ORIGINAL ARTICLE

**ORGANISMS
DIVERSITY &
EVOLUTION**

On the phylogenetic position of the palaeopteran Syntonopteroidea (Insecta: Ephemeroptera), with a new species from the Upper Carboniferous of England

Jakub Prokop · André Nel · Andrew Tenny

Abstract A new syntonopterid, *Anglolithoneura magnifica* gen. et sp. n., is described from a siderite concretion (nodule) from the Late Carboniferous (Langsettian) of Lancashire County (UK). The new genus is diagnosed on hind wing venation and compared with other syntonopterid genera. The new species is the first syntonopterid formally described from the Late Carboniferous of Europe. The systematic positions of other potential Syntonopteroidea (*Miracopteron mirabile*, *Bojophlebia prokopi*, and specimens described in 1985 by J. Kukalová-Peck from Obora in the Czech Republic) are reconsidered. Wing venation synapomorphies are proposed for the Syntonopteroidea (sensu novo), and for a potential clade ((Ephemeroptera+ Syntonopteroidea)+Odonatoptera) separated from the Palae-odictyopterida. The close relations of the new species with *Lithoneura lameerei* Carpenter, 1938 from Mazon Creek (Illinois, USA) provide additional support for a Euramerican connection during the Late Carboniferous.

J. Prokop (✉)
Department of Zoology, Faculty of Science,
Charles University in Prague,
Viničná 7,
128 44 Praha 2, Czech Republic
e-mail: jprokop@natur.cuni.cz

A. Nel
CNRS UMR 7205, Muséum National d'Histoire Naturelle,
CP 50, Entomologie, 45 rue Buffon,
75005 Paris, France
e-mail: anel@mnhn.fr

A. Tenny
6 Kay Street, Smithy Bridge,
Littleborough, Lancashire OL14 5TD, UK
e-mail: atenny@sky.com

Introduction

The small family Syntonopteridae Handlirsch, 1911 presently includes the two Paleozoic genera *Syntonoptera* Handlirsch, 1911 and *Lithoneura* Carpenter, 1938. It is a crucial group for the resolution of phylogenetic relationships among the palaeopteran taxa Ephemeroptera, Palaeodictyopterida, and Odonatoptera, as well as more generally for Palaeoptera and Neoptera (Grimaldi and Engel 2005; Kukalová-Peck 1985; Willmann 1999).

The Palaeoptera were erected as a taxon by Martynov (1924), but since then their monophyly has been debated, based on morphological or molecular datasets and various analyses (Beutel and Gorb 2006; Boudreaux 1979; Haas and Kukalová-Peck 2001; Hennig 1981; Klass 2007, 2009; Kristensen 1991, 1995; Kukalová-Peck 1991; Terry and Whiting 2005; Wheeler 1989; Wheeler et al. 2001). The recent works by Hovmöller et al. (2002) and Ogden and Whiting (2003), both attempting to solve the 'Palaeoptera problem', provided conflicting results. Contributions by Kjer (2004), Kjer et al. (2006), and Whitfield and Kjer (2008), dealing with higher insect phylogeny based on different analyses of mainly molecular datasets, provided support for monophyly of Palaeoptera to a varied extent. In conclusion, the monophyly of Palaeoptera has remained a doubtful issue of insect phylogeny.

Soldán (1997) has provided a comprehensive review of potential apomorphies of Ephemeroptera within a presumed palaeopteran lineage, and discussed possible relationships with other groups. Apart from the three major groups,

Ephemeroptera, Odonatoptera, and (extinct) Palaeodictyopterida, the Palaeoptera also include several fossil taxa (Syntonopteridae, Bojophlebiidae, and Namuroningxiidae) that exhibit a 'mosaic' of apomorphies of more than one of the major groups, which renders them difficult to place in the classification system (Prokop and Ren 2007). The Syntonopteridae and Bojophlebiidae are currently combined to the higher taxon Syntonopterida, as their wing venation patterns are considerably different from those of the true mayflies. Originally Syntonopterida had been erected by Handlirsch (1911) for Syntonopteridae alone, which was later followed by Rasnitsyn (2002). Note that Rasnitsyn (2002: 89) indicated that no synapomorphy is known for the Syntonopterida.

The known distribution of Syntonopteridae was restricted to the Late Carboniferous of North America (Mazon Creek, Illinois; *Lithoneura* and *Syntonoptera*) and the Middle Permian of France (Var, Provence; *Gallolithoneura*). The family was first attributed to Palaeodictyoptera by Handlirsch (1911, 1919) on the basis of fragmentary remains of *Syntonoptera schucherti* Handlirsch, 1911 from the Late Carboniferous of Mazon Creek. Later Edmunds and Travers (1954) considered Syntonopteridae to be placed "between" Palaeodictyoptera and Ephemeroptera due to intermediate character states. Laurentiaux (1953) erected a new order, Syntonopterodea, without indicating diagnostic characters. The current systematic position of Syntonopteridae within Ephemeroptera was proposed first by Kukalová-Peck (1985), and supported by Willmann (1999), but other authors separated the two groups and treated Syntonopteridae as Palaeoptera or Pterygota incertae sedis (Carpenter 1987; Kluge 2004). Some elements of syntonopterid wing venation were poorly known and controversial at the time (e.g. presence or absence of a strut between M and CuA). Kluge (2004) classified *Syntonoptera* as "Pterygota incertae sedis" because he considered several characters to be of "unclear phylogenetic status", i.e. insufficient to support an attribution to the Euephemeroptera, because they are either plesiomorphies or present in many other clades. For example, Sc and RA nearly reach the wing apex (probably a plesiomorphy in Palaeoptera), RA and RP begin as separate stems, MA is convex, MP concave, CuA convex, and CuP concave (also probably plesiomorphies in palaeopteran groups; see Béthoux et al. 2007; Kukalová-Peck 1991; Lameere 1922).

Bojophlebiidae was erected by Kukalová-Peck (1985) for the gigantic mayfly, *Bojophlebia prokopi* Kukalová-Peck, 1985, which shares apomorphies with Syntonopteridae. Both families were placed in a superfamily Syntonopteroidea characterized by the hind wing being broader than the forewing, by a very gently arched subcostal brace, a strong brace between AA and CuP (with anterior branch of AA1+2 and CuP fused in Kukalová-Peck's interpretation, but see below), the posterior branch of AA1+2 diverging from CuP as an arch, and by a dense network of irregular crossveins (Kukalová-Peck 1985: 939).

