), emended in a conservative way, without further hypothesis on the nature of the veins of the areas of AA and AP, *i.e.*, the composite nature of AA1+2 and AA3+4 stems, *sensu* Haas & Kukalová-Peck (2001) is considered as not clearly demonstrated.

Archaeorthoptera Béthoux & Nel, 2002

Protophasmatidae Brongniart, 1885
(*nom. correct.* Carpenter, 1992, *pro* Protophasmida Brongniart, 1885)

Protophasmida Brongniart, 1885, p. 59.
Protophasmidae Brongniart, 1893, p. 423.
Protophasmidae Lameere, 1917, p. 170.
Protophasmidae Laurentiaux, 1953, p. 449.
Protophasmidae Sharov, 1962, p. 117 (translated in Sharov, 1991, p.147).
Protophasmatidae Carpenter, 1992 p. 130.
Protophasmatidae Rasnitsyn, 2002a, p. 82.
Protophasmatidae Rasnitsyn, 2002b, p.258-260.

Composition

Type genus.— *Protophasma* Brongniart, 1879.

Diagnosis.— **Forewings**: M simple, at least basal of its mid-length; CuA + CuPa with numerous branches covering large part of posterior wing margin, but not organized in clear pattern of ramification; occurrence of well-developed AP area densely covered by veins and cross-veins. **Hindwings**: some branches of RP reaching RA; M forked very distally; contact between CuA and CuP limited to a simple point; CuA slightly arched towards CuP at this point and distally diverging from CuP; CuP branched distal of its mid-length; area between CuP and first AA vein broad, with secondary convex veins between them; two convex veins in AA area; AP area densely covered by veins and cross-veins; posterior margin nearly straight at level of anal fan. **Both wing pairs**: cross-veins reticulated except in AP area.

Discussion

The Protophasmatidae can be attributed to the Archaeorthoptera after the occurrence in the forewings of a fusion of CuA (from M + CuA) with the anterior branch of CuP (CuPa) into a composite common stem. Nevertheless, most of the venational features of this family can be considered as plesiomorphies within Archaeorthoptera or cannot be reliably polarized (see below). A possible apomorphy of this family would be 'in hindwings, CuP branched distal of its mid-length'.

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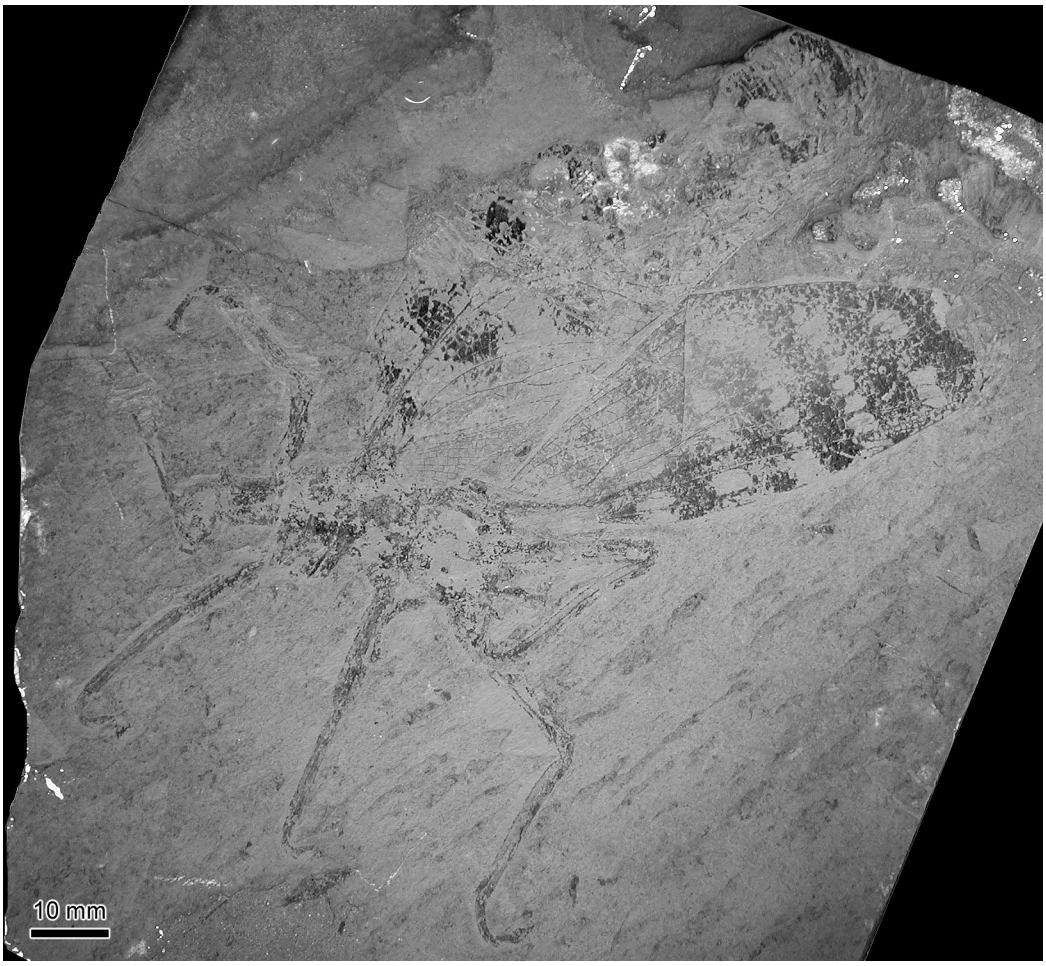


