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Lodetiella magnifica nov. gen. and nov. sp. (Insecta: Palaeodictyoptera; Permian), an extreme situation in wing morphology of palaeopterous insects

Lodetiella magnifica nov. gen. et nov. sp. (Insecta : Palaeodictyoptera ; Permien), un cas extrême dans la morphologie alaire des insectes paléoptères

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Received 30 May 2005; accepted 22 April 2006

Available online 23 January 2007

Abstract

Based on published data and review of *Mecynoptera splendida* Handlirsch, 1904, a wing venation ground plan applicable to most taxa of the Palaeozoic superorder Palaeodictyopteroidea is proposed, where each major vein system has a simple anterior sector, and, primitively, a dichotomously branched posterior sector. *Lodetiella magnifica* nov. gen. and sp. is described, based on an isolated hind wing from the Salagou Formation (Middle to Late Permian; Hérault, France). The venation of *Lodetiella magnifica* conforms to the predicted ground plan, but differs by its simple posterior cubitus sector. This character is diagnostic of the family Calvertiellidae (Palaeodictyoptera), whose diagnosis is updated. Wing movement in flight is inferred from the peculiar wing vein organization of *Lodetiella magnifica*. Some ecological preferences might explain the relative rarity of calvertiellids in the fossil record.

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Résumé

D'après les données publiées et la révision de *Mecynoptera splendida* Handlirsch, 1904, un plan de base de nervation alaire, applicable à la plupart des taxons du super-ordre paléozoïque Palaeodictyopteroidea, est proposé, où chacun des systèmes de nervures majeurs a un secteur antérieur simple et, plésiomorphiquement, un secteur postérieur branché dichotomiquement. *Lodetiella magnifica* nov. gen. et sp. est décrit, d'après une aile postérieure isolée provenant de la Formation Salagou (Permien moyen à supérieur ; Hérault, France). La nervation de *Lodetiella magnifica* est conforme au plan de base décrit, mais en diffère par son secteur postérieur du cubitus simple. Ce caractère est diagnostique de la famille Calvertiellidae (Palaeodictyoptera), dont la diagnose est remise à jour. Le mouvement de l'aile en vol est déduit de l'organisation particulière de la nervation alaire de *Lodetiella magnifica*. Certaines préférences paléocéologiques pourraient expliquer la rareté relative des calvertiellides dans le registre fossile.

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Keywords: Palaeoptera; Calvertiellidae; *Mecynoptera*; *Carryzopteryx*; Lodève basin; Flight mode; Ecological preference

Mots clés : Palaeoptera ; Calvertiellidae ; *Mecynoptera* ; *Carryzopteryx* ; Bassin de Lodève ; Type de vol ; Préférences écologiques

1. Introduction

The insect super-order Palaeodictyopteroidea, currently nested within the 'Palaeoptera' complex, is known only from the Late Paleozoic. It includes the orders Palaeodictyoptera Goldenberg, 1877, Megaseoptera Brongniart, 1885, and

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Diaphanopteroidea Handlirsch, 1919. The latest representatives of the super-order show a wide array of wing structures apparently related to flight abilities (Wootton and Kukalová-Peck, 2000). The overall wing designs of several specimens are very similar, though nonhomologous, to those of highly derived recent groups. Indeed, wing structure led some early authors to consider some orders as closely related to Hymenoptera (Tillyard, 1924).

Here we describe a new Permian Palaeodictyoptera, discovered by one of us (J. W. Schneider) in the Salagou Formation (Hérault, France; Middle to Late Permian) belonging to the family Calvertiellidae Martynov, 1931. Prior to the emendation of the family and the description of the new taxon, we propose an insect wing venation ground plan that is relevant to the whole super-order Palaeodictyopteroidea. Modifications of this ground plan, which is applicable to the Calvertiellidae, will be indicated in the diagnosis of this family.

2. Wing venation ground plan in Calvertiellidae and related taxa

Interpretation of the wing venation of *Lodetiella magnifica* nov. gen. and sp. proposed herein is based upon observations made on taxa supposed to be closely related. We follow the insect wing venation nomenclature proposed by Kukalová-Peck (1991), and use the following abbreviations: 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; A, Analis; AA, anterior Analis; AP, posterior Analis; J, Jugal. The term ‘system’ is used herein as defined by Béthoux (2005). The presence of a jugal area barely has been demonstrated, and few references or photographs of corresponding material are available (but see Béthoux and Nel, 2003a: Fig. 4), though described by Kukalová-Peck (1991) in her theoretical insect plan of the insect wing. The wing venation of *Mecynoptera splendida* Handlirsch, 1904 (Late Carboniferous; Belgium; Fig. 1) yields additional evidence of a jugal area in the ground plan of insect wing venation. The only available specimen is probably a forewing. If not, it probably belongs to an insect in which both wing pairs were very similar (as in Dictyoneuridae Handlirsch, 1906a or Eugereonidae Handlirsch, 1906b for example; see Carpenter, 1992). In wings of *M. splendida* the radial, median, cubital, and anal systems are easily recognisable by their uniform pattern of branching (all anterior sectors simple, all posterior sectors branched; see below), and their very distinct basal stems. A well-developed system occurs basal to the anal area, which we interpret herein as a jugal area. Such a well-developed jugal area is a probable symplesiomorphy for the whole Pterygota, but this hypothesis needs further investigation.