Moreover, some exceptionally preserved Paleozoic fossils exhibit some body characters other than the venation pattern that have attracted several authors to review and more broadly consider the relationships with other palaeopteran Paleozoic groups. *Lithoneura lameeri* Carpenter, 1938 is one of these very well-preserved fossils (Carpenter 1938, 1987; Kukalová-Peck 1985; Willmann 1999).

The aim of the present paper is to describe a new syntonopterid taxon from the Langsettian (Westphalian A) of England based on a well-preserved hind wing. As this is the first Late Carboniferous European syntonopterid, it is of great interest to studies of the evolution of wing venation and the paleobiogeography of these insects. Based on this newly discovered species we therefore also provide a broader discussion of the evolution of the wing venation pattern, as well as of the systematic placement of the Late Paleozoic taxa more or less related to Syntonopteroidea (Syntonopteridae, Bojophlebiidae, and Miracopteridae).

Material and methods

The description of the new species is based on a single specimen (imprint, counterpart, and cast of counterpart) from Crock Hey opencast pit located near Manchester (Lancashire). This is one of the major currently investigated localities in the UK at which insects in siderite concretions have been preserved. Its fossil fauna, as well as data on geology and stratigraphy, have been treated extensively by Anderson et al. (1999).

Morphological observations were made under WILD TYP 308700 and OLYMPUS SZX-9 stereomicroscopes in dry state or in ethyl alcohol. The venation pattern was drawn directly using a camera lucida, then readjusted to the photograph scales using image-editing software (Adobe Photoshop). Photographs were made using Nikon CoolPix 4500 and Nikon D80 digital cameras with a Nikon AF-S VR Micro-Nikkor 105 mm macro lens, and single-sided cross-light exposure.

We follow the wing venation nomenclature of Kukalová-Peck (1991) and Willmann (1999), with reserves concerning the possible fusion and relative positions of CuP and AA1+2 (see below). Abbreviations of wing veins: AA = anal anterior, AP = anal posterior, C = costa, CuA = cubitus anterior, CuP = cubitus posterior, 'IN-' = concave vein between AA1+2 and AA3+4, MA = media anterior, MP = media posterior, RA = radius anterior, RP = radius posterior, ScA = subcosta anterior, ScP = subcosta posterior. The addition '+' indicates a convex vein (elevated to dorsal), '−' a concave vein (sunken to ventral).

Systematics section

Superfamily Syntonopteroidea Kukalová-Peck, 1985

This includes the families Syntonopteridae Handlirsch, 1911, and Miracopteridae Novokshonov, 1993 (newly placed here; see "Discussion" below). Bojophlebiidae Kukalová-Peck, 1985 is excluded (see below).

Family Syntonopteridae Handlirsch, 1911

This includes the following genera and species (after Carpenter 1987): *Syntonoptera* Handlirsch, 1911 (type and only included species: *S. schucherti* Handlirsch, 1911); *Lithoneura* Carpenter, 1938 (type species: *L. lameeri* Carpenter, 1938; other species: *L. mirifica* Carpenter, 1944, *L. carpenteri* Richardson, 1956, *L. clayesi* Kukalova-Peck, 1985 (based on larva), *L. piecko* Kukalova-Peck, 1985 (based on larva)).

Genus *Anglolithoneura* gen. n.

Type species

Anglolithoneura magnifica sp. n.

Etymology

The genus name is derived from *Anglia*, the Latin name for England, and from the genus name *Lithoneura*. Its gender for the purposes of nomenclature is feminine.

Diagnosis

[Only hind wing characters known.] Anal area narrow, with relatively short and zigzagged veins; MA not fused with RP but closely approaching and touching it for a short distance (T in Fig. 1); CuP straight, not distally sigmoidal; concave vein 'IN-' not approximating AA1+2.

Anglolithoneura magnifica sp. n.

Etymology

The species epithet reflects the wonderful state of preservation of the fossil. It is to be treated as adjectival for the purposes of nomenclature.

Material

Holotype specimen II.3037 (imprint of a hind wing), NHM Palaeont. Dept. II, The Natural History Museum, London (UK); counterpart in private collection of Andrew Tenny, Littleborough (UK); cast of holotype in Muséum national d'Histoire naturelle, Paris (France).

Age and outcrop

The fossil was found in a nodule in the tips at Crock Hey opencast pit (accessible 2001–2005), roof shales of Ru's coal seam 2b, Langsettian (Westphalian A), Late Carboniferous, Lancashire, UK (Anderson et al. 1999).

Diagnosis

As for the genus.

Description

[Only basal part of hind wing known; Figs. 1, 2 and 3.] Wing without trace of coloration, probably hyaline; holotype wing fragment 26 mm wide. Wing corrugate, no archedictyon. Area between ScP and C with one row of cross-veins; no convex ScA distinct from vein along

