

The Upper Carboniferous *Lithoneura lameerei* (Insecta, Ephemeroptera ?)

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With 12 figures

Zusammenfassung: Die Nachuntersuchung des Typus von *Lithoneura lameerei* aus dem Oberkarbon von Mazon Creek (Illinois) hat ergeben, daß Pflanzenreste und anorganische Strukturen irrtümlich als Antennen und Prothorakalloben interpretiert worden sind; andere Teile des Tieres wie der Kopf und die Flügelgelenksklerite wurden hinsichtlich ihrer Ausbildung nicht richtig erkannt. Diese Erkenntnisse haben erhebliche Konsequenzen für unser Bild von der frühen Evolution der Pterygota. Nach derzeitiger Kenntnis spricht nichts gegen die Tatsache, daß es sich bei *Lithoneura* um eine frühe Ephemeroptere handelt. Die angebliche Eintagsfliege *Triplosoba* aus dem Karbon von Frankreich ist möglicherweise kein Vertreter dieser Gruppe.

Abstract: Re-examination of the type specimen of *Lithoneura lameerei* (Upper Carboniferous, Mazon Creek, Illinois) has revealed that plant remains and inorganic structures have been misinterpreted by a previous author as antennae, a haustellate beak and prothoracic lobes, and some parts of the animal have not been interpreted correctly (e. g. eyes, pteralia). Though no characters shared by *Lithoneura* and the Ephemeroptera are, according to current knowledge, doubtless synapomorphies, the results of the re-examination are compatible with the view that *Lithoneura* is a mayfly. The alleged early mayfly *Triplosoba* from the Carboniferous of France is possibly not an ephemeropteran. The new results have some bearing on our view of general early pterygote evolution.

Introduction

The sister group relationships among the basal branches of the pterygotes (Ephemera, Odonata, and Neoptera) have been the subject of debate since the advent of phylogenetic systematics. Characters have been interpreted in favour of all possible sister group relationships. Excluding the extinct Palaeodictyopteroidea (Palaeodictyoptera, Diaphanopteroidea and Megasecoptera), the different assumptions have their supporters as follows. HENNIG (1953) and KRISTENSEN (e.g. 1981: 141; 1989: 301; see also HENNIG 1986) believed that the hypothesis of a sister group relationship between the Odonata and the Neoptera is best supported. For the respective superordinate taxon the name Metapterygota is available. BOUDREAUX (1979) was in favour of a sister group rela-

tionship between the Ephemeroptera and the Neoptera (together the Chiasmomyaria, Opisthoptera). The most popular view is that of a monophylum consisting of the Odonata and the Ephemeroptera, the two together constituting a taxon bearing the well-known name Palaeoptera. MARTYNOV, who introduced this name, however, did not necessarily believe in what we today call the monophyly of the group, as he thought that the palaeopteran condition is primitive in relation to the neopteran wing. Authors dealing with fossil insects also include the Palaeodictyopteroidea in the Palaeoptera.

It is not my intention to review the arguments for or against one hypothesis or another. For more recent reviews see KRISTENSEN (1991, 1995) and SOLDÁN (1997), who consider the question of basic pterygote sister group relationships as unsolved.

The affinities of a number of Palaeozoic palaeopteran insects are not clear. One of the species concerned is *Lithoneura lameerei*. The species was described by CARPENTER in 1938, based on a very well preserved specimen from the Upper Carboniferous of Mazon Creek (Illinois, Westphalian D). It has provoked considerable interest since it has some bearing on assumptions about character evolution in the early pterygotes. Some authors have considered *Lithoneura* as belonging to the Ephemeroptera, others as a member of the Palaeodictyoptera.

Description of *Lithoneura lameerei*

CARPENTER (1938) gave a detailed description of the wings of *Lithoneura lameerei*. He made only scant mention of other structures.

In 1985, KUKALOVÁ-PECK published the results of a new examination of the holotype. She regarded *Lithoneura* as an ephemeropteran. Her drawings and description resulted in a lot of interest, as they show the specimen as bearing very long antennae and other features not present in recent Ephemeroptera. The long antennae are of particular interest as short antennae have often been mentioned as a possible synapomorphy of Odonata and

Ephemeroptera and have thus been used to bolster the assumption that the two taxa are sister groups. Long antennae in early members of one of the two taxa would, of course, weaken this hypothesis.

My own re-examination of the specimen showed, however, that several of the characters mentioned or figured by KUKALOVÁ-PECK as being parts of the fossil are either inorganic structures or organic remains which do not belong to the specimen. Because of its importance, a detailed description of *Lithoneura lameerei* is presented here. My examination is based on both the part and counterpart of the holotype specimen (MCZ 4537, Fig. 1 a, b). As the part shows portions of the left wings only, the following description is presented as if it was based on the more complete counterpart. 'Left' and 'right' refer to the counterpart (Fig. 1 a) and were reversed in the living animal.

Head (not mentioned by CARPENTER): KUKALOVÁ-PECK figured the head as being large, having large round compound eyes which protrude beyond the width of the prothorax (not taking into consideration the alleged prothoracic lobes). From between the eyes, almost from their medial margin, she believed the antennae arose (KUKALOVÁ-PECK 1985: fig. 11; Fig. 5 herein).

I have been unable to confirm KUKALOVÁ-PECK's observations. The head appears to be a much smaller structure within the area circumscribed by the alleged left antenna (Fig. 2). The supposed eyes are not very large as compared to the size of the head, the left one being clearly visible (Fig. 3). Between the eyes, dorsofrontal parts of the head capsule are preserved showing no details that could be interpreted with certainty, but the frontal portion is suggestive of the clypeolabral area. What KUKALOVÁ-PECK interpreted as the left eye is a smooth structure of the slab and is not of organic origin (Figs. 1 and 2). Moistening of the slab confirms that there is no organic matter beyond the head region as shown in Fig. 5 (compare Fig. 1 b).

Antennae: According to KUKALOVÁ-PECK, the antennae are clearly visible and very long, the right one being preserved with its basal section only and showing eleven anuli (Fig. 5 herein). The other antenna is illustrated as being much longer, though broken, and its distal section is shown as being overlain by the right wings. According to KUKALOVÁ-PECK, 20 anuli are present, each anulus being slightly longer than wide.

However, what KUKALOVÁ-PECK describes as the left antenna shows a clear longitudinal striation (Figs. 4 a, b), while there is not a single structure that could be interpreted as an antennomere. This so-called antenna is clearly a plant remain. The nature of what KUKALOVÁ-PECK figured as the right antenna is at best an elevation of the rock surface without any relation to structures of organic origin.

The only structures which could be remains of an antenna are preserved immediately in front of the left eye. In this

area, there is, as Fig. 3 shows, a dark almost rectangular spot, which is divided by the margin of the head capsule. This could be a basal antennomere, and another one may be indicated by weak sutures on the rock surface. I should like to stress, however, that the various fine linear structures preserved in this area are difficult to interpret, and I am not stating that any definite antennal remains are preserved.

Mouth parts: No mouth parts are preserved. Whether this is indicative of small mouth parts is unclear, but I do believe that no particularly strong mouth parts were present in the living animal. A short distance from the front margin of the left eye there is a little elongate structure which is included in fig. 11 of KUKALOVÁ-PECK's paper (1985; Fig. 5 herein) but which is not mentioned in her text. It is probably the structure which she interpreted as a beak in 1980 (see below). I have been unable to confirm that this structure was part of the specimen. As it shows longitudinal striae, it appears more probable that it is a small fragment of plant origin. It is definitely not a part of one of the mouth parts. Hence, no indication of a beak is preserved in the type specimen of *Lithoneura lameerei*.

Prothorax: The tergite of the prothorax is preserved as an elongate negative imprint probably not showing the actual margins of the sclerite which may have been a little broader in the living insect.