Fig. 1. *Protophasma dumasii* Brongniart, 1879, holotype specimen MNHN-LP-R.51150: photograph of whole specimen (under alcohol).

Protophasma Brongniart, 1879

Protophasma Brongniart, 1878, p. 58, *nom. nud.*
Protophasma Brongniart, 1879, p. 99, pl. IV, figs 1-4, 6, 9.

Composition

Type species.— *Protophasma dumasii* Brongniart, 1879

Diagnosis.— That of the family.

Protophasma dumasii Brongniart, 1879
Figs 1-4

Protophasma dumasii Brongniart, 1878, p. 58, *nomen nudum*.
Protophasma dumasii Brongniart, 1879, p. 99, pl. IV, figs 1-4, 6, 9.
Protophasma dumasii Brongniart, 1893, p. 427, pl. XLIX (33), figs 1-3.
Protophasma dumasi Carpenter, 1992, p. 130.
Protophasma dumasi Rasnitsyn, 2002b, p.359, fig. 359 (new figuration).

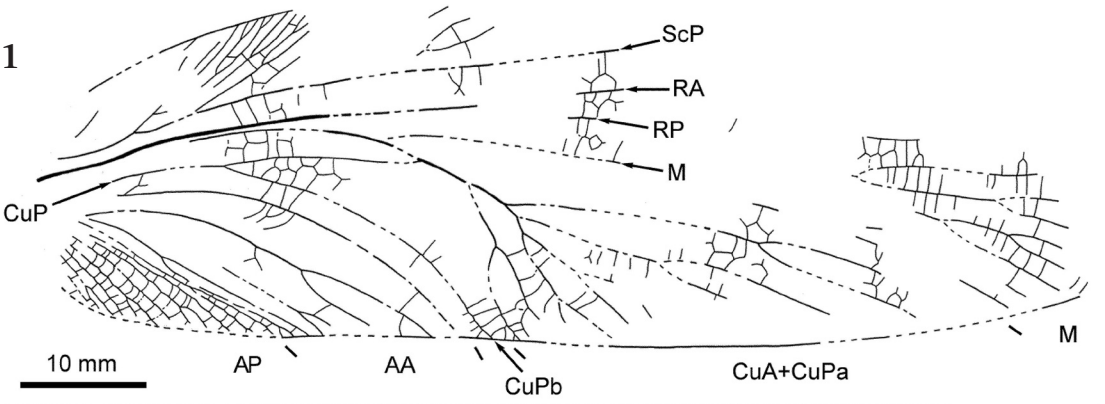
Diagnosis.— By monotypy, that of the genus.

Material.— Holotype specimen MNHN-DHT-R51150; specimen MNHN-DHT-R51334.

Short descriptions.— A description is rendered necessary because of a new preparation of the type specimen (October 2002), and our new interpretation of the wing venation. Also, the most recent illustration of the holotype and interpretation of the wing venation, provided by Rasnitsyn (2002b: fig. 359), were incomplete and partly erroneous.