Fig. 1 *Anglolithoneura magnifica* gen. et sp. n., holotype; composite line drawing of hind wing. Scale bar 10 mm. For abbreviations of wing veins, see the "Material and methods" section
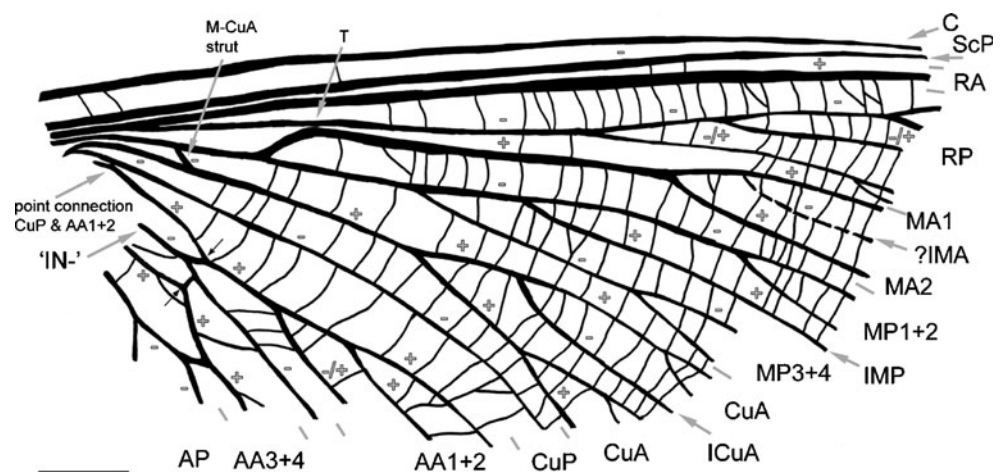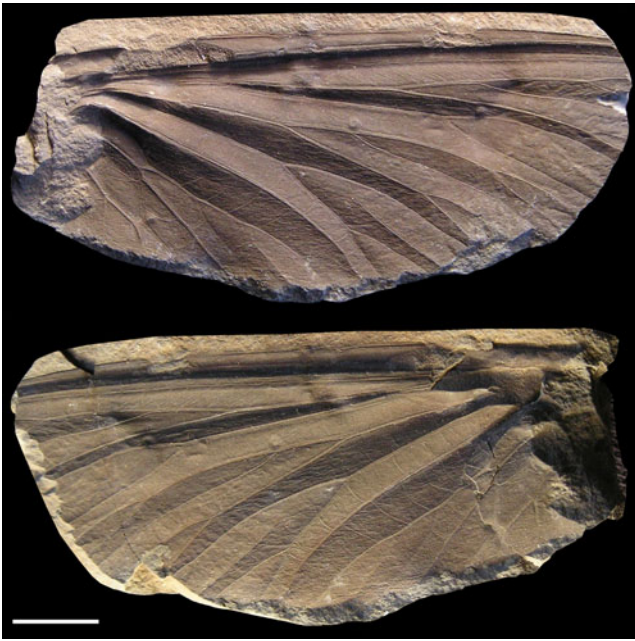
Fig. 2 *Anglolithoneura magnifica* gen. et sp. n., holotype; photograph of counterpart (*top*; coll. A. Tenny) and imprint (*bottom*; II.3037, Natural History Museum, London, UK). Scale bar 10 mm

and concave intercalary vein IMA between them; concave MP with two main branches, each secondarily bifurcated and intercalary convex vein IMP between main branches; convex CuA strongly approximates M, with a visible strut between them (M-CuA strut in Figs. 1 and 3a), CuA and its branches convex, dichotomously branched with four preserved branches, with an intercalary concave vein ICuA between the two main stems branches; CuP simple (as far as preserved), strongly concave and only weakly curved, not sigmoidal; convex AA1+2 touching CuP in one point near wing base (Figs. 1 and 3a, b); a constriction of the area between AA1+2 and convex AA3+4, and a constriction of the area between AA3+4 and first branch of concave AP at the same point; a strongly concave longitudinal vein between AA1+2 and AA3+4 ending on posterior wing margin, interpreted as "?A2" by Willmann (1999) and as "IN-" by Kukalová-Peck (1985); AA1+2 with three preserved branches; branches of AP short and zigzagged, with 1–2 rows of cells in anal area between each pair of neighbouring veins.

Discussion

Taxonomic content of Syntonopteridae

Anglolithoneura gen. n. has the combination of the main diagnostic characters of Syntonopteridae, i.e. wing corrugate; no archedictyon but a simple and relatively straight pattern of cross-veins between the longitudinal veins [also present in Odonatoptera and some Palaeodictyoptera (e.g. Breyeriidae)]; CuP simple; MA with a strong anterior curve at its base, touching RP for a short distance; most anterior

anterior wing margin; concave ScP straight, nearly parallel to anterior wing margin and reaching it probably near wing apex; RA straight; fork/dichotomy between RA and RP about 11.6 mm from wing base; RP with four main branches visible (there could have been one more distally); first branch forked near its apex; convex MA emerging from M-stem 7.1 mm estimated from wing base, directed towards RP and touching it for a short distance, not fused with it; MA with two branches visible, with a broad area

Fig. 3 *Anglolithoneura magnifica* gen. et sp. n., detail photographs of hind wing base. a Imprint (II.3037, Natural History Museum, London, UK). b Counterpart (coll. A. Tenny). Scale bars 5 mm
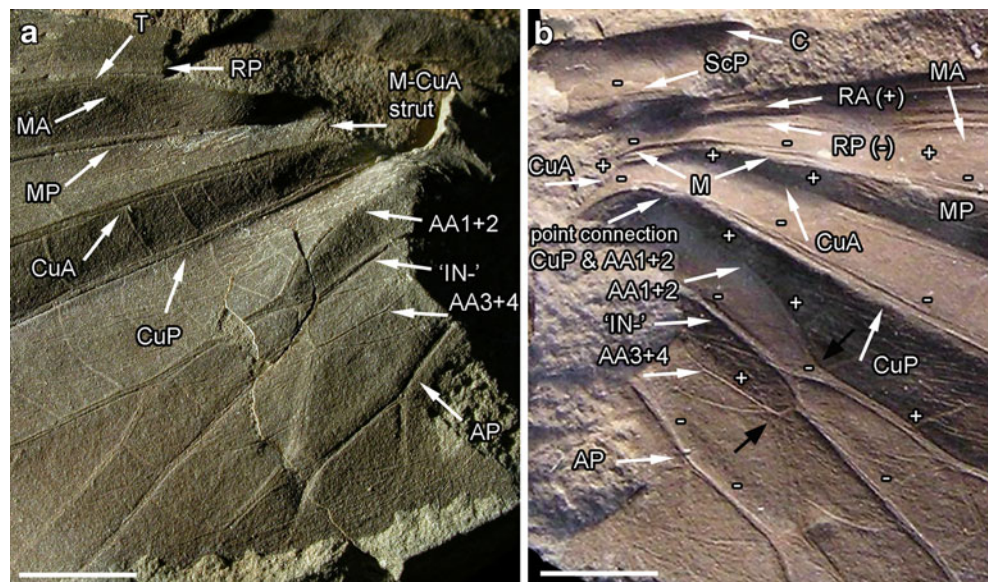
branch of AA with a strong curve ('zigzag') and touching CuP in one point.