According to CARPENTER 1938, "prothoracic lobes are clearly shown, and are 2.5 mm wide and 4 mm long (i.e., parallel to the longitudinal body axis)." HUBBARD & KUKALOVÁ-PECK (1980) also stated that "the prothorax carried a pair of large prothoracic winglets of the palaeodictypteroid type" (see also KUKALOVÁ-PECK 1985: 140). But in fact, no prothoracic lobes are present. CARPENTER was misguided by a smooth area of the rock surface near the prothorax which he interpreted as part of the fossil and which he considered as the left pronotal lobe (right lobe in the living animal) (Figs. 1 a, 2). In addition, a portion of the rock is broken away, and the resulting structures also contribute to the impression that a prothoracic lobe might be present (WILLMANN 1998). When I realised this during my examination together with the late Prof. CARPENTER, he did not object to my interpretation. My figures show the structures under different illumination, Fig. 2 b showing their artefactual nature best. (Just to indicate that comparable inorganic structures are common on the slab, a similar smooth (though much larger) area on the rock surface can be seen behind the fossil in Fig. 1 a). On the right side of the prothorax, no structures are present that could be interpreted as pronotal lobes.

Meso- and metathorax: Both meso- and metathorax are large (Fig. 1 a). The legs are not preserved.

Wings: As the membrane is partly wrinkled, it is difficult to reconstruct the fine venation and even the position of many crossveins. The longitudinal veins are gen-

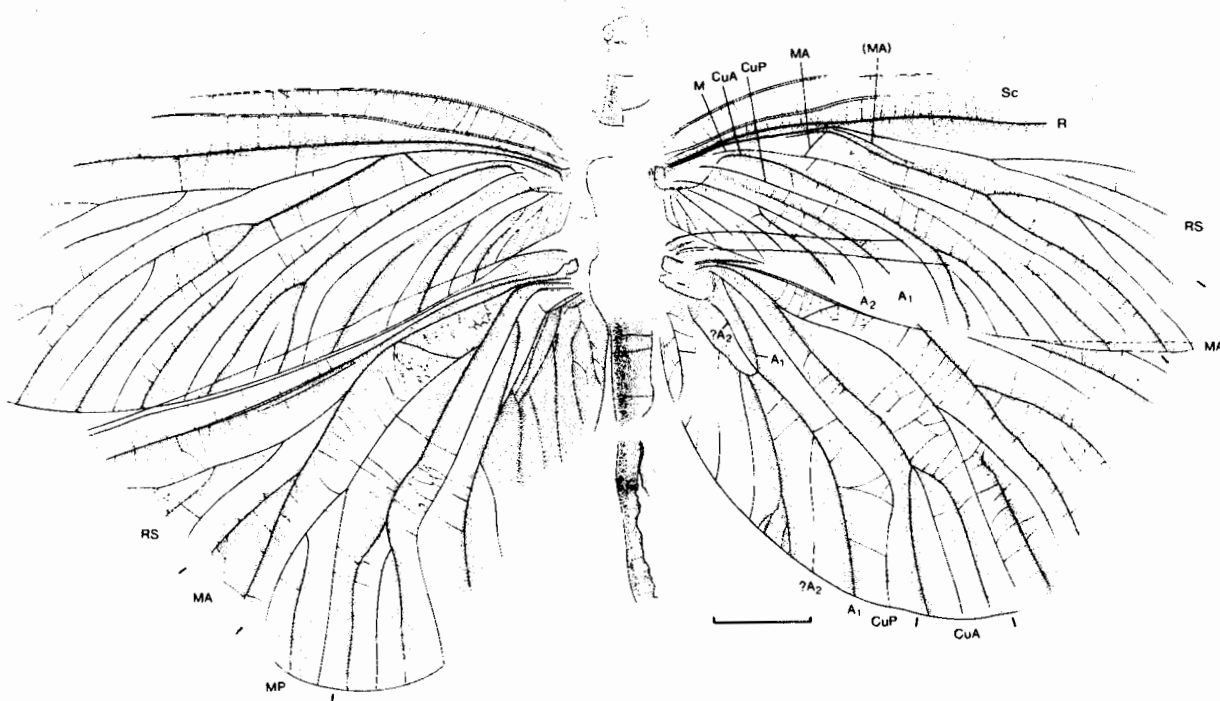


Fig. 1a, b. *Lithoneura lameerei* CARPENTER 1938, holotype (MCZ 4537), counterpart. Wing span as preserved 6.4 cm. A. anal vein; CuA, CuP, anterior and posterior cubitus; M, media; MA, media anterior, (MA) in Fig. 1b, doubling of the media anterior due to preservation. Such doubling also occurs in RS and part of MP: for conditions in the living animal, see other fore wing. - R, radius; RS, radial sector; Sc, subcosta. - Scale bar = 5 mm.

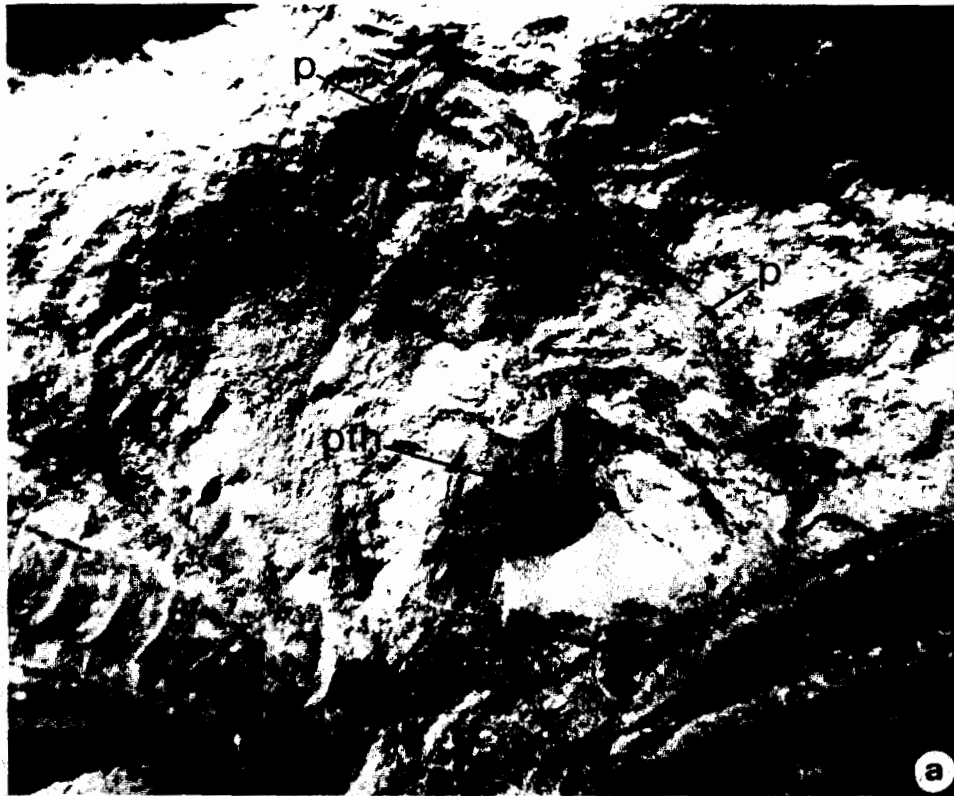


Fig. 2a, b. *Lithoneura lameerei*. Head (h) and prothorax (pth) under different illumination with plant remains (p) in front. The smooth structure on the left side of the prothorax is due to the breaking off of pieces of the slab and was misinterpreted as prothoracic lobes by earlier authors. The small head is hardly visible in Fig. 2 a, compare Fig. 4. - Scale bar = 1 mm.

erally well preserved. To facilitate comparison, the venational terms used here are sometimes augmented by those of KUKALOVÁ-PECK in parenthesis.

Fore wing, costal area. – According to KUKALOVÁ-PECK there is a branched additional vein, ScA, between the wing margin and Sc (her ScP). What she interprets as the anterior branch of ScA is indeed visible on the part of the specimen, but whether or not this is a veinlet is hardly possible to decide. What KUKALOVÁ-PECK views as a posterior branch of ScA (ScA_{3,4}) is, in my opinion, the fore margin of Sc, which is considerably broadened near the wing base (see below: fore and hind wings, pteralia). The broadened base of Sc is the basisubcostale sensu BRODSKY (1994).