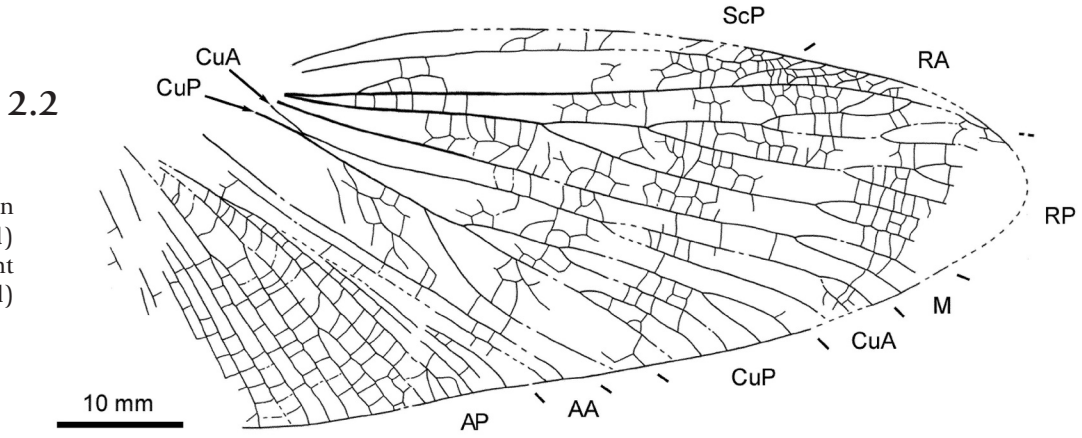
Holotype specimen MNHN-DHT-R51150.— (Figs 1-3): individual with head, thorax, 5 legs, counterpart of the left forewing and part of the left hindwing (with AP area folded), with relief of wing veins weakly preserved. **Left forewing** (Fig. 2.1): wing incomplete and damaged; preserved length 82.8 mm, width about 27.1 mm; area between anterior wing margin and ScP broad, 6.1 mm wide; ScP with numerous parallel and dense veins in preserved part; RA and RP probably diverging opposite first branch of CuA + CuPa; RP very probably distally branched; M + CuA close but distinct from R at wing base; CuA + CuPa with at least 11 branches reaching posterior wing margin, without clear pattern of ramification; branches of CuA + CuPa covering about second third of posterior wing margin; CuPa long (15.6 mm) basal of its fusion with CuA; CuPb simple; first vein in AA area simple (AA1?); other veins in this area branched, arising from common point; AP area with dense net of veins and cross-veins; cross-veins reticulated and less dense in other parts of wing. **Left hindwing** (Figs 2.2, 3): wing almost complete, estimated length 73.5 mm, width (opposite end of first AA vein) 28.1 mm; area between anterior wing margin and ScP narrow; RA with 5 distal anterior branches; RA and RP diverging basally; RP posteri-

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2.1: Reconstruction (coloration omitted) and photograph of the left forewing (counter-print, under alcohol).





2.2: Reconstruction (coloration omitted) and photograph (print reversed, under alcohol) of the left hindwing.

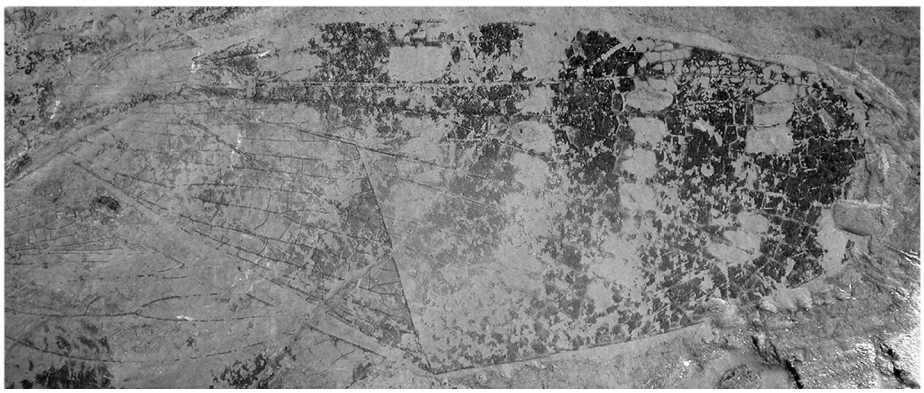


Fig. 2. *Protophasma dumasii* Brongniart, 1879, holotype specimen MNHN-LP-R.51150.

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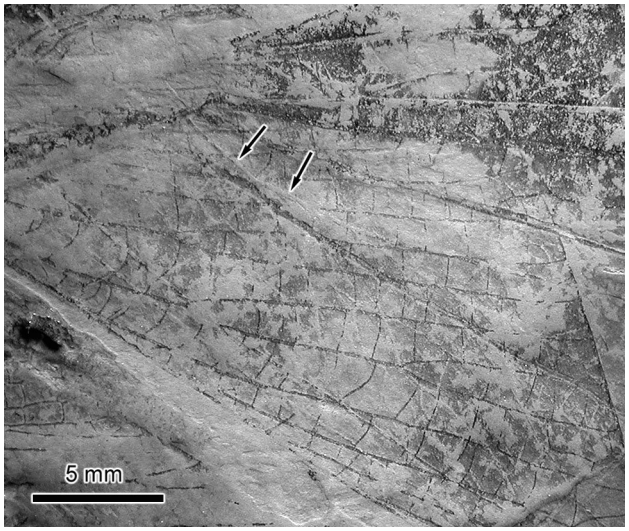