The *Anglolithoneura* hind wing shares with that of *Lithoneura* a characteristic concave vein between the two convex veins AA1+2 and AA3+4. The exact nature of this vein remains controversial; Kukalová-Peck (1985) interpreted it as a fold ("IN-"), Willmann (1999) as "?A2". Willmann's hypothesis implies that a branch of AA is concave, which is debatable. Nevertheless, the distal part of this structure is more clearly visible in *Anglolithoneura* than in *Lithoneura*, because it is completely separated from AA1+2 and AA3+4 in the former versus strongly approximating AA1+2 and separating more distally from it in the latter. *Anglolithoneura* and *Lithoneura* also share a constriction of the area between the first and the second convex branches of AA (AA1+2 and AA3+4 sensu Kukalová-Peck 1991), with a strong brace between them (see black arrows in Figs. 1, 3b, and 5). On the basis of the anal area pattern being similar to that of the hind wing of *Lithoneura*, we consider the holotype of *A. magnifica* sp. n. as a hind wing. Unfortunately, the wing bases are not preserved in *Syntonoptera*; thus it is not possible to determine whether it has similar structures. Nevertheless, the characters are synapomorphies of (at least) *Anglolithoneura* and *Lithoneura*.

The hind wing of *Anglolithoneura* differs from that of *Lithoneura* in its narrower anal area, with relatively short and zigzagged veins; MA not fused with RP; CuP straight; and concave vein 'IN-' not approximating AA1+2.

The data above show that the genera *Syntonoptera*, *Lithoneura*, and *Anglolithoneura* are similar in wing morphology, and likely closely related as they also share several apomorphies. They are thus adequately combined in a single family, Syntonopteridae. In contrast, Willmann (2007: 124, 125) doubted the assignment of *Lithoneura* to Syntonopteridae; instead, he created a new group Ephemeronta (= *Lithoneura*+Reticulata) on the basis of three synapomorphies: (1) A1 simple in forewings; (2) MA and RP fused; (3) proximal part of anal area part wider in hindwings.

Kukalová-Peck (1985) attributed two fossil ephemeroptera-like nymphs to the genus *Lithoneura*, i.e. *L. piecko* and *L. clayesi*. Carpenter (1987) doubted these attributions because he supposed that *Lithoneura* is not an ephemeropteran, which is debatable (see below). In any case, the wing tracheation of these nymphs is unknown, and that character system is the only one that could potentially yield arguments allowing those nymphs to be considered as (relatives of) Syntonopteridae. We therefore consider *L. piecko* and *L. clayesi* as Pterygota incertae sedis.

Kukalová-Peck (1985) also assigned an apical part of a wing from the Lower Permian of Obora (Moravia) to Syntonopteroidea incertae sedis. However, unlike the other Syntonopteridae that wing has a dense network of cross-veins, an 'archaedictyon'—likely a plesiomorphy. On the other hand, no clear apomorphy shared with syntonopterids has been documented. Garrouste et al. (2009) reported another wing fragment attributable to the Syntonopteridae from the Upper Permian of Var (France), under the name *Gallolithoneura butchlii*.

Demoulin (1954) revised the holotype specimen of *Aedophasma anglica* Scudder, 1885 and attributed this taxon to Syntonopteridae. However, this was based on an apical wing fragment only (see Fig. 4) and therefore is rather uncertain. Nevertheless, the venation pattern corresponds well with that in the wing apex of syntonopterids, as there are intercalary veins in addition to a dense network of cross-veins. Still, we prefer to follow Carpenter (1992) in placing this taxon in Palaeoptera incertae sedis, due to its fragmentary state of preservation.

Fig. 4 *Aedophasma anglica* Scudder, 1885; photograph of plaster cast of holotype (No. 18378, Natural History Museum, London; original at Liverpool Museum, UK). Scale bar 10 mm
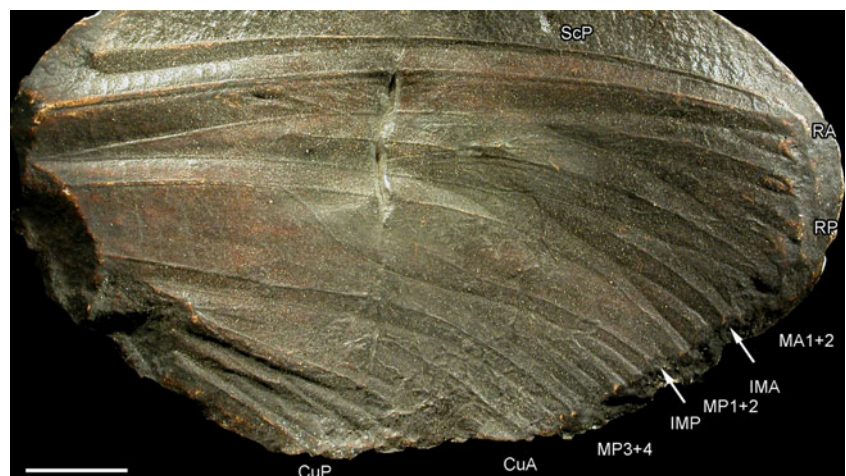
Phylogenetic relationships of Syntonopteridae and related families

*Clarification of some characters in Syntonopteridae*

Willmann (1999: fig. 1b) hypothesized that the posterior branch of AA (A2 in his terminology) in the hind wing of *Lithoneura lameerei* is represented by the vein just posterior to his AA1 ("?A2" in his drawing), but this vein is clearly concave and cannot correspond to a branch of AA. It is a supplementary vein in the cell between AA1+2 and AA3+4 (indicated by a dotted line in Kukalová-Peck 1985: fig. 37). This concave longitudinal vein IN- lying between AA1+2 and AA3+4 is clearly visible in *Anglolithoneura magnifica*. It can be compared to the concave longitudinal vein 'Cuspl' that occurs in the hindwing 'anal loop' of the modern Odonatoptera-Libellulidae (*Libellula*, *Tramea*, etc.). The libellulid anal loop is an area limited by a convex branch of AA and a convex branch of CuA. The whole structure transversely reinforces the wing and has a mechanical function during flight. A similar function can be assumed for the large transverse cell between AA1+2 and AA3+4 crossed by the longitudinal concave vein IN- in *Lithoneura* and *Anglolithoneura* (see Figs. 1 and 5a, b). By similarity with the Libellulidae, this cell could be termed the anal loop, even if there is no homology between the two structures. One may suspect that—similar to Libelluloidea—some unknown taxa of the syntonopterid lineage could have had a more rudimentary anal loop and vein IN- than found in *Lithoneura* and *Anglolithoneura*.