In several families of the order Palaeodictyoptera (at least the Dictyoneuridae Handlirsch, 1906a, Lithomanteidae Handlirsch, 1906a, Megaptilidae Handlirsch, 1906b, Eugereonidae Handlirsch, 1906b, Calvertiellidae Martynov, 1931, Lycocercidae Handlirsch, 1906a, Breyeriidae Handlirsch, 1906b, and Tchirkovaeidae Sinitshenkova, 1979), the anterior sectors of the main systems (i.e. RA, MA, CuA, and AA) are simple, while the

posterior sectors (i.e. RP, MP, CuP, AP) are very generally branched. This pattern is obvious in *M. splendida* (Fig. 1). Wootton and Kukalová-Peck (2000: 151) already noticed this pattern and discussed its morphofunctional implications, but without mentioning its potential phylogenetic significance.

Although the posterior sectors are generally simple in members of the orders Megasecoptera and Diaphanopteroidea, which also belong to the Palaeodictyopteroidea, several taxa in these orders have branched MP and CuP (e.g. in *Aspidothorax* Brongniart, 1893, *Diaphanoptera* Brongniart, 1893; see Béthoux and Nel, 2003b for a revision of the latter genus), a state we interpret as plesiomorphic for these orders. We propose that the above-mentioned pattern applies to a part of the Palaeodictyoptera and the orders Megasecoptera and Diaphanopteroidea.

In the Palaeodictyoptera, though the branching of the posterior sectors does not strictly conform to a pattern, it is frequently dichotomous. Such a branching pattern is obvious in the genera *Dictyoptilus* Brongniart, 1893 (see Kukalová, 1969) and *Breyeria* de Borre, 1875 (see Kukalová, 1959), for example. The recurrence of branching of the first posterior branch of RP in the palaeodictyopterid families cited above also supports the hypothesis of a primitively dichotomous branching pattern. The wing venation of the Calvertiellidae follows this pattern. We consider this pattern plesiomorphic for the family, based upon its occurrence in all putative sistergroups (families cited above). Modifications of this pattern that are typical of the Calvertiellidae are detailed in the new diagnosis of the family (see below).

It is difficult to polarize the character states of the pattern described above, for several reasons. First, the ordinal position of many Late Paleozoic paleopterous species (including those Palaeodictyoptera that do not conform to the above-cited pattern) is yet uncertain (see for example Béthoux and Nel, 2003a; Willmann, 1999). The relationships of the Palaeodictyopteroidea with respect to other ‘paleopterous’ orders are unknown. Additionally, the ‘most basal’ modern neopterous taxon, usable as sister-group for ‘paleopterous’ orders, is undetermined, due to difficulties to resolve the basal Neoptera phylogeny. Moreover, knowledge of fossil ‘basal’ Neoptera is chronically incomplete, due to incomplete descriptions (for example, the re-description of *Protophasma dumasii* Brongniart, 1879 in Béthoux, 2003, reveals unexpected significance of this taxon among polyneopterous orders) and a lack of fossils of the earliest winged insects (Lower Carboniferous or earlier; Engel and Grimaldi, 2004; Grimaldi, 2001).

The ‘Gryllones–Scarabaeones’ hypothesis developed by Rasnitsyn (Rasnitsyn and Quicke, 2002) regarding relationships of fossil insect orders, provided some hypotheses about the closest relatives of the Palaeodictyoptera, Megasecoptera, and Diaphanopteroidea. However, this hypothesis posits a diphyletic Neoptera, viz. the ‘Gryllones’, which includes the orders commonly referred to as Polyneoptera, was hypothesized to be sister group to the ‘Scarabaeones’, including all other winged orders (i.e. paleopterous orders, Paraneoptera and Holometabola). We follow Terry and Whiting (2005) and Grimaldi and Engel (2005), among others, and we consider the ‘Gryllones–Scarabaeones’ (i.e. diphyletic Neoptera) hypothesis unsustainable.