Fig. 3. *Protophasma dumasii* Brongniart, 1879, holotype specimen MNHN-LP-R.51150: photograph (under alcohol) of the hindwing base; arrows indicate the course of CuA basal and distal of connection with CuP.

orly pectinate with 4 main branches distally branched; nearly all anterior branches of RP reaching RA; M forked very distally; contact between CuA (convex) and CuP (strongly concave) limited to a single point, just distal of divergence of RA and RP; CuA slightly arched towards CuP at this point and distally diverging from CuP; CuA forked 24.9 mm distal of this contact; CuP branched 14.8 mm distal of this contact, with 5 branches, without clear pattern of ramification; area between CuP and first AA vein broad, 5.2 mm wide, of unvarying width, and filled with secondary convex veins; AA area with 2 simple and straight veins; AP area with dense net of veins and cross-veins; cross-veins less dense and reticulated in other parts of wing.

Specimen MNHN-DHT-R51334.— (Fig. 4; very probably the specimen figured by Brongniart, 1893: pl. XLIX (33), fig. 3): poorly preserved right forewing probably superimposed with remains of another wing; AP area folded, tentatively but arbitrarily replaced on the reconstruction; preserved length about 57.0 mm; area between anterior wing margin and ScP broad, 4.9 mm wide; ScP with a dense net of veins in its basal part, but less dense in its distal part; RP strongly arched 15.4 mm distal of its origin (probable teratology?); M with an anterior branch (or secondary vein?) 22.4 mm distal of its divergence from CuA; CuA + CuPa with at least 9 branches reaching posterior margin, but not organized into clear pattern of branching; area between CuA + CuPa and CuPb with secondary strengthened veins; CuPb simple; AP area with dense net of veins and cross-veins; except in AP area, cross-veins reticulated.

Geological settings.— Commentry Basin, Allier, France; Stephanian B-C, Upper Carboniferous (Doubinger & Vetter 1985); insect-biostratigraphy zone: *Sysciophlebia-praepilata*-Zone (Schneider 1982).

Phylogenetic implications

The homologization of the forewing area labeled 'AP' must be discussed. The relief of the veins is altered and there is no clear evidence that veins in this area were concave, as expected from veins of the posterior sector. Nevertheless, their organization strongly differs from veins in the AA area, and is very similar to that occurring in the undisputable AP area of the hindwings. Thus, I interpret this area as that of AP. Kukalová-Peck (1991) considered that convex veins could be branches of AP in the 'polyneopterous' orders. This contradicts her ground-plan pattern of Pterygota. Furthermore, these veins do not show the typical organization shown by the AP veins in *Protophasma*. Thus, at least for 'polyneopterous' orders, I propose that the veins interpreted as AP by Kukalová-Peck are AA veins, after the organization of true AP veins in *Protophasma*.

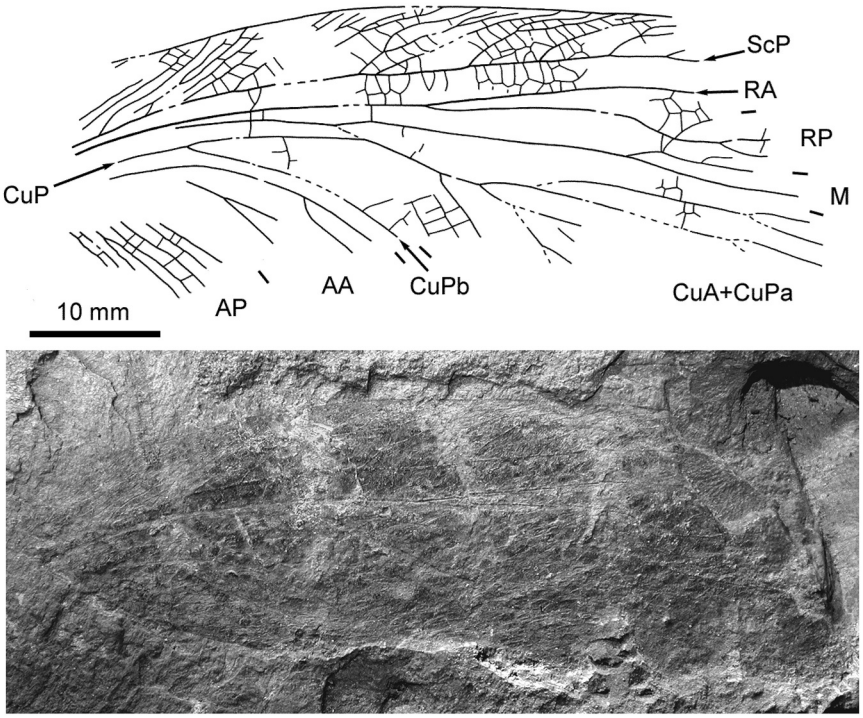


Fig. 4. *Protophasma dumasii* Brongniart, 1879, specimen MNHN-LP-R.51334: reconstruction (coloration omitted) and photograph (composite of photographs dry and under alcohol) of the right forewing (counter-print, reversed).