Fore wing, R (= R₁) and RS. – CARPENTER (1938) has drawn R₁ and RS as being fused near the wing base. The two veins are, however, entirely separate. CARPENTER (1943: 14) remarked that R and RS are completely independent in the larger species *Lithoneura mirifica*, adding that “this condition undoubtedly existed in *lameerei* but it was not clearly visible in the type.” Fortunately, I can confirm that the latter is not the case (see also KUKALOVÁ-PECK 1985: fig. 12). RS is fused over a short distance with M (clearly visible only in the left fore wing, as the right wing seems to have moved a little immediately after embedding, thus doubling impressions of some veins and obscuring details; see Figs. 1 a, b).

Fore wing, M and Cu. – According to KUKALOVÁ-PECK (1985: fig. 12), M and the base of CuA are connected by a short strut. As Figs. 6 and 7 show, there is no such structure, but there is a raised area of the membrane in this part of the wing (preserved as a furrow in the counterpart). If one proceeds from the wing margin to the base, CuA leaves the raised area of the wing to meet CuP, while the raised wing area continues towards M without altering its course. CuP is markedly bent before reaching the wing margin.

Fore wing, anal area. – Basal to the cubital and anal veins, there is an elongate depression (preserved as a raised area in the counterpart). According to KUKALOVÁ-PECK, this field is separated from the anal area by the first anal vein (AA_{1,2} of her nomenclature). In the type specimen of *Lithoneura*, however, no such vein is preserved; what she interprets as the first anal vein is obviously a fold. The fold becomes less pronounced before reaching CuP which is visible in the hind wings.

In the fore wing, the base of A₁ sensu CARPENTER (1938; AA₂ sensu KUKALOVÁ-PECK 1985) obviously meets CuP (CuP + AA₁ sensu KUKALOVÁ-PECK). This is difficult to see as there are several wrinkles in the membrane obscuring the connection in the left wing, and irregularities in the rock suggestive of a connection in the right wing further confuse the situation. CARPENTER had drawn CuP and A₁ as being entirely separate.

What KUKALOVÁ-PECK interprets as a concave fold (f

in her figs. 12-13) crossing the area basal to Cu and A is more likely a true vein. According to KUKALOVÁ-PECK, it continues into the anal area as an intercalary vein and the alleged fold mentioned above is more likely exactly that vein. CARPENTER (1938) considered it to be A₂, and I agree with his view.

Hind wing. – As with the fore wing, KUKALOVÁ-PECK interprets the broad base of Sc as two veins, and again I cannot confirm the existence of the strut which she believes to occur between M and the base of CuA. CuA is basally fused to the stem of the media (in contrast to the fore wing, where the two veins are entirely separate). CuP is markedly bent, even stronger than in the fore wing. As in the fore wing, there is obviously no vein surrounding the elevated area at the wing base (depression in the living animal if seen from the dorsal side), but only a marked fold.

A₂ is obviously fused over a short distance with A₁. It is difficult to judge the nature of this vein, but comparison with the fore wing contributes to its homologization. It is obviously the branched vein interpreted as A₂ in the fore wing, which extends, if one proceeds from the wing margin to the base, into the depression (elevated area in the fossil) at the wing base.

Fore and hind wing, pteralia. – In both the fore and hind wing some pteralia can be recognized. No true plate is visible at the base of Sc. However, the base of Sc is enlarged, and therefore the two furrows accompanying Sc are far apart in this area. This led KUKALOVÁ-PECK to assume that there are two branches to Sc which she called ScA and ScP (see above; Fig. 9a). The radial plate lies a little behind the base of Sc and behind the beginnings of R and RS, which are separate from the radial plate. There is no indication of the pteralia called median basivenale, cubital basivenale, anal basivenale and jugal basivenale by KUKALOVÁ-PECK which she shows in her figs. 12 and 13 (1985). Figs. 6 - 7 show the respective areas of the left and right fore wings under different illumination; for the hind wing see Fig. 10 a-b (see also Fig. 8).

Abdomen: CARPENTER (1938) described the abdomen only briefly, as it is only weakly preserved, writing “The abdomen is slender, being about 2 mm wide.” Indeed only a few segments are discernible. The end of the abdomen is not preserved.

Comparison with other species: Only the hind wing is known of the much larger Carboniferous *L. mirifica* CARPENTER 1943. In this species, there is no longitudinal vein between C and Sc, R and RS are separate, MA touches RS, CuA and the stem of M are fused, CuP is strongly bent shortly before the wing margin. In these characters as well as in many additional details, there is total agreement with the hind wing of *L. lameerei*, thus confirming the results obtained during the re-examination of this species. While in *L. lameerei* A₁ and A₂ are fused over a short distance, the two veins are close to one another though separate in *L. mirifica* (CARPENTER 1943).

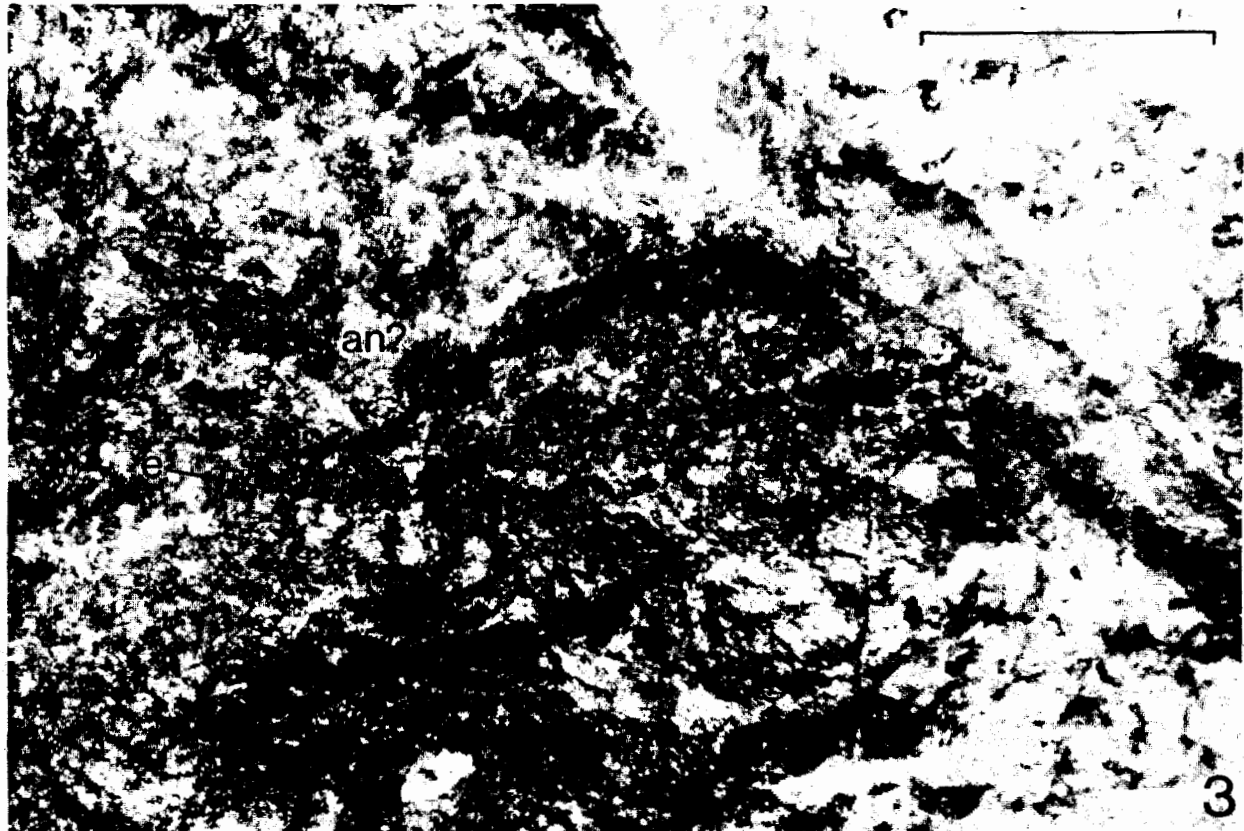
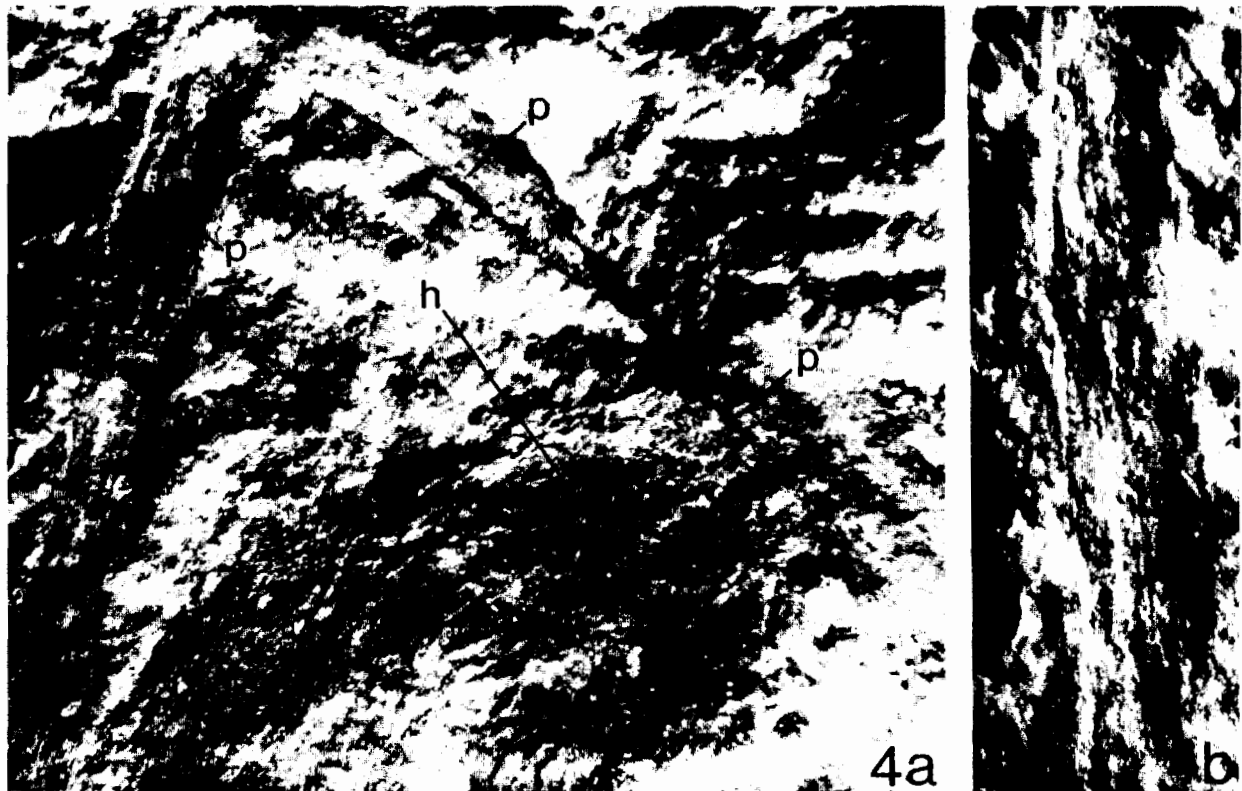