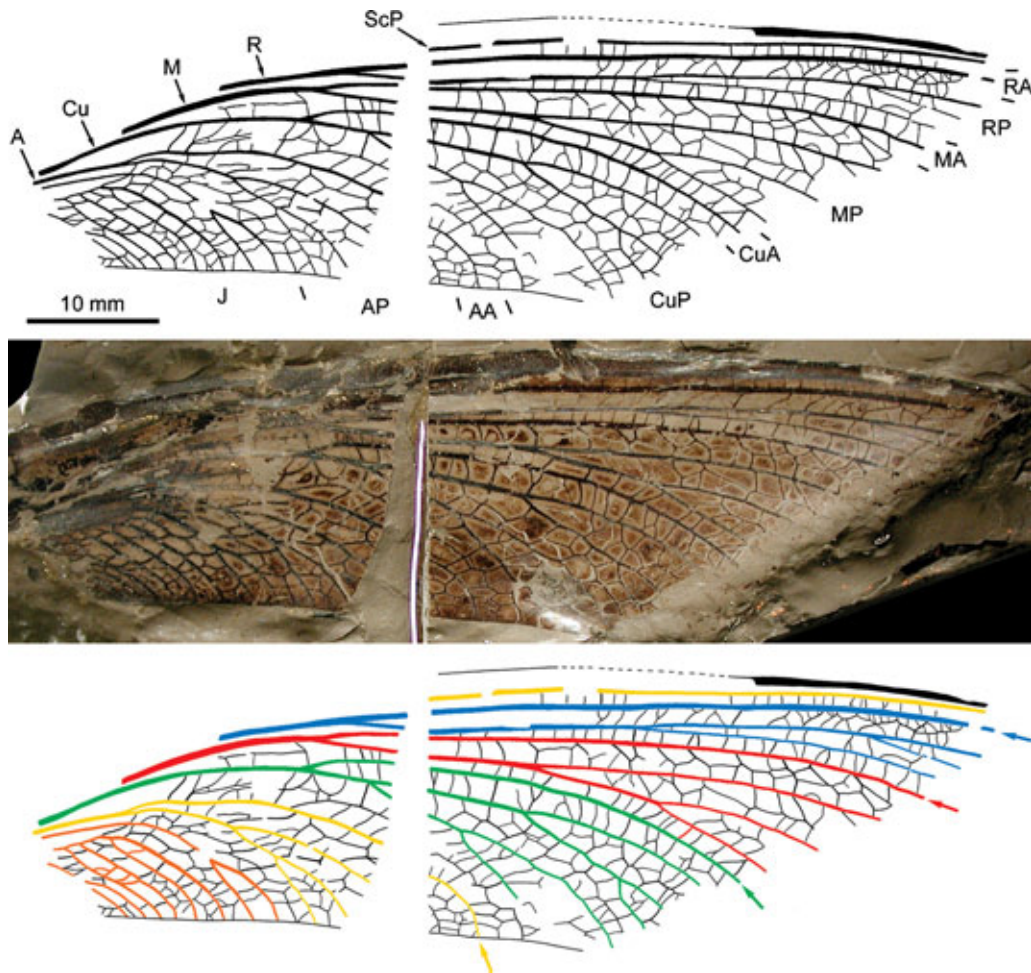


Fig. 1. *Mecynoptera splendida* Handlirsch, 1904: left forewing, reconstruction, photograph (positive imprint, reversed, under alcohol), and colorized vein systems pattern (color-coding following Kukalová-Peck and Lawrence, 2004): yellow for the Subcosta (Sc) system; blue for the Radius (R) system; red for the Media (M) system; green for the Cubitus (Cu) system; yellow for the Analis (A) system; and orange for the Juga (J) system; arrows indicate anterior sectors, all simple (holotype RBINS a7690; Royal Belgian Institute of Natural Sciences, Brussels, Belgium); Late Carboniferous, Belgium.

Fig. 1. *Mecynoptera splendida* Handlirsch, 1904 : aile antérieure gauche, reconstruction, photographie (empreinte positive, inversée, en immersion à l'alcool), et patron de systèmes de veines colorisé (code de couleur d'après Kukalová-Peck and Lawrence, 2004) : jaune pour le système Subcosta (Sc) ; bleu pour le système Radius (R) ; rouge pour le système Media (M) ; vert pour le système Cubitus (Cu) ; jaune pour le système Analis (A) ; et orange pour le système Juga système (J) ; les flèches indiquent les secteurs antérieurs, tous simples (holotype RBINS a7690 ; Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgique) ; Carbonifère supérieur, Belgique.

Finally the sister group of the Palaeodictyopteroidea is yet undetermined, and the character states of the pattern we discussed above cannot be polarized at the level of the Pterygota. Nevertheless, it is unarguably a major insect wing venation ground plan.

3. Material and methods

We followed the drawing and photographic procedures described in Béthoux et al. (2004).

4. Systematic palaeontology

Family CALVERTIELLIDAE Martynov, 1931

Synonymy list: Calvertiellidae Martynov, 1931: p. 146; Mongolodictyidae Sinitshenkova, 1992: p. 98.

New diagnosis: In fore- and hind wings: ScP ending on RA (i.e. ScP does not reach the anterior wing margin as an independent vein); first posterior branch of RP branched; CuP simple; presence of a strengthened cross-vein located in the area between R and M, connecting the point of divergence of RA, RP, and M (either at the point of divergence of MA and MP or basal to it; 'ct' after Kukalová, 1964; absent in *Carrizopteryx* Kukalová-Peck, 1976 in Kukalová-Peck and Peck (1976), in which the stems of R and M are connected instead; see Fig. 2); presence of a strengthened cross-vein connecting M (either at the point of divergence of MA and MP or basal to it, usually in prolongation of 'ct') and CuA ('cv' after Kukalová, 1964; absent in *Calvertiella* Tillyard, 1925, in which CuA fuses with M at length; the origin of CuA is unknown in *Carrizopteryx*). The area of the strengthened cross-veins is elevated somewhat roof-like. In addition, several representatives of the Calvertiellidae have more or less organized intercalary convex veins,