The hind wing of *Anglolithoneura magnifica* exhibits a convex CuA that diverges from CuP and strongly approx-imates M, with a visible strut between them (M-CuA strut in Figs. 1 and 3a). This structure agrees with the interpretation of the bases of the cubital and median veins by Kukalová-Peck (1985: fig. 12), contrary to Willmann (1999), who interpreted M and CuA as basally fused in the hind wing of *Lithoneura lameerei*. The separation between CuA and MP is visible on the photograph of the left hind wing of *L. lameerei* in Willmann (1999: fig. 10a), and also in the present Fig. 5a.

Willmann (1999) indicated that *Lithoneura* has no convex costal brace, unlike the true Ephemeroptera. On the basis of the preserved basal wing part the same situation occurs in *Anglolithoneura*. In contrast, Rasnitsyn (2002: 88) proposed the presence of a costal brace as a potential synapomorphy of 'Syntonopterida' and Ephemerida. A costal brace (convex ScA, vein Ax0) is also present in Odonatoptera (Bechly 1996), thus would constitute a synapomorphy of the whole group Libelluliformes sensu Rasnitsyn (2002) or Hydropalaeoptera Rohdendorf, 1968 (= Ephemeroptera+Odonatoptera) (see also Kukalová-Peck et al. 2009). Thus the inclusion of Syntonopteroidea in Hydropalaeoptera would imply a reversal for this character. However, the polarity of this character is not well established; it may more likely be a pterygote plesiomorphy, if one follows the ground pattern of wing venation of Kukalová-Peck (1991). The polarisation of related characters for such basal Pterygota is difficult to achieve, because all potential outgroup taxa are apterous (Zygentoma, Archaeognatha). All Neoptera and Paoliida cannot be used as outgroup taxa, because the absence of the brace in Neoptera may just as well be a synapomorphy of the Neoptera themselves.

Fig. 5 *Lithoneura lameerei* Carpenter, 1938, holotype (No. MCZ 4537, Museum of Comparative Zoology at Harvard University, Cambridge, MA, USA). **a** Detail photograph of left hind wing base. **b** Line drawing of left hind wing base. Scale bars 5 mm
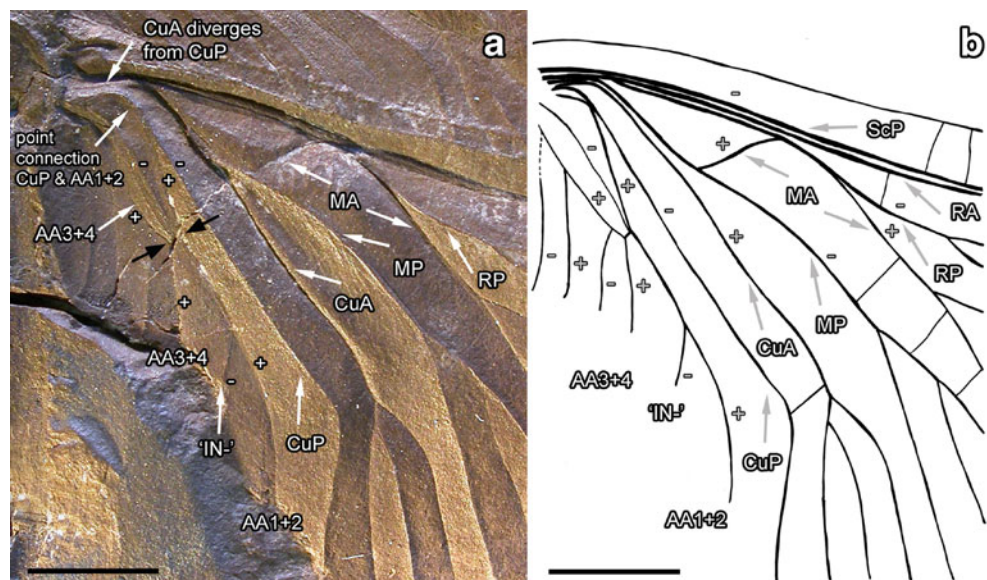
Syntonopteridae and some potentially related smaller taxa: the Syntonopteroidea

Some palaeopteran taxa could be more closely related to Syntonopteridae than to any other clade. These are:

(1) *Miracopteron* Novokshonov, 1993 (the sole genus of Miracopteridae Novokshonov, 1993). This is an enigmatic Lower Permian taxon based on isolated wings (see Novokshonov 1993; and Fig. 6). The Miracopteridae share with the Syntonopteridae the presence of a characteristic constriction of the area between AA1+2 and AA3+4, the presence of a concave longitudinal vein between them (vein IN-), and a constriction of the area between AA3+4 and the first branch of the concave AP at the same point, plus very similar overall wing venation patterns (see Fig. 6). Rasnitsyn (2002: 89) suggested that *Miracopteron* could belong to the 'Syntonopterida', and be closely related to the Syntonopteridae, without giving a precise argument. The main difference between *Miracopteron* and Syntonopteridae is the presence of posterior branches of CuP in the former.

(2) *Bojophlebia* Kukalová-Peck, 1985 (Bojophlebiidae Kukalová-Peck, 1985). Following Kukalová-Peck's (1985) interpretation, the wing in this taxon would lack the above-mentioned peculiarities of the anal area, and have a distinct convex costal brace, unlike that of *Lithoneura*. However, Kukalová-Peck's (1985) interpretation is far from convincing, as the holotype specimen of *Bojophlebia* is very poorly preserved (Fig. 7). In fact, it is impossible to see whether there is a ScA, and the basal part of the anal area is hardly preserved.

Fig. 6 *Miracopteron mirabile* Novokshonov, 1993, holotype (No. 2/135, Paleontological Institute, Russian Academy of Sciences, Moscow); photograph of counterpart. Scale bar 10 mm

Fig. 7 *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype (No. 1/1985, National Museum Prague, Czech Republic); photograph of counterpart. Scale bar 50 mm

Thus we newly propose here to exclude Bojophlebiidae from the Syntonopteroidea, considering it as Pterygota incertae sedis instead, and to characterize Syntonopteroidea by the presence of the specialized structures of the hind wing anal area listed above. We also propose to include *Miracopteron* and the Miracopteridae within the Syntonopteroidea.