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The occurrence of a well-developed AP area in forewings is unknown in all other representatives of the Archaeorthoptera and, actually, in the whole of Neoptera. Polarized after the putative sister-groups of Neoptera (*e.g.*, the 'paleopterous' orders), this character must be considered as a plesiomorphy within Pterygota.

Protophasma shows some other features unknown in Archaeorthoptera. Among them, the most prominent is the absence of fusion of CuA with (a branch of) CuP in the hindwings, also absent in Blattodea. Because this last order is a putative sister group of the Archaeorthoptera, this character must be considered as a plesiomorphy within Archaeorthoptera. It must be noted that both veins CuA and CuP are connected near the wing base, which could be considered as a 'transitional' state toward the more complete fusion occurring in other Archaeorthoptera.

In the hindwings, the M, long, simple and not clearly differentiated into MA and MP, is a character unknown in other Archaeorthoptera, in which it is branched near its origin. Nevertheless, this structure can be found in some Blattodea (Schneider 1984). Possibly, this structure could be a plesiomorphy within the Archaeorthoptera.

The character state in hindwings, 'CuP branched distal of its mid-length' is unknown in all the 'polyneopterous' orders. In Blattodea, CuP is simple (in both fore and hindwings), but branched near the wing base in Archaeorthoptera (in both fore and hindwings). Thus, the state 'CuP branched distal of its mid-length' cannot be polarized. Its apomorphic status in Protophasmatidae is debatable: it may be a state 'transitional' between Blattodea and Archaeorthoptera.

Furthermore, the hindwing 'anojugal lobe' of the Protophasmatidae is similar to that defined for Blattodea and Isoptera by Haas & Kukalová-Peck (2001), *viz.* 2 simple convex veins occurring in the AA area, separated from the AP area by the 'anal fold', along which the hindwing is folded, as in the holotype specimen of *Protophasma dumasii* (see Figs 2.2, 3). Thus, the AA area is very reduced: it is the 'partial anojugal lobe' *sensu* Haas & Kukalová-Peck (2001). In 'Orthoneoptera' *sensu* Haas & Kukalová-Peck (2001) (a group that comprises at least all the representatives of the Archaeorthoptera), the AA area is well developed, contributing to the 'full anojugal lobe'. Following Haas & Kukalová-Peck (2001) but emendating them, I consider that the 'partial anojugal lobe' is present in 'Blattoneoptera', 'Hemineoptera', 'Endoneoptera' but also in basal 'Orthoneoptera' (*i.e.*, Protophasmatidae) and must then be considered as plesiomorphic within Neoptera.

In conclusion, the hindwings of the Protophasmatidae retain many plesiomorphic features linkable with the hindwing venation pattern of Blattodea, despite the fact that their forewings already show the typical and complex medio-cubital pattern of the Archaeorthoptera.

Conclusion

Following the present work, the Protophasmatidae are assigned to the Archaeorthoptera but must be considered as belonging to the stem group of this supraordinal clade, and potential sister-group of the whole clade. It will be necessary to include *Protophasma* in future attempts at phylogenetic analyses of the Archaeorthoptera (in prep.). The Protophasmatidae could be considered as a model of a 'link' between the Archaeorthoptera and the 'dictyopterid' orders.

The Protophasmatidae were contemporaneous with much more derived Archaeorthoptera (*e.g.*, Orthoptera and Caloneurodea — an extinct Paleozoic order). Thus, by its numerous putative plesiomorphies, this family seems to have been a 'relict' taxa during the Upper Carboniferous. Because the record of Lower Carboniferous insects is very sparse, such remains are of great help in phylogenetic attempts.

Acknowledgments

I thank Dr. A. Nel (MNHN, Paris) for his advice. I thank Prof. J. W. Schneider (Freiberg University of Mining and Technology, Germany) and an anonymous referee for their constructive comments on the manuscript. This work was supported by the grant 'Germaine Cousin' of the 'Société Entomologique de France' and by UMR 5143 and UMR 5120 of CNRS.

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