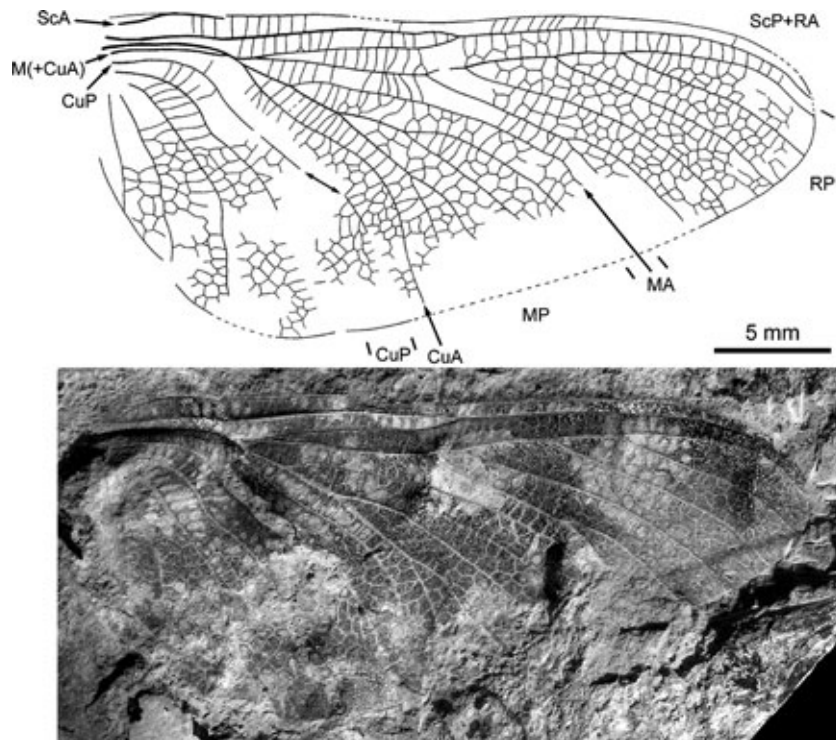


Fig. 2. *Carryzopteryx arroyo* Kukalová-Peck in Kukalová-Peck and Peck (1976). Right hind wing, reconstruction and photograph (negative imprint, light-mirrored, composite) (holotype UNM 3157; University of New Mexico, Albuquerque, NM, USA); Virgilian, Late Carboniferous, NM, USA.

Fig. 2. *Carryzopteryx arroyo* Kukalová-Peck dans Kukalová-Peck et Peck (1976). Aile postérieure droite, reconstruction et photographie (empreinte négative, lumière inversante, composite) (holotype UNM 3157; université du Nouveau Mexique, Albuquerque, NM, États-Unis); Virgilien, Carbonifère supérieur, NM, États-Unis.

occurring only between the branches of the posterior sectors. In other words, there are no intercalary veins in the areas surrounding the anterior sectors.

Composition: Included genera: *Calvertiella* Tillyard, 1925, *Mongolodictya* Sinitshenkova, 1992, *Sharovia* Sinitshenkova, 1977 (in Sharov and Sinitshenkova, 1977), *Moravia* Kukalová, 1964, *Moraviptera* Kukalová, 1955, *Carryzopteryx* Kukalová-Peck, 1976 (in Kukalová-Peck and Peck, 1976), *Lodetiella* nov. gen.

Discussion: This new diagnosis is based on literature data (Kukalová, 1964; Kukalová-Peck and Peck, 1976; Sinitshenkova, 1979, 2002) and direct observation of holotypes of *Calvertiella permiana* Tillyard, 1925, *Carryzopteryx arroyo* Kukalová-Peck, 1976 (in Kukalová-Peck and Peck, 1976) (Fig. 2), and *Lodetiella magnifica* nov. sp. (Fig. 3).

The family Mongolodictyidae Sinitshenkova, 1992 is based on one genus and species, *Mongolodictya callida* Sinitshenkova, 1992. The type specimen is a fragment of the mid part of a wing, with the apex of ScP, bases of branches of RP, median part of MA and three branches of MP preserved (Sinitshenkova, 1992). Nothing is known of the structure of its wing base, especially the organization of the cubital vein. *Lodetiella* nov. gen. shares with *Mongolodictya* its typical fusion of ScP and RA, the only putative apomorphy of the Mongolodictyidae. *Lodetiella* n. gen. is a genuine Calvertiellidae (see below). Based upon our more complete material, we consider the Mongolodictyidae as a junior synonym of Calvertiellidae stat. nov.

The interpretation of the cubito-anal area in the hind wings of Calvertiellidae poses a problem of homology. Several convex branches of AA are present in forewings of the representatives of the family, suggesting that CuP is simple. However, in hind wings, the presence of four concave branches basal to CuP contradicts the pattern of alternation of anterior-convex and posterior-concave sectors. These veins either belong to AA and their relief has been reversed, maybe as a result of biomechanical constraints, or AA is absent and these branches belong to AP (as suggested by the occurrence of convex intercalary veins between them). An example of an increasing reduction of AA area is known in blattids (Schneider, 1984a: Pl. 4), though AA is always present.

Genus *Lodetiella* nov. gen.

Type species: *Lodetiella magnifica* nov. sp.

Etymology: After the town 'Lodève' and the end of the genus name *Calvertiella*.