Fig. 3. *Lithoneura lameerei*. Head. e. eye; an?, basal portion of left antenna (interpretation uncertain, see text). — Scale bar = 1 mm.



The phylogenetic position of *Lithoneura lameerei*

The exact phylogenetic position of *Lithoneura* must remain unresolved pending better knowledge of early pterygote evolution. Quite a number of important questions can be answered now, however, and some earlier assumptions appear unlikely now.

CARPENTER (1938) believed that *Lithoneura* belonged to the Palaeodictyoptera and within this taxon, to the Syntonopteridae. This does not mean much in terms of phylogenetic relationships, however, as he regarded the Palaeodictyoptera as what we would today call a paraphyletic group: in 1943 (p. 14) he wrote that "the evidence still indicates that [the Syntonopteridae] were related to the stock which produced the Plectoptera" (Plectoptera = little used name for mayflies). Other authors considered the Syntonopteridae to be palaeodictyopteroids as well (e.g. HANDLIRSCH 1911, 1919; RICHARDSON 1956; KUKALOVÁ-PECK in several publications, see KUKALOVÁ-PECK 1985: 939), while WOOTTON (1981: 328), EDMUNDS & TRAVER (1954) and SHAROV (1966) favoured the view that they belong to the Ephemeroptera (see also KRISTENSEN 1981: 141 for *Lithoneura*). LAURENTIAUX (1953) constituted a new order 'Syntonopterodea', but this did not contribute to the discussion about where the Syntonopteridae belong.

Phylogenetic significance of the mouth parts

It appears possible that the Palaeodictyopteroidea (Palaeodictyoptera, Megasecoptera and Diaphanopteroidea) are a monophyletic group as they have a haustellate beak, which is sometimes considered to be an autapomorphy of the group. When CARPENTER placed the Syntonopteridae in the Palaeodictyoptera again in 1992, he did so because "KUKALOVÁ-PECK (HUBBARD & KUKALOVÁ-PECK, 1980) has reported the presence of a haustellate beak in the type specimen of the syntonopterid genus *Lithoneura*. All the Palaeozoic Ephemeroptera known had normal, dentate mandibles." This would have been a good argument indeed, but in fact no such beak is preserved in *L. lameerei* (Figs. 1, 3, 4), and I am convinced that it was not present in the living animal, either (see above). HUBBARD & KUKALOVÁ-PECK (1980: 27) considered *Lithoneura* to be a palaeodictyopteroid which is "strongly convergent in venation and in

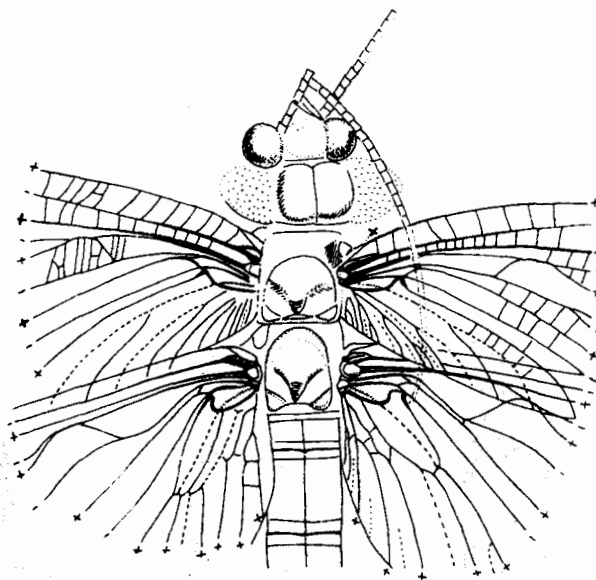


Fig. 5. *Lithoneura lameerei*. KUKALOVÁ-PECK'S (1985) drawing of the holotype for comparison with the description given in the present paper.

the body shape to mayflies". They believed the head to be "palaeodictyopteroid with long heavy antennae, bulging eyes, ... a swollen clypeus where the cibarial muscles were attached", and as having "small remnants of a beak" and viewed these structures as decisive for deriving the phylogenetic position of the species. Unfortunately, the structures interpreted as remnants of a beak were neither described by HUBBARD & KUKALOVÁ-PECK (1980) nor by KUKALOVÁ-PECK (1985), but fig. 11 in KUKALOVÁ-PECK (1985 [Fig. 5 in the present paper]) shows an elongate structure in front of the head which is probably what she had interpreted as a beak in 1980. But as any reference to the structure is omitted from KUKALOVÁ-PECK'S 1985 description of *Lithoneura*, and as she gives some qualifications on p. 939, it is possible that she had, in the meantime, realised that the structure is at least not a beak.

With respect to other characters discussed by HUBBARD & KUKALOVÁ-PECK (1980) it should be mentioned that no bulging eyes are present in the fossil, and there is also no indication of a "swollen clypeus" which might be used to argue in favour of a close relationship to the Palaeodictyopteroidea (see under 'description').