Putting Miracopteridae and Syntonopteridae into a superfamily or order is an arbitrary choice at this stage, because their relationships with Ephemeroptera and Odonatoptera remain rather uncertain (see below). Rasnitsyn (2002) proposed to maintain order rank for the "considerable phenetic distance from the true mayflies as well as their probable paraphyletic (ancestral) position in respect to both mayflies and dragonflies." Such arguments to create or maintain orders are not well-grounded, because 'phenetic distance' is a subjective concept. Moreover, we follow the rule that sister-taxa should be of the same rank.

Relationship between Syntonopteroidea and other major palaeopteran groups

A group (Triplosobida+(Syntonopteroidea+Ephemerida)) (= Ephemeridea Latreille, 1810 sensu Rasnitsyn 2002) was defined by Rasnitsyn (2002: 88). In the following, we discuss four main aspects of that proposal.

(1) **Affinities of Syntonopteroidea with the Triplosobida (= Triplosobidae, only including *Triplosoba pulchella* (Brongniart, 1883)).** Prokop and Nel (2009) excluded this option, as this family has been transferred from the Hydropalaeoptera to the Rostropalaeoptera (= Palaeodictyopterida).

(2) **Affinities of Syntonopteroidea with Ephemerida (= Ephemeroptera plus the extinct Protereismatina and Euplectoptera).** Rasnitsyn (2002) proposed a

group including the Syntonopteroidea (under the name "Syntonopterida") and Ephemerida, on the basis of the supposed presence of a costal brace. As the Syntonopteridae have no costal brace, Rasnitsyn probably based that grouping on the alleged presence of a costal brace in *Bojophlebia*, after an assumption of Kukalová-Peck (1985). However, as we noted above both the phylogenetic position of *Bojophlebia* and its possession of such a costal brace are very uncertain. Consequently, there is no potential synapomorphy supporting the grouping of Syntonopteroidea with Ephemerida.

(3) **Affinities of Syntonopteroidea with the Ephemeroptera (and possibly Bojophlebiidae?).** These taxa share the presence of a distinct anterior curve or 'zigzag' of AA1+2, although this can be pronounced to a varied extent (Kukalová-Peck 1985: fig. 2, 1997; Willmann 1999: fig. 1b; Zhou 2007). The feature is absent in Odonatoptera and constitutes a potential synapomorphy of the former groups.

(4) **Affinities of *Lithoneura* with Odonatoptera, Ephemeroptera, and Protereismatidae.** Several potential synapomorphies (items a–c below) have been proposed by various authors to support a grouping comprising these taxa. One should keep in mind here that, considering extant taxa alone, a clade Odonatoptera+Ephemeroptera receives some support from molecular studies but is at least debatable from a morphological viewpoint (Bechly 1996; Hovmöller et al. 2002; Kjer 2004; Klass 2009; Wheeler et al. 2001).

  (a) Willmann (1999: fig. 12) listed four potential synapomorphies. Three of them concern structures unknown from *Lithoneura*. The fourth putative synapomorphy is a composite character state "simple CuP (plesiomorphic character?), with MA and RP being fused over a short distance and with intercalary veins (character state uncertain)." While this is true for *Miracopteron* and *Lithoneura* among the Syntonopteroidea, MA only touches RP in one point (but is not fused) in *Anglolithoneura* (T in Fig. 1), suggesting that this character is subject to reversals or homoplasy. Still the one-point touch in *Anglolithoneura* could be an initial state of longer fusion, and this could be a synapomorphy of a clade Syntonopteroidea+Odonatoptera+Ephemeroptera, together with the presence of intercalary veins.
  (b) Absence of an archedictyon and presence of a regular pattern of cross-veins are similar in Syntonopteridae and in Odonatoptera and Ephemeroptera, suggesting a possible synapomorphy.
  (c) Complete fusion of the most anterior branch of AA with CuP, resulting in a concave vein, has been

proposed by Kukalová-Peck (1985, 1991) as a synapomorphy for a clade Ephemeroptera +Odonatoptera+Bojophlebiidae+Syntonopteridae. Concerning Syntonopteroidea, Kukalová-Peck's (1985) opinion was based on the assumption that AA1+2 should always separate in two branches. In *Lithoneura*, the presence of one point of contact between the convex AA1+2 and the concave CuP, and the fact that these veins maintain their respective convexity in their distal parts, support the hypothesis of Willmann (1999: fig. 1b) that there is no fusion CuP+AA1, contrary to Kukalová-Peck (1985: figs. 11, 14) (Fig. 5a, b). The only argument favouring the possible fusion of AA1 with CuP is the presence in *Miracopteron* of a distal posterior branch of CuP that seems to be less concave than the main CuP (see Fig. 6). This branch would be (?) AA1 re-emerging from CuP. But this vein is clearly not as convex as the genuine branches of AA; its interpretation as AA1 is uncertain. In *Anglolithoneura* AA1+2 separates near the posterior wing margin into two convex branches that can be interpreted as AA1 and AA2, without any capture of a branch by CuP (Fig. 1). Thus, the situation greatly varies among Syntonopteroidea.

A fusion of CuP with AA is obviously present in the Meganisoptera (and more advanced Odonatoptera) (see, e.g., Nel et al. 2009), where the concave CuP 'vanishes' into the main longitudinal convex AA to separate again further distally into a convex AA and a concave CuP. In the most basal Odonatoptera—*Eugeropteron* Riek in Riek & Kukalová-Peck, 1984—there is a brace between AA, CuP and CuA, but no obvious fusion of a branch of CuP to AA.

In Ephemeroptera, Bojophlebiidae (after Kukalová-Peck's 1985: fig. 2), there is a strong convex brace between AA and CuP, but there is no CuP fused to a convex AA, and also no direct evidence of a branch of AA completely fused with a concave CuP.