Diagnosis (based on hind wing): Costal margin basally widened, ScP reaching RA, with RA apparently ending in ScP; only the two bases of the two first branches of RP are basal to the point of fusion of ScP and RA; MA with a distinct curve at the middle of the wing; presence of long longitudinal concave intercalary veins between branches of the posterior sectors of main veins; the two posterior branches of MP, the intercalary vein between them, CuA, CuP, branches of anal vein, and intercalary veins between them strongly sigmoidal (autapomorphy); cubito-anal area very broad; basal part of CuA

aligned with basal part of CuP (not bent towards M); R, M, and Cu well separated at wing base.

Discussion: *Lodetiella* nov. gen. can be attributed to the Palaeodictyoptera: Calvertielloidea sensu Sinitshenkova (2002: 117, Fig. 138) on the basis of the following characters: wing wide basally, broad, with intricate archaediectyon; main veins arching basally; ScP scarcely extending beyond wing mid-length; CuP simple. Sinitshenkova (2002) included the two families Mongolodictyidae Sinitshenkova, 1992 and Calvertiellidae Martynov, 1931 in this superfamily. However, we propose to synonymize them (see above).

It is premature to make a phylogenetic analysis of the Calvertiellidae because some species are based on forewings, while others are known from hind wings only, and some even on the basis of very incomplete fragments of wings (see below). We attempt here a direct comparison of *Lodetiella* nov. gen. to known taxa.

Mongolodictya Sinitshenkova, 1992 differs from *Lodetiella* nov. gen. in the location of the bases of the branches of RP, which are mostly basal to the point of fusion of ScP with RA. In addition, MA is straight below the base of the first posterior branch of RP, instead of being curved as in *Lodetiella* nov. gen.

The genus *Calvertiella* Tillyard, 1925 (monotypic: *C. permiana* Tillyard, 1925) is based on a complete forewing from the Wellington shale, Lower Permian of Kansas, USA (Tillyard, 1925; Kukulová, 1964). It differs from *Lodetiella* nov. gen. by M and CuA partly fused with R in a ‘cuticular thickening’ sensu Kukulová (1964: Text-fig. 1). Its MP has only three curved branches, instead of four in *Lodetiella* nov. gen. *Calvertiella* has veins in the anal area somewhat sigmoidal, but less than in *Lodetiella* nov. gen. Additionally the network of cross-veins is less dense in *Calvertiella* than in *Lodetiella* nov. gen.

Sharovia Sinitshenkova, 1977 in Sharov and Sinitshenkova (1977), with two species (*S. sojanica* Sinitshenkova, 1977, Kazanian of Soyana, and *S. tshekardica* Ivanov, 2000, Kungurian, Middle Urals, Russia), is based on the apical halves of wings (see Sharov and Sinitshenkova, 1977: Fig. 6; Ivanov, 2000). Nothing is known about the form of veins CuA, CuP, the anal area, and the basal half of M. *Sharovia sojanica* differs from *Lodetiella* nov. gen. in that only the base of the first branch of RP is basal to the apex of ScP, and MA is straight below the base of the first branch of RP. In *S. sojanica* the posterior-most main branches of MP are not strongly sigmoidal, unlike in *Lodetiella* nov. gen. Lastly, its RA is not ending in ScP. *S. tshekardica* is based on a very fragmentary apex of the wing, with no diagnostic structure preserved, though ‘similar’ to *S. sojanica* (after Ivanov [2000: S289, Fig. 1]). We consider it as a Palaeodictyopteroidea incertae sedis nov. stat.

Moravia Kukulová, 1964 (with two species *M. convergens* Kukulová, 1964 from the Lower Permian of Moravia, and *M. grandis* Carpenter, 1979 from the Lower Permian, Oklahoma, USA) is based on hind wings (Kukulová, 1964; Carpenter, 1979). Both differ from *Lodetiella* nov. gen. in the area between ScP and C being basally not widened, its most posterior main branches of MP, CuA, CuP and anal veins not

strongly sigmoidal. *Moravia* shares with *Lodetiella* nov. gen. the basal part of CuA not perpendicular to Cu.

Moraviptera Kukulová, 1955 (monotypic: *M. reticulata* Kukulová, 1955, Lower Permian, Moravia) is based on the costo-apical half of a wing. It differs from *Lodetiella* nov. gen. in its short fork of the first posterior branch of RP, by the lack of long secondary longitudinal veins between branches, and in the absence of long secondary longitudinal veins between the branches of MP. Also, CuA is, apparently, partly fused with M and R, though this character is ambiguous since this part of the wing is poorly preserved (Kukulová, 1955: Fig. 3).

Two species are assigned to the genus *Carrizopteryx* Kukulová-Peck, 1976 (in Kukulová-Peck and Peck, 1976). *C. arroyo* Kukulová-Peck, 1976 (in Kukulová-Peck and Peck, 1976) is based on a complete hind wing from the Carboniferous-Permian transition of New Mexico (USA; Lucas and Krainer, 2004; Schneider et al., 2004). We provide a new figure of the holotype of *C. arroyo* (Fig. 2) because the original description was partly erroneous. *C. lucasi* Sinitshenkova, 2004 (in Rasnitsyn et al., 2004) is based on a small fragment of a fore wing (?) from the same locality as *C. arroyo*. However, no familial diagnostic character is preserved in the type of *C. lucasi*. Furthermore, in all Calvertiellidae the first posterior branch of RP is forked distal to the origin of the second posterior branch of RP, unlike in *C. lucasi* (assuming that the two most basal branches belonging to RP in *C. lucasi* arises from a single stem). Hence, we consider *C. lucasi* as a Palaeodictyopteroidea incertae sedis nov. stat.