Significance of the antennae

Short, bristle-like antennae in the Odonata and Ephemeroptera have been interpreted as a synapomorphy of the Ephemeroptera and Odonata. This is why LAMEERE subsumed the Ephemeroptera and Odonata under the name 'Subulicornia'. The character, however, applies to Palaeozoic Palaeoptera only with limitations, as in early odonates, the antennae were somewhat longer than in Recent species (BRAUCKMANN & ZESSIN 1989). If

Fig. 4a, b. Plant remains (p) in front of the head (h) of *Lithoneura lameerei*, misinterpreted as an antenna by an earlier author. The head is hardly visible under the chosen illumination. Fig. 4b shows the left portion of the plant fragment shown in Fig. 4a under different illumination and further enlarged. There is no evidence of antennomeres as figured by KUKALOVÁ-PECK (1985), while a longitudinal striation typical of plant remains is clearly visible. For the size of the plant remains, compare Fig. 2.

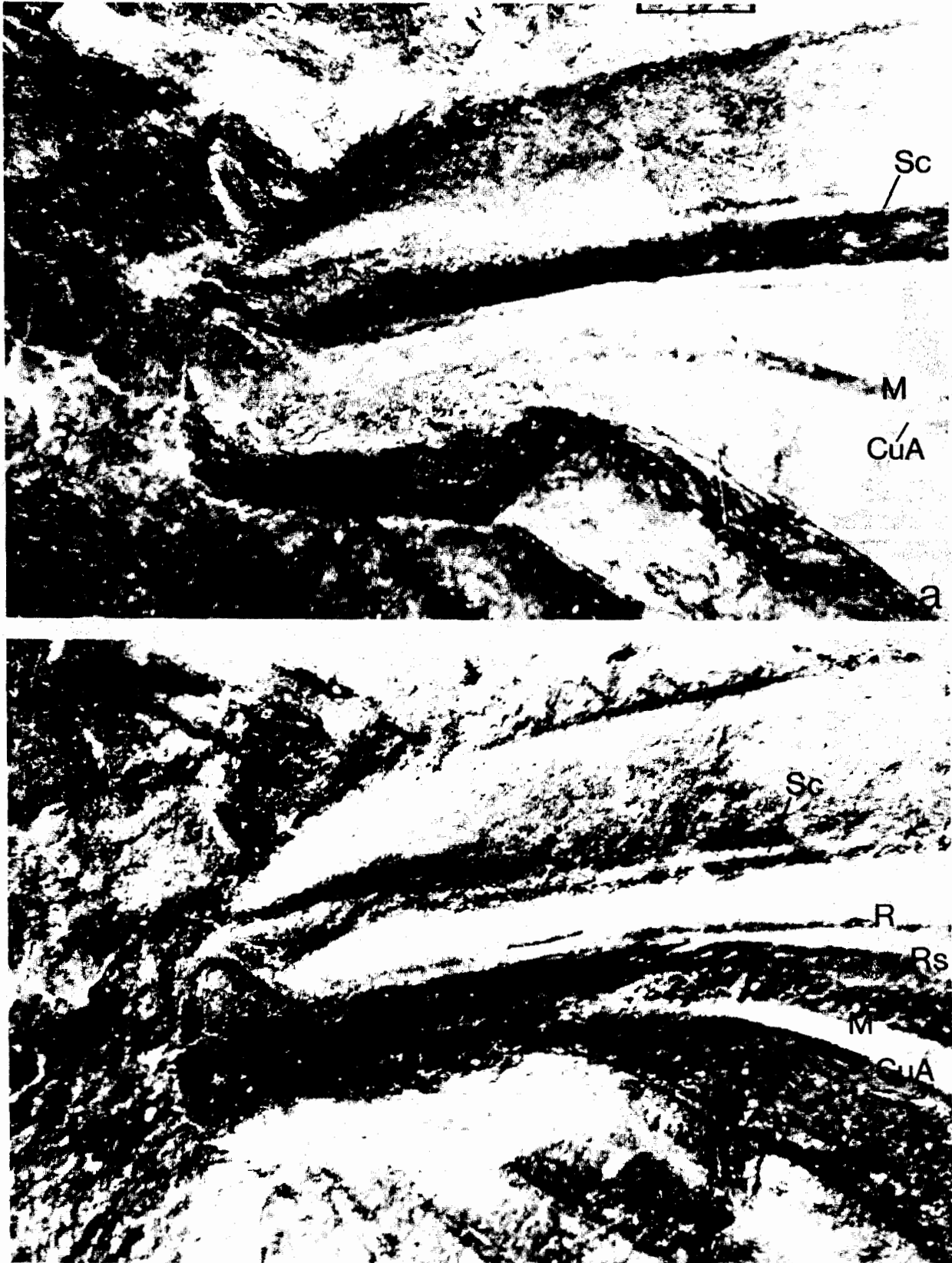


Fig. 6a, b. *Lithoneura lameerei*. Base of right fore wing (counterpart: left forewing of the living animal). Fig. 6b shows the same area with light reversed; negative structures of Fig. 6a therefore appear as positives and vice versa. This would be the condition in the living animal if the wing is seen from dorsal view. Fig. 6b shows particularly well the enlarged base of Sc and the radial plate behind it. There is no indication of the plates called median basivenale, cubital basivenale, anal basivenale and jugal basivenale which KUKALOVÁ-PECK shows in her fig. 13 (1985; here Fig. 9b). What she interprets as a concave fold (f) crossing the Cu-AA area continuing into the anal area as an intercalary vein behind AA₁ (Fig. 9 herein) is more likely a true vein. — Sc, subcosta; R, radius; RS, radial (sector); M, media; CuA, cubitus anterior. — Scale bar = 1 mm.



Fig. 7. *Lithoneura lameerei*, type. Base of left fore wing (right fore wing of the living animal). Illumination as in Fig. 6a. - CuP, cubitus posterior; A₂, second anal vein. - Scale bar = 1 mm.

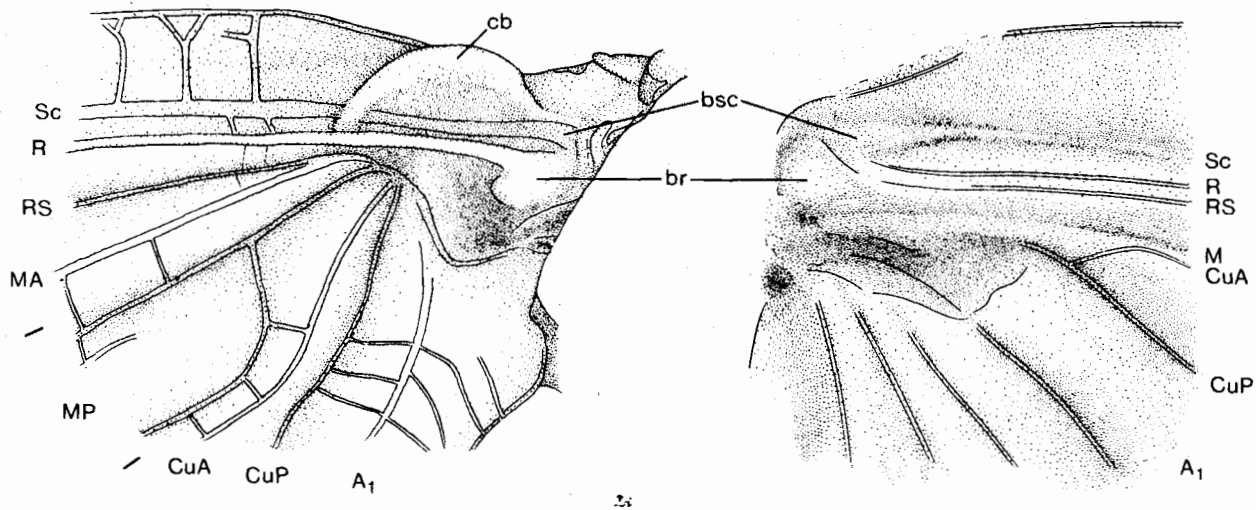


Fig. 8. Base of fore wing of *Lithoneura lameerei*, type (on the right), and of the Recent species *Ephemera danica*. Ephemeroptera (Niemetal near Göttingen, Germany; dorsal view) (on the left). Concave and convex folds are reversed in the fossil (negative impression). A major difference between the two is the lack of a costal brace (cb) and the more numerous anal veins in the former species (plesiomorphies) and the fusion of MA and RS near the wing base in *Ephemera*.