The presence of a strong convex brace or a contact between AA and CuP is a possible synapomorphy of Ephemeroptera, Syntonopteroidea, and Odonatoptera, which would separate them from the Palaeodictyoptera [Note that nothing similar to a strong convex brace between AA and CuP can be found in the Palaeodictyoptera, in which AA is completely separated from CuP (Kukalová 1969a, 1969b, 1970). The only known exception is a rather strong cross-vein between AA and Cu, aligned with a crossvein between Cu and M, occurring as a kind of arculus in the eugereonid *Dictyoptilus sepultus* (Kukalová 1969b). This is clearly not homologous to what can be observed in Ephemeroptera, Odonatoptera, and Lithoneuridae.] Kukalová-Peck (1997: 265) proposed a "cup-aa1"

brace as a "strong" synapomorphy of the Ephemeroptera and Odonatoptera. This potential synapomorphy supports the hypothesis of Kukalová-Peck (in Wootton and Kukalová-Peck 2000) of a basal division of Palaeoptera in two taxa, Hydropalaeoptera (Ephemeroptera and Odonatoptera) and Rostropalaeoptera (Palaeodictyopterida).

However, a similar connection between veins CuP and AA1 is also present in the modern Plecoptera (e.g. Béthoux 2005). Haas and Kukalová-Peck (2001: fig. 14) interpreted this brace as AA1 distally fused and vanishing in CuP, but Kukalová-Peck and Lawrence (2004) did not.

New data on other body structures and/or on larval characters shall be necessary to definitely solve the problem of classification of the Palaeopterous insects.

Palaeogeographical significance

Anglolithoneura magnifica is the first syntonopterid described from the Upper Carboniferous of Europe. It exhibits a pattern of wing venation similar to that in *Lithoneura lameeri* (Westphalian D/Cantabrian; Mazon Creek, Illinois, USA). The close affinities between these two taxa support the well-known Euramerican connection during the Late Carboniferous. Other insects, such as *Anglopterum magnificum* Prokop, Smith, Jarzembowski & Nel, 2006 (Palaeodictyoptera: Homoiopteridae) and chelicerates such as *Euproops danae* (Meek & Worthen, 1865), *Pleophrynus verrucosa* (Pocock, 1911) and *Adelophthalmus imhofi* Jordan & Meyer, 1856), are known from Late Carboniferous basins both in the UK and at Mazon Creek, supporting a Euroamerican connection as well (Anderson 1994; Dunlop 1994; Proctor 1999; Prokop et al. 2006).

References

Anderson, L. I. (1994). Xiphosurans from the Westphalian D of the Radstock Basin, Somerset Coalfield. In E. A. Jarzembowski (Ed.), Writhlington Special Issue, the South Wales Coalfield and Mazon Creek, Illinois. *Proceedings of the Geologists' Association, 105*, 265–275.

Anderson, L. I., Dunlop, J. A., Eagar, R. M. C., Horrocks, C. A., & Wilson, H. M. (1999). Soft-bodied fossils from the roof shales of the wigan four foot coal seam, Westhoughton, Lancashire, UK. *Geological Magazine, 135*, 321–329.

Bechly, G. (1996). Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der phylogenetischen Systematik und des Grundplanes der *Odonata. *Petalura (Böblingen), Special Volume, 2*, 1–402.

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

Béthoux, O., Nel, A., Schneider, J. W., & Gand, G. (2007). *Lodetiella magnifica* nov. gen. and nov. sp. (Insecta: Palaeodictyoptera; Permian), an extreme situation in wing morphology of palaeopterous insects. *Geobios, 40*, 181–189.

Beutel, R. G., & Gorb, S. N. (2006). A revised interpretation of the evolution of attachment structures in Hexapoda with special emphasis on Mantophasmatodea. *Arthropod Systematics & Phylogeny, 64*, 3–25.

Boudreaux, H. B. (1979). *Arthropod phylogeny with special reference to insects*. New York: Robert E. Krieger, John Wiley & Sons.

Carpenter, F. M. (1938). Two Carboniferous insects from the vicinity of Mazon Creek, Illinois. *American Journal of Science, Fifth Series, 36*, 445–452.

Carpenter, F. M. (1987). Review of the extinct family Syntonopteridae (order uncertain). *Psyche, 94*, 373–388.

Carpenter, F. M. (1992). Superclass Hexapoda. In R. C. Moore & R. L. Kaesler (Eds.), *Treatise on invertebrate paleontology, Part R, Arthropoda 4* (pp. 1–655). Boulder: Geological Society of America and University of Kansas.

Demoulin, G. (1954). *Aedophasma anglica* Scudder, syntonopteroide méconnu (Insecta: Paléodictyoptères). *Bulletin et Annales de la Société Royale de l'Entomologie de Belgique, 90*, 278–281.

Dunlop, J. A. (1994). The palaeobiology of the Writhlington trigonotarbid arachnid. In E. A. Jarzembowski (Ed.), Writhlington Special Issue, the South Wales Coalfield and Mazon Creek, Illinois. *Proceedings of the Geologists' Association, 105*, 287–296.

Edmunds, G. F., Jr., & Travers, J. R. (1954). The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. *Journal of the Washington Academy of Sciences, 44*, 390–400.

Garrouste, R., Nel, A., & Gand, G. (2009). New fossil arthropods (Notostraca and Insecta: Syntonopterida) in the Continental Middle Permian of Provence (Bas-Argens basin, France). *Comptes rendus palevol, 8*, 49–57.

Grimaldi, D. A., & Engel, M. S. (2005). *Evolution of the insects*. New York: Cambridge University Press.

Haas, F., & Kukalová-Peck, J. (2001). Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). *European Journal of Entomology, 98*, 445–509.

Handlirsch, A. (1911). New Paleozoic insects from the vicinity of Mazon Creek, Illinois. *American Journal of Science, Fourth Series, 31*, 297–378.

Handlirsch, A. (1919). Revision der paläozoischen Insekten. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien, 96*, 511–592.

Hennig, W. (1981). *Insect phylogeny*. Chichester: Wiley.

Hovmöller, R., Pape, T., & Källersjö, M. (2002). The Paleoptera problem: basal pterygote phylogeny inferred from 18S and 28S rDNA sequences. *Cladistics, 18*, 313–323.

Kjer, K. M. (2004). Aligned 18S and insect phylogeny. *Systematic Biology, 53*, 506–514.

Kjer, K. M., Carle, F. L., Litman, J., & Ware, J. (2006). A molecular phylogeny of Hexapoda. *Arthropod Systematics & Phylogeny, 64*, 35–44.

Klass, K.-D. (2007). Die Stammesgeschichte der Hexapoden: eine kritische Diskussion neuerer Daten und Hypothesen. *Denisia, 20*, 413–450.