As redefined, *Carrizopteryx* differs from *Lodetiella* nov. gen. in the absence of a widened costal area, the absence of sigmoidal veins, the absence of secondary longitudinal veins between branches of RP and MP, the absence of strengthened cross-veins between R and M, and the more distal branching of MA and MP.

Lodetiella magnifica nov. sp.

Fig. 3

Material: Holotype specimen Ld LAP 679 (La Lieude 4a/97/13, S. Roque Longue), Coll. Lapeyrie, housed at the Musée of Lodève (Hérault, France).

Type locality and horizon: Lodève basin, north of La Lieude farm, Rieupeyre valley, south of Roque Longue (Gand et al., 1997); Merifons Member, Salagou Formation; Late Early to Middle Permian.

Description: Negative imprint of a nearly complete right hind wing, 36.7 mm long, 20.0 mm wide; the fossil is an imprint of the lower and upper cuticules of the wing, which are slightly displaced respective to each other and therefore not perfectly overlapping (one being characterized by cross-veins as depressions, the other by cross-veins as tubular structures). Posterior margin with distinct small lobes between apices of veins; basal part of the anterior wing margin missing; ScA preserved at the wing base, with a small part of the wing membrane between it and C (which is missing); ScP reaching RA 18.9 mm from wing base, with RA apparently ending in ScP; area between ScP and C basally widened, 1.4 mm wide, distally narrowing, 0.5 mm wide at level of fusion of ScP with

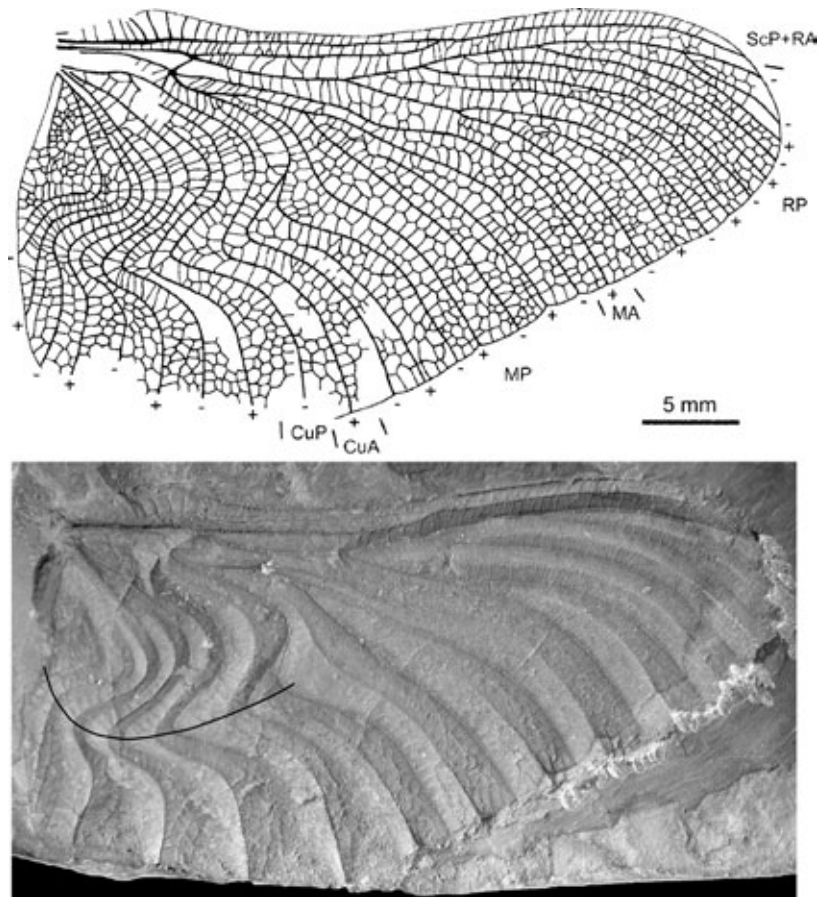


Fig. 3. *Lodetiella magnifica* nov. gen. and nov. sp.: right hind wing, reconstitution and photograph (negative imprint, reversed, light-mirrored) (holotype Ld LAP 679; Fleury Museum of Lodève, Hérault, France); Middle to Upper Permian, France.

Fig. 3. *Lodetiella magnifica* nov. gen. et nov. sp. : aile postérieure droite, reconstruction et photographie (empreinte négative, inversée, en lumière inversante) (holotype Ld LAP 679 ; Musée Fleury de Lodève, Hérault, France) ; Permien moyen à supérieur, France.