Lithoneura is an early ephemeropteran. very long antennae in this taxon would of course weaken the assumption that the mayflies and odonates are sister groups. As mentioned above, however, the alleged long left antenna in the type of *Lithoneura lameerei* is a plant remain. The true antennae are unknown (see also WILLMANN 1997).

Significance of the prothorax

Many Palaeodictyopteroidea (Palaeodictyoptera, Megasecoptera, Diaphanopteroidea) had prothoracic lobes. Contrary to earlier descriptions, no such lobes are preserved in *Lithoneura*. Taking this character and further

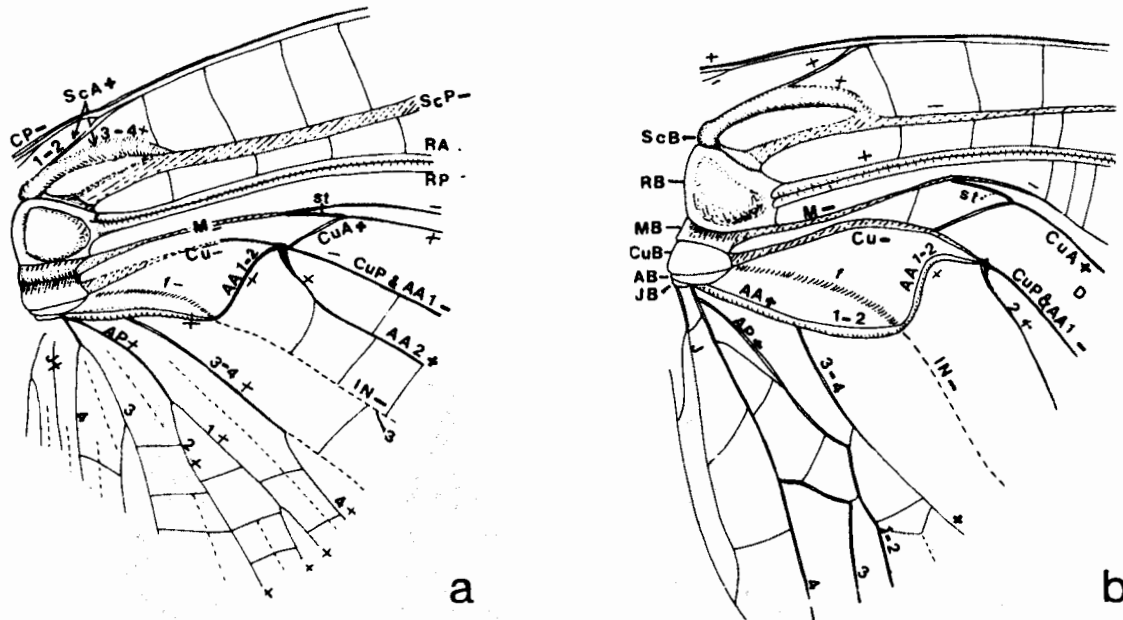


Fig. 9. *Lithoneura lameerei*, type specimen, bases of wings after KUKALOVÁ-PECK 1985. – a, fore wing; b, hind wing.

evidence (absence of a beak; separate R and RS, for the latter character, see below) into consideration, it is obvious that *Lithoneura* is not a palaeodictyopteroid.

Significance of the structure of R and RS

In the Neoptera and Palaeodictyopteroidea, R and RS are fused near the wing base. In *Lithoneura*, R is completely independent from RS. As R and RS are also independent in mayflies and odonates, FORBES (1943) believed the Palaeodictyoptera and Megasecoptera to be allied closer to the Neoptera (see also HENNIG 1969: 148). Thus he regarded the independence of R and RS as plesiomorphic, as did EDMUNDS & TRAVER (1954: fig. 8). In the opinion of CARPENTER (1963: 127-128), however, this is a derived character of Recent mayflies. In *Triplosoba*, usually considered to be a Carboniferous mayfly (e. g. CARPENTER 1992: 19, CARPENTER & BURNHAM 1985: 303; WOOTTON 1981), R and RS are fused near the wing base. This is considered as primitive by CARPENTER (1963), and he believed that the separation of R and RS occurred in more derived Ephemeroptera by migration of the origin of RS towards the wing base. This is also the theory of TILLYARD (1932: 104-105). The situation in the alleged mayfly *Triplosoba* was important for this interpretation, but in actual fact, its phylogenetic position is uncertain, and it is possibly not a mayfly. FORBES (1943) views the fusion of R and RS as being derived, concluding that *Triplosoba* "certainly belongs in the company of Palaeodictyoptera" (1943: 398). Thus no definite mayfly is known which has R and RS primarily fused.

The discussion shows that two conflicting interpretations have been published:

R and RS as separate veins may be either (1) a synapomorphy of odonates and ephemeropterans or (2) a symplesiomorphy. Under possibility (1) species with separate R and RS can be Odonata and Ephemeroptera or stem-group representatives of the Odonata + Ephemeroptera. Under assumption (2) such species can be either stem-group representatives of the pterygotes, or they are odonates, or mayflies, or representatives of their stem group (if the two combined are a monophylum), or they belong to those stem groups that would have to be assumed if the odonates or the mayflies are more closely related to the remaining pterygotes, or they are early species of the stem group of the Palaeodictyopteroidea + Neoptera. (Things would be more complicated if fusion of R and RS had occurred more than once, as in that case the Palaeodictyopteroidea and Neoptera need not be closely related.)

I am inclined to think that a third interpretation with respect to the separation of R and RS, namely convergence is less likely as the character does not occur in any other insect group which possibly indicates that it is for some reason difficult to separate the two veins. It must be mentioned, however, that with respect to both Palaeozoic mayflies and odonates the descriptions and illustrations are sometimes not clear as to whether or not R and RS are fused. The convergence hypothesis would, of course, be supported if some species both primitive mayflies and odonates had the two veins united at the wing base. Separate R and RS would be a convergent character if CARPENTER was right in assuming that it is derived in Recent mayflies.