Klass, K.-D. (2009). A critical review of current data and hypotheses on hexapod phylogeny. *Proceedings of the Arthropodan Embryological Society of Japan, 43*, 3–22.

Kluge, N. (2004). *The phylogenetic system of Ephemeroptera*. Dordrecht: Kluwer Academic.

Kristensen, N. P. (1991). Phylogeny of extant hexapods. In I. D. Naumann (Ed.), *The insects of Australia, vol. I* (2nd ed., pp. 125–140). Melbourne: Melbourne University Press.

Kristensen, N. P. (1995). Forty years' insect phylogenetic systematics: Hennig's "Kritische Bemerkungen..." and subsequent developments. *Zoologische Beiträge (Neue Fassung), 36*, 83–124.

Kukalová, J. (1969a). Revisional study of the order palaeodictyoptera in the Upper Carboniferous shales of commentry, France. Part 1. *Psyche, 76*, 163–215.

Kukalová, J. (1969b). Revisional study of the order palaeodictyoptera in the Upper Carboniferous shales of commentry, France. Part 2. *Psyche, 76*, 439–486.

Kukalová, J. (1970). Revisional study of the order palaeodictyoptera in the Upper Carboniferous shales of commentry, France. Part 3. *Psyche, 77*, 1–44.

Kukalová-Peck, J. (1985). Ephemeroid wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemerida). *Canadian Journal of Zoology, 63*, 933–955.

Kukalová-Peck, J. (1991). Fossil history and the evolution of hexapod structures. In I. D. Naumann (Ed.), *The insects of Australia, vol. I* (2nd ed., pp. 141–179). Melbourne: Melbourne University Press.

Kukalová-Peck, J. (1997). Arthropod phylogeny and 'basal' morphological structures. In R. A. Fortey & R. H. Thomas (Eds.), *Arthropod relationships* (pp. 249–268). London: Chapman & Hall.

Kukalová-Peck, J., & Lawrence, J. F. (2004). Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. *European Journal of Entomology, 101*, 95–144.

Kukalová-Peck, J., Peters, G., & Soldán, T. (2009). Homologisation of the anterior articular plate in the wing base of Ephemeroptera and Odonatoptera. *Aquatic Insects, 31*(Supplement 1), 459–470.

Lameere, A. (1922). Sur la nervation alaire des insectes. *Bulletin de la Classe des Sciences, Académie Royale de Belgique, 5*, 138–149.

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

Martynov, A. V. (1924). Über Zwei Grundtypen der Flügel bei den Insekten und ihre Evolution. *Zeitschrift für Morphologie und Ökologie der Tiere, 4*, 465–501.

Nel, A., Fleck, G., Garrouste, R., Gand, G., Lapeyrie, J., Bybee, S. M., et al. (2009). Revision of Permo-Carboniferous griffenflies (Insecta: Odonatoptera: Meganisoptera) based upon new species and redescription of selected poorly known taxa from Eurasia. *Palaeontographica (A), 289*, 89–121.

Novokshonov, V. G. (1993). New insects (Insecta) from the lower permian of chekarda (Central Urals). *Paleontological Journal, 27*, 172–178.

Ogden, T. H., & Whiting, M. F. (2003). The problem with "the Paleoptera problem:" sense and sensitivity. *Cladistics, 19*, 432–442.

Proctor, C. J. (1999). An Upper Carboniferous eurypterid from the writhlington geological nature reserve. *Proceedings of the Geologists' Assocation, 110*, 263–265.

Prokop, J., & Ren, D. (2007). New significant fossil insects from the Upper Carboniferous of Ningxia in northern China (Insecta: Palaeodictyoptera, Archaeorthoptera). *European Journal of Entomology, 104*, 267–275.

Prokop, J., & Nel, A. (2009). Systematic position of *Triplosoba*, hitherto the oldest mayfly from Upper Carboniferous of commentry in Central France (Insecta: Palaeodictyopterida). *Systematic Entomology, 34*, 610–615.

Prokop, J., Smith, R., Jarzembowski, E. A., & Nel, A. (2006). New homoiopterids from the late carboniferous of England (Insecta: Palaeodictyoptera). *Comptes rendus palevol, 5*, 867–873.

Rasnitsyn, A. P. (2002). 2.2.1.1. Cohors Libelluliformes Laircharting, 1781 (= Subulicornes Latreille, 1807, = Hydropalaeopaloptera Rohdendorf, 1968). In A. P. Rasnitsyn & D. L. J. Quicke (Eds.), *History of insects* (pp. 85–89). Dordrecht: Kluwer Academic.

Soldán, T. (1997). The Ephemeroptera: whose sister-group are they? In P. Landolt & M. Sartori (Eds.), *Ephemeroptera & Plecoptera. Biology, ecology, systematics* (pp. 514–519). Fribourg: MTL.

Terry, M. D., & Whiting, M. F. (2005). Mantophasmatodea and phylogeny of the lower neopterous insects. *Cladistics, 21*, 240–257.

Wheeler, W. C. (1989). The systematics of insect ribosomal DNA. In B. Fernholm (Ed.), *The hierarchy of life* (pp. 307–321). Amsterdam: Elsevier.

Wheeler, W. C., Whiting, M., Wheeler, Q. D., & Carpenter, J. M. (2001). The phylogeny of the extant hexapod orders. *Cladistics, 17*, 113–169. + 404 (erratum).

Whitfield, J. B., & Kjer, K. M. (2008). Ancient rapid radiations of insects: challenges for phylogenetic analysis. *Annual Review of Entomology, 53*, 449–472.

Willmann, R. (1999). The Upper Carboniferous *Lithoneura lameerei* (Insecta, Ephemeroptera?). *Paläontologische Zeitschrift, 73*, 289–302.

Willmann, R. (2007). Die Stammgruppenvertreter der Ephemeroptera und ihre systematische Stellung (Insecta). *Species, Phylogeny and Evolution, 1*, 109–128.

Wootton, R. J., & Kukalova-Peck, J. (2000). Flight adaptations in Palaeozoic Palaeoptera (Insecta). *Biological Reviews, 75*, 129–167.

Zhou, C.-F. (2007). The bracing and fusing pattern of longitudinal veins at base in living mayflies (Insecta: Ephemeroptera). *Acta Entomologica Sinica, 50*, 51–56.