RA; numerous cross-veins in costal area, few of them forked; RA and RP fused in a basal stem, 6.7 mm long; R, M, and Cu basally well separated, though R and M are very close; presence of strong ‘arched transverse bridge’ sensu Kukalová (1964: Text-fig. 4), i.e. two convex cross-veins ‘ct’, 1.2 mm long between M and R, and ‘cv’, 0.9 mm long, between M and Cu; RA simple; RP with five concave branches; bases of the two basal branches basal to the point of fusion of ScP with RA; bases of other branches of RP distal to this point; first posterior branch of RP with two long branches and a convex intercalary longitudinal vein; presence of long convex intercalary veins between branches of RP; convex MA simple, with a distinct curve opposite the base of the first posterior branch of RP; concave MP, dichotomously branched, with four long branches and three long intercalary veins between them; the two more basal branches of MP and the intercalary vein between them strongly sigmoidal; part of CuA basal to ‘cv’ aligned with basal part of Cu; CuA and CuP simple and strongly sigmoidal; four concave branches in the anal area, all strongly sigmoidal, with long convex sigmoidal intercalary veins between them; cubito-anal area between Cu and posterior wing margin very broad, 16.1 mm wide.

Discussion: Occasionally fossil insect wings are preserved as two imprints that are not perfectly overlapping, as is the

holotype of *L. magnifica*. We (O. Béthoux and A. Nel) observed such preservation on a few specimens from the deposit at Commentry and from the Lodève basin. In a modern stonefly individual studied by Béthoux (2005: Fig. 22) the hind wing was dissected and the two layers partly separated. It has also been observed (J. W. Schneider) that, during preparation of modern cockroach wings, after the decay of nonchitinous organic substances between the two cuticles (by natural decay in water or made by hydrogen peroxide), both cuticle membranes could be moved against each other between the main veins. In dysaerobic to anaerobic sediments, such as in black shale, the decay of chitin was also observed. As a result, wings are preserved as poor imprints, termed ‘shadows’. A partial decay during the taphonomic process might have led to this peculiar preservation.

5. Possible flight mechanics

The highly specialized organisation of the veins of the cubito-anal area of *Lodetiella*, with veins strongly sigmoidal, parallel, and alternatively concave and convex, is very similar to that of the hind wing cubito-anal area of *Jarzembowskiiaeschnidium polandi* Fleck and Nel, 2003, a dragonfly of the Mesozoic family Aeschnidiidae from the Early Cretaceous of

England (Fleck and Nel, 2003). This convergence is probably a similar adaptive response relating to flight, but the structural complexity of the hind wings of *Lodetiella* renders morpho-functional interpretation speculative. Wootton and Kukalová-Peck (2000: 157) inferred that, in Calvertiellidae, a ‘strong’ curvature of the cubital and anal veins serves to hold down the trailing edge when the distal part of the wing undergoes pronatory (leading-edge down) twisting. Then the sigmoidal course of the veins could have reduced the compliance of the anal area. Nevertheless, a slightly different interpretation is possible with *Lodetiella*. The line that can be traced along the climax of the veins bending (Fig. 3) might have functionally separated the most posterior part of the anal area from the base of the wing. Although less obvious, if continued, the above-mentioned line crosses the bending of MA and reaches the point of fusion of ScP and RA. Then, the postero-basal part of the cubito-anal area, isolated from the wing base, might have behaved together with the distal part of the wing in cambering dorsally during downstroke. It would have resulted in enhancing lift.

In insects, lift production related to augmentation of the hind wing surface is usually based on a vannus-like area (see Wootton, 1979, for a definition of this term), functionally separated from the rest of the wing (remigium) by series of close, simple, straight, and parallel veins, with strong pleating. Such a pattern might be convergent within Polyneoptera (Kukalová-Peck and Lawrence, 2004). Very generally, the vannus is filled with veins radiating from the wing base. If our morphofunctional interpretation of the hind wing of *Lodetiella* is correct, this taxon (and maybe *Jarzewowskiaeschnidium* as well) developed a unique way of enhancing lift production by extending the hind wing surface.

6. Palaeoecology and palaeogeography of Calvertiellidae

Discoveries like *Lodetiella* reveal that only a fraction of the palaeoentomofauna is known, especially for the Late Early to Upper Permian. *Carrizopteryx* (Carizzo Arroyo, Bursum Form., New Mexico; Carboniferous/Permian transition) is the earliest known representative of the Calvertiellidae. *Moravia* and *Moraviptera*, both from the Obora insect bed of Moravia (Sakmarian), are more than 10 m.y. younger. *Moravia grandis* (from the Elmo insect bed, Wellington shales, Oklahoma; Leonardian) is 10 m.y. younger than the Obora calvertiellids. Of similar age is *Sharovia tshekardica* (Tsherkarda, western Urals; Kungurian). *Sharovia sojana* (Soyana, Arkhangelsk region, northern European Russia, early Kazanian), is about 5 m.y. younger. *Mongolodictya* (Bor-Tologoy, Central Gobi Aymag, Mongolia; Kazanian or Tatarian), is nearly of the same age, but might be about 5 m.y. younger. *Lodetiella*, described herein, could be of Kungurian (Leonardian) to Capitanian age (Late Early to Middle Permian).