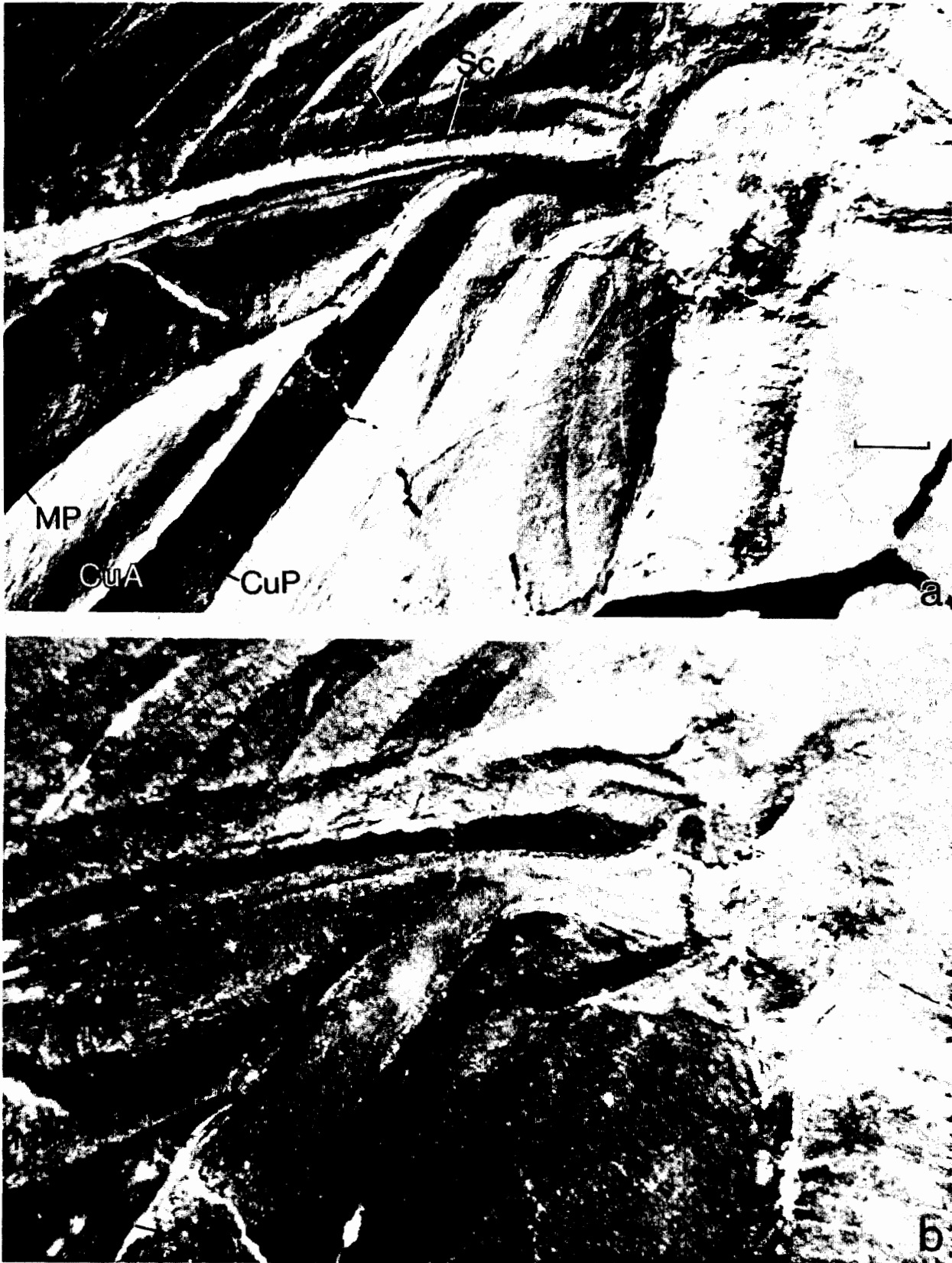


Fig. 10a, b. *Lithoneura lameerei*. Base of left hind wing (right hind wing of the living animal) under different illumination, in Fig. 10b more enlarged than in 10a. Illumination in Fig. 10a is chosen in such a way that the impression of a dorsal view of the living animal is achieved, while Fig. 10b shows the condition in the fossil (counterpart). – MP, media posterior; CuA, cubitus anterior, CuP, cubitus posterior. – Scale bar = 1 mm.



Fig. 11. *Lithoneura lameerei*. Portion of left fore wing, showing wrinkling of the membrane. Front margin of the wing above. The upper middle section of the photo shows fusion of MA and RS. Abbreviations as in previous figures. — Scale bar = 1 mm.

Significance of the pteralia

The base of Sc is broad which led KUKALOVÁ-PECK to assume that there are remnants of two branches to Sc (ScA_{3,4} and ScP in her terminology). There is, however, no evidence of two branches (Figs. 6 and 8). The radial plate lies behind the base of Sc, and R and RS are separate from the radial plate. As mentioned above, there is no evidence of the pteralia called median basivenale, cubital basivenale, anal basivenale and jugal basivenale by KUKALOVÁ-PECK. *Lithoneura* had only few pteralia, and the wing base was very similar to Recent mayflies. If R and RS are primarily separate in the Pterygota (see discussion in the preceding section) and if the Palaeodictyopteroidea are more closely related to the Neoptera because they have R and RS fused at the wing base, there were originally no 32 pteralia that became partially fused in many taxa, but a much smaller number. This view stands in contrast to what KUKALOVÁ-PECK believes. If 32 pteralia were present in some Palaeodictyoptera (as stated by KUKALOVÁ-PECK), this number must be interpreted as derived.

Significance of fusion of MA and RS

In *Lithoneura* and the Ephemeroptera, MA is partially fused to RS. In the Odonata including the "Protodonata", this fusion occurs as well (TILLYARD 1932: 104), but the branching pattern is different which may be due to the narrowing of the wings (narrowing as a derived character of "Protodonata": FORBES 1943: 399). It is not clear whether the fusion is a synapomorphy of the Odonata and Ephemeroptera. If not, *Lithoneura* is a mayfly. In the fore wing of *Triplosoba*, MA meets the base of R+RS, while MA is remote from RS and fused to MP in the hind wing (CARPENTER 1963). This condition is quite different from that in *Lithoneura*, the Ephemeroptera and the Odonata, and because of this and other evidence (fusion of R and RS, see above) I do not believe that *Triplosoba* is a mayfly.

Ephemeropteran affinities of *Lithoneura*

As mentioned above, *Lithoneura* is often considered to be an ephemeropteran. But at present, no certain synapomorphy shared by *Lithoneura* and Recent Ephemeroptera is known, although the triads formed by RS, M, and CuA are suggestive of those in the mayflies, and the fusion of MA and RS is similar. On the other hand, several characters known to be autapomorphies of the Recent Ephemeroptera were not yet developed in *Lithoneura*: (1) *Lithoneura* had no costal brace. The statement of KUKALOVÁ-PECK (1985: 940) that a "gently arched but very strong subcostal brace" (ScA) is present, is not correct. I view the structure under consideration as part of the broad base of Sc (see above). A costal brace is present in Permian Ephemeroptera like the Protoreismatidae and Misthodotidae (TILLYARD 1932). Their costal brace does not yet reach the costa. (2) The hind wing is large in *Lithoneura*, while it is much smaller in Recent mayflies. (3) The hind wing of *Lithoneura* has a pronounced anal area, while the anal fan is smaller in other Ephemeroptera with large hind wings, e.g. Protoreismatidae. Many decisive structures (mouth parts, antennae, legs, abdomen) are not or not sufficiently well preserved in the type of *Lithoneura lameerei*, and the character states of many wing structures of early pterygotes still need to be worked out.

Conclusions

Lithoneura lameerei does not belong to the Palaeodictyopteroidea but is obviously closely related to the Odonata and Ephemeroptera, sharing with them independent R and RS, fusion of MA with RS over a short distance and a wing base similar to that in the Ephemeroptera (Fig. 12). Although the triads formed by RS, M and CuA are suggestive of the Ephemeroptera, it is not entirely clear whether *Lithoneura* belongs here as the character may have been present in the stemgroup of the Ephemeroptera + Odonata (provided the two are sister