Most of these localities had distinct environmental conditions. Carizzo Arroyo, at the Carboniferous/Permian transition, was located in a coastal plain environment, episodically transgressed by the sea. It belonged to the palaeotropical zone,

but the conifer-dominated flora associated with the diverse insect fauna point to seasonally dry climate (DiMichele et al., 2004, Schneider et al., 2004). This environment was very different from that of the common Carboniferous coal swamp insect localities of the time (Mazon Creek, Saar-Lorain, Saale basin, Writhlington, among others). With few exceptions such as Mazon Creek, the latter localities were ‘blattid’ dominated, though palaeodictyopterids were not rare. The Late Carboniferous (Westphalian/Stephanian) coal swamp faunas belonged to the ‘equatorial and tropical everwet biome’ of Ziegler (1990). Caused by continental drift to the north and the beginning of global warming, this tropical ‘coal swamp area’ changed increasingly into the ‘tropical and subtropical summerwet biome’ of monsoonal climate during the Late Pennsylvanian (Late Stephanian or Gzhelian to earliest Permian). Palaeodictyopterids are still common in the Late Stephanian ‘blattid-dominated’ entomofaunas such as at Commentry (Schneider, 1983b), but they are missing or are very rare in the Stephanian basins of Montceau-les-Mines, Saar-Lorain, Plötz-Wettin (Saale basin, East Germany).

During the Early Permian (Late Asselian, Sakmarian, and Artinskian) a smooth transition took place, with tropical to subtropical ‘desert biome’ becoming increasingly dry, characterized by outspreading red beds. From this time interval was a diverse Obora entomofauna of the Boskovice graben in Moravia that is unique in Europe (Kukalová, 1963). The Late Carboniferous and Early Permian deposits of the intramontane Boskovice graben, like other European insect sites, are dominated by blattids (Schneider, 1983a), up to the sudden appearance of the Obora entomofauna. Blattids are still common in the faunal spectra but are mostly represented by xeromorphic mylacrids (Schneider, 1980, 1984b). This fits well with the dominance of xerophilous plants such as conifers in the Obora insect bed.

The insect bearing limestone of the Elmo insect beds was deposited in an extended shallow lake system under arid to semiarid climatic conditions. Arid climate with seasonal to episodic precipitation is proposed for the playa red beds of the Salagou Formation (Körner et al., 2003). In the latter deposit, the insects were fossilized in small decimetre-wide channels, which were filled with water during the rainy season. Insect habitats were possibly situated in the sparse vegetated border of this playa, which itself was virtually free of any vegetation. The deposit at Chekarda, in the western Urals belongs to the Subangaran phytogeographic province, with nearly 30% endemic plants and a mixture of typical Late Permian Angaran and Euramerican forms (Naugolnykh, 1998). The insect bearing section belongs to an alluvial to marine delta-fan environment, close to the sea, deposited under arid climate conditions (Ponomaryova, 1998). In contrast, Bor-Tologoy (Mongolia) was situated in the Asian microcontinent assemblage, where warm intertropical conditions prevailed regionally up to the end of the Permian. Concluding from this, calvertiellids seem to be an advanced group, based on their wing venation and northern Pangean-wide distribution, with lineages adapted to wet as well as dry environments. However, dry environments with mesophilous to xerophilous floras might have been their

preferred habitats. During the Late Carboniferous, such environments were situated outside the basins of the equatorial tropical to subtropical belt. Drought-adapted plants evolved outside of the basins, in extrabasinal or upland floras. They migrated during the Carboniferous/Permian transition into the known depositional areas (Schneider, 1989, among others). This might well be the case of many insect groups, including the calvertiellids.

7. Conclusion

A previous discovery from the Permian of southern France already showed how Late Paleozoic insects could be unexpectedly disparate (Béthoux et al., 2003). *L. magnifica* belongs to the order Palaeodictyoptera, whose apogee in taxonomic diversity was apparently in the Late Carboniferous, but which disappeared at or around the Permian–Triassic boundary. In such case, *L. magnifica* is one of the very last representatives of the order. Also, this species exhibits a complex and unique wing morphology that might have been involved in an enhancement of lift production during the downstroke.

In Permian times the last palaeodictyopteroid lineages exhibited a wide range of wing morphologies, ranging from reduced wing venation (for example the megasecopterid Eukulojidae, see Sinitshenkova, 2002: Fig. 146) to extremely complex ones, such as *Lodetiella*. Last but not the least, they were all based on a relatively simple wing venation pattern that lasted for at least 70 m.y. (maybe 150 m.y., depending upon the date of divergence of the Palaeodictyopteroidea). Surely, ‘phylogenetic analysis of the Palaeodictyopteroidea would [...] be very promising’ (Grimaldi, 2001: 1157), especially with respect to the diverse evolutionary trends of the group. Unfortunately, such an attempt would be premature before significant taxonomic updates of the Carboniferous representatives of the group are made.

Acknowledgements

We thank D. Grimaldi (AMNH, USA) and an anonymous referee for insightful comments on the manuscript. We thank Barry S. Kues, (Department of Earth and Planetary Sciences, University of New Mexico, USA) for the loan of the holotype of *Carryzopteryx arroyo*. We thank Dr Annie V. Dhondt and Dr Jacques Godefroid (RBINS, Brussels) for their help during the visit of one of us in collections of the Royal Belgian Institute of Natural Sciences (March 2003, O. Béthoux). This work was partly supported by an ABC-project grant (RBINS; European Community, Access to Research Infrastructure action of the Improving Human Research Potential Programme, 2003). J. W. Schneider thanks the Deutsche Forschungsgemeinschaft for support by the grant Schn 408/7–1 and 2.

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