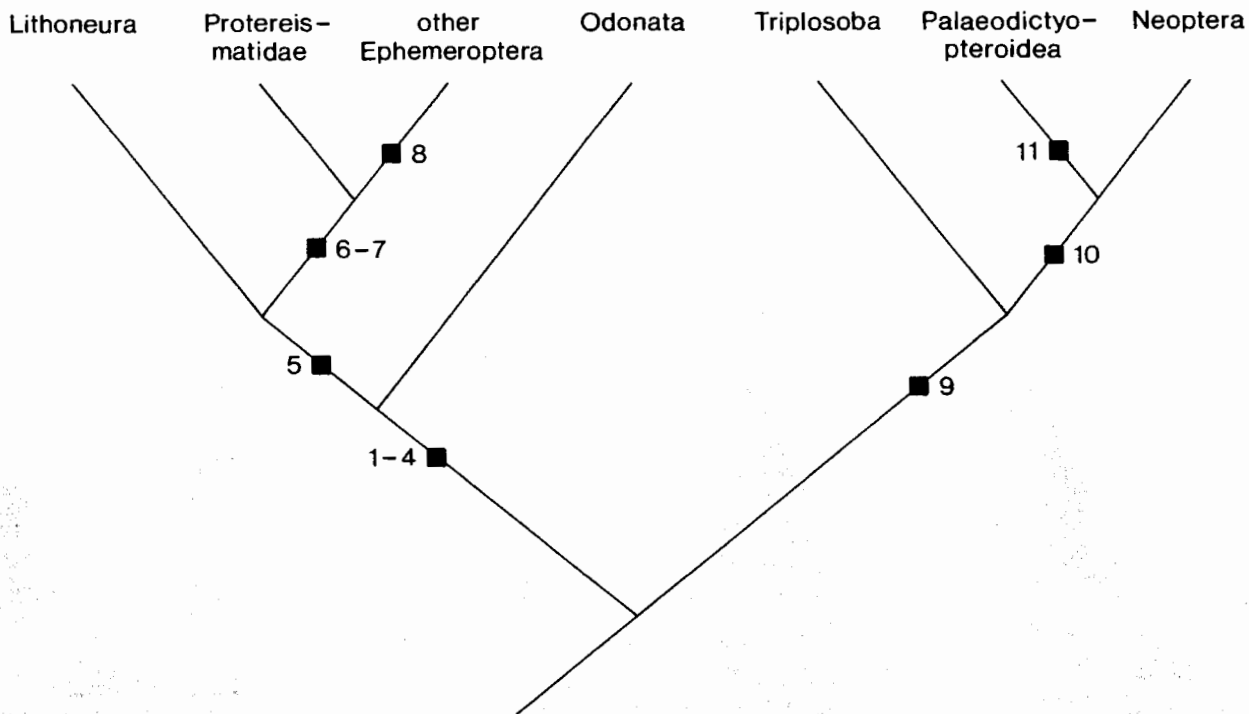


Fig. 12. One of several hypotheses about the relationships among the lower Ptergota. Note that several of the characters indicated here as derived may well be interpreted in different ways (see text; for a review of concurring views on the affinities of Recent basal pterygote groups: see SOLDÁN 1997). Only taxa mentioned in the text are considered. – Apomorphies: 1: wings with simple CuP (plesiomorphic character?), with MA and RS being fused over a short distance and with intercalary veins (character state uncertain). 2: short antennae. 3: galea and lacinia fused. 4: aquatic larva. 5: triads formed by RS, M, and Cu. 6: costal brace. 7: anal fan of hind wing small. 8: hind wing small. 9: stems of R and RS fused near wing base. 10: loss of caudal (= terminal) filament. 11: haustellate beak.

groups). Apart from this structure, no possible autapomorphy of Recent mayflies is visible. *Lithoneura* shows no autapomorphy of the Odonata (sensu lato, including the Protodonata [= Meganisoptera]). Again, the results of the restudy of *Lithoneura lameerei* mean that there is currently no evidence that large prothoracic lobes were ever present in the Ephemeroptera, if *Lithoneura* belongs to this group, as, contrary to earlier descriptions, no such structures are preserved in *Lithoneura*. Should *Lithoneura* belong in the stemgroup of the Odonata + Ephemeroptera (provided the two are sister-groups), there would be no evidence of such lobes even among the common ancestors of the mayflies and odonates. Finally, there is still no evidence for particularly long antennae in early representatives of the Odonata or Ephemeroptera. Among others, the structures previously considered as being antennae and prothoracic lobes were misinterpreted in the type specimen of *Lithoneura lameerei*.

Triplosoba from the Upper Carboniferous of France, sometimes regarded as the only true mayfly of that age, is probably not an ephemeropteran.

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References

- BOUDREAUX, H. 1979. Arthropod phylogeny with special reference to insects. – 320 pp., New York, Chichester, Brisbane (J. Wiley & sons).
- BRAUCKMANN, C. & ZESSIN, W. 1989. Neue Meganeuridae aus dem Namurium von Hagen-Vorhalle (BRD) und die Phylogenie der Meganisoptera (Insecta, Odonata). – Deutsche entomologische Zeitschrift, neue Folge 36: 177-215, Berlin.
- BRODSKY, A. 1994. The evolution of insect flight. – 229 pp., Oxford (Oxford University Press).
- CARPENTER, F.M. 1938. Two Carboniferous insects from the vicinity of Mazon Creek, Illinois. – American Journal of Science, (5) 36: 445-452, New Haven.
- 1943. Carboniferous insects from the vicinity of Mazon Creek, Illinois. – Illinois State Museum, Scientific Papers 3: 9-20, Chicago.
- 1963. Studies on Carboniferous insects from Commentry, France. Part IV. The genus *Triplosoba*. – Psyche 70: 120-128, Cambridge/Mass.
- 1992. Superclass Hexapoda. – Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, vols. 3 and 4, Boulder/Col. (Geological Society of America), Lawrence/Ks. (University Press).

- CARPENTER, F.M. & BURNHAM, L. 1985. The geological record of insects. – *Annual Review of Earth and Planetary Sciences* **13**: 297-314, Palo Alto.
- EDMUNDS, G. & TRAYER, J. 1954. The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. – *Journal of the Washington Academy of Science* **44**: 390-400, Washington/DC.
- FORBES, T. 1943. The origin of wings and venational types in insects. – *American Midland Naturalist* **29**: 381-405, Notre Dame.
- HANDLIRSCH, A. 1911. New Paleozoic insects from the vicinity of Mazon Creek, Illinois. – *American Journal of Science*, (4) **31**: 297-326, 353-377, New Haven.
- 1919. Revision der palaeozoischen Insekten. – *Denkschriften der Kaiserlichen Akademie der Wissenschaften Wien, mathematisch-naturwissenschaftliche Klasse* **96**: 511-592, Wien.
- HENNIG, W. 1953. Kritische Bemerkungen zum phylogenetischen System der Insekten. – *Beiträge zur Entomologie* **3** (Sonderheft): 1-85, Berlin.
- 1969. Die Stammesgeschichte der Insekten. – 436 pp., Frankfurt (W. Kramer).
- 1986. Wirbellose II. Gliedertiere. – *Taschenbuch der Speziellen Zoologie*, – 2: 335 pp., Thun, Frankfurt. [4th ed.].
- HUBBARD, M. & KUKALOVÁ-PECK, J. 1980. Permian mayfly nymphs: New taxa and systematic characters. – [In:] FLANAGAN, J. & MARSHALL, K. [eds.] *Advances in Ephemeroptera biology*: 19-31, New York.
- KRISTENSEN, N. 1981. Phylogeny of insect orders. – *Annual Review of Entomology* **26**: 135-157, Palo Alto.
- 1989. Insect phylogeny based on morphological evidence. – [In:] FERNHOLM, B.; BREMER, K. & JÖRNVALL, H. [eds.] *The hierarchy of life*: 295-307, Amsterdam, New York, Oxford (Elsevier).
- 1991. Phylogeny of extant hexapods. – [In:] *The insects of Australia*, – 1: 125-140, Ithaca, New York (Cornell University Press). [2nd ed.].
- 1995. Forty years' insect phylogenetic systematics. HENNIG's "Kritische Bemerkungen..." and subsequent developments. – *Zoologische Beiträge, neue Folge* **36**: 83-124, Berlin.
- KUKALOVÁ-PECK, J. 1985. Ephemeroid wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemeroptera). – *Canadian Journal of Zoology* **63**: 933-955, Ottawa.
- LAURENTIAUX, D. 1953. Classe des insectes. – [In:] PIVETEAU, J. [ed.] *Traité de Paléontologie*, – 3: 397-527, Paris.
- RICHARDSON, E. 1956. Pennsylvanian invertebrates of the Mazon Creek area, Illinois. – *Fieldiana (Geology)* **12**: 3-76, Chicago.
- SHAROV, A. 1966. *Basic Arthropodan Stock: with special reference to insects*. – 271 pp., Oxford (Pergamon Press).
- SOLDÁN, T. (1997): The Ephemeroptera: whose sister-group are they? – [In:] LANDOLT, P. & SARTORI, M. [eds.] *Ephemeroptera & Plecoptera, Biology - Ecology - Systematics*. – *Proceedings of the VIIIth International Conference on Ephemeroptera and XIIth International Symposium on Plecoptera*, Lausanne, Aug. 1995: 514-519, Fribourg.
- TILLYARD, R. J. 1932. Kansas Permian insects. Part 15. The order Plecoptera. – *American Journal of Science*, (5) **23**: 97-134; 237-272, New Haven.
- WILLMANN, R. 1997. Phylogeny and the consequences of phylogenetic systematics. – [In:] LANDOLT, P. & SARTORI, M. [eds.] *Ephemeroptera & Plecoptera, Biology - Ecology - Systematics*. – *Proceedings of the VIIIth International Conference on Ephemeroptera and XIIth International Symposium on Plecoptera*, Lausanne, Aug. 1995: 499-510, Fribourg.
- 1998. Advances and problems in insect phylogeny. – [In:] FORTEY, R. & THOMAS, R. [eds.] *Arthropod relationships*: 269-279, London, Weinheim, New York (Chapman & Hall).
- WOOTTON, R. 1981. Palaeozoic insects. – *Annual Review of Entomology* **26**: 319-344, Palo Alto.

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