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Revision of the giant pterygote insect *Bojophlebia prokopi* Kukalová-Peck, 1985 (Hydropalaeoptera: Bojophlebiidae) from the Carboniferous of the Czech Republic, with the first cladistic analysis of fossil palaeopterous insects

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The holotype is redescribed of the giant pterygote insect *Bojophlebia prokopi* Kukalová-Peck, 1985 from the Pennsylvanian of the Czech Republic. Multiple errors in the original description are documented and corrected. *Bojophlebia prokopi* has neither any visible traces of a costal brace nor an anal brace, but it does show triadic branchings of MA, MP, CuA, and even, as rare a plesiomorphy, of CuP. It is therefore rejected as a fossil stem mayfly and attributed as sister group of all other Hydropalaeoptera. The first cladistic analysis of fossil palaeopterous insects, including different palaeodictyopterid groups, is presented. A revised phylogeny of Hydropalaeoptera and the stem line of Ephemeroptera are suggested. Palaeodictyopterida is recognized as sister group of Neoptera; thus Palaeoptera *s.l.* is rejected as a paraphyletic taxon. Four new higher taxa – Paranotalia, Euhydropalaeoptera, Neopterygota and Litophlebioidea superfam. nov. – are introduced, as well as the new family Lithoneuridae.

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Keywords: Ephemerida; Palaeodictyopterida; Palaeoptera; Pterygota; Syntonopteroidea; phylogeny

Introduction

Bojophlebia prokopi Kukalová-Peck, 1985, from the Pennsylvanian of the Czech Republic, was originally described by Kukalová-Peck (1985), along with its alleged larva. Both were attributed to Ephemerida (*sensu* Kukalová-Peck 1985) as the only representatives of a newly erected family Bojophlebiidae. The larval paratype was later removed from Ephemerida, named *Carbotriplura kukalovae* Kluge, 1996, and attributed to Zygentoma (Kluge 1996). In a recent revision, *C. kukalovae* was recognized as a putative sister group to Pterygota and placed in a separate order, Carbotriplurida (Staniczek *et al.* 2014).

Kukalová-Peck's (1985) interpretation of the wing venation of *Bojophlebia prokopi* was subsequently adopted by several authors, who relied on the original description and thus all placed *Bojophlebia* as the most basal lineage within stem group mayflies (Rasnitsyn 2002; Grimaldi & Engel 2005; Willmann 2007a, b). More recently, the description published by Kukalová-Peck (1985) was reported to include several errors by authors who had seen the holotype (Prokop *et al.* 2010; Staniczek *et al.* 2011). This resulted in an uncertain phylogenetic status for *Bojophlebia*, being considered as Pterygota *incertae sedis* (Prokop *et al.* 2010) or Hydropalaeoptera *incertae sedis* (Staniczek *et al.* 2011). However, despite the fact that the interpretation of *B. prokopi* could be of crucial importance to the phylogeny of basal pterygotes, no detailed investigation of the holotype has been undertaken since its original description.

The present study presents an in-depth re-examination of the holotype to check the validity of characters stated by Kukalová-Peck (1985) and to clarify the systematic position of *Bojophlebia prokopi* within Pterygota. Based on this reinvestigation, the first cladistic study of fossil palaeopterous insects is here presented.

Material and methods

The holotype of *Bojophlebia prokopi* is housed in the National Museum (Národní muzeum), Prague, Czech Republic, catalogue number 36338/1955. It was found in tuffites of the middle Pennsylvanian/Moscovian (Silesian, Westphalian C) near Vrapice, Czech Republic (Kukalová-

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Peck 1985). The site of discovery was specified by Kukalová-Peck (1985) as the President Antonín Zápotocký Mine near Vrapice, in accordance with the original report of its discovery (Zázvorka 1956). Most probably it refers to the coal mine shaft 'Antonín IV', also called 'Prago IV', which is indeed located near Vrapice. This is part of a larger mining facility that is known under different names: originally called 'František Josef', it became known as 'Antonín Zápotocký' in the 1950s, and later was also named 'Prago-Tragy' (Roman Hájek pers. comm.).

According to Prokop & Nel (2010), this deposit is the so-called Whetstone Horizon from the continental basins of the Bohemian Massif represents a peat mire ecosystem with a shallow lake that was gradually filled by re-deposited volcanic ashes from the Bolsovian of western Bohemia (Czech Republic). The Whetstone Horizon has been dated by Hess *et al.* (1985) with the Ar/Ar method as 309 ± 3.7 Ma.

The specimen was studied under an Olympus SZX 9 (Olympus Corporation, Tokyo) stereomicroscope and photographed in different focal layers with a Nikon 60mm f/2.8 G ED AF-S Micro lens on a Nikon D800E (Nikon Corporation, Tokyo) digital camera. It was entirely covered with a layer of ethanol to achieve better contrast of the fossilized structures. In Adobe Photoshop version CS6 (Adobe Systems Incorporated, San Jose), focus stacks of photographs were subsequently merged to give compound images. These were sharpened and adjusted in contrast and tonality.

Abbreviations for the wing veins used throughout the text are as follows: **C**: costa; **ScP**: subcosta posterior; **R**: radius; **RA**: radius anterior; **RP**: radius posterior; **M**: media; **MA**: media anterior; **MP**: media posterior; **Cu**: cubitus; **CuA**: cubitus anterior; **CuP**: cubitus posterior; **AA**: analis anterior; **I**: intercalary vein. As the holotype of *Bojophlebia prokopi* is preserved in ventral aspect, the pleating is reversed and convex veins appear to be sunken in folds, while concave veins appear to be on top of folds on the photographs.

Systematic palaeontology

Class **Insecta** Linnaeus, 1758
Subclass **Pterygota** Lang, 1888
Infraclass **Hydropalaeoptera** Rohdendorf, 1969
Family **Bojophlebiidae** Kukalová-Peck, 1985
Genus ***Bojophlebia*** Kukalová-Peck, 1985
Bojophlebia prokopi Kukalová-Peck, 1985
(Figs 1−10)

Figure 1. *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype, overview (scale bar = 4 cm). The elevations appear to be reversed due to lighting from below, so that the legs only seem to be lower than the wing and ScP only seems to be concave (as in Figs 5, 6, 7 and 9A).

Material. The holotype and single known specimen is rather poorly preserved, as already indicated by previous authors who had briefly re-examined the fossil (Prokop *et al.* 2010; Staniczek *et al.* 2011).

The fossil is visible from its ventral side, because legs are superimposed on the wing veins, thoracic sternites are clearly visible, and the corrugation of the wing veins is reversed (concave veins are convex and vice versa). Head, thorax, proximal part of abdomen, fragments of legs, and basal parts of all four wings are preserved (Fig. 1). For measurements see Table 1.

Table 1. Measurements of *Bojophlebia prokopi* (holotype).

Measurement	mm
Length of body*	94.70
Length of head	14.78
Width of head	17.60
Length of labial palp	12.18
Length of prothorax	13.31
Width of prothorax	17.65
Length of mesothorax	19.64
Width of mesothorax	22.32
Length of metathorax	18.23
Width of metathorax	20.34
Length of right forewing*	103.48
Width of right forewing	68.55
Length of left forewing*	167.38
Width of left forewing	71.07
Length of right hind wing*	69.38
Width of right hind wing*	65.87
Length of left hind wing*	168.12
Width of left hind wing	76.05
Length of right forefemur	21.39
Length of right foretibia	32.65
Length of right foretarsus*	10.58
Length of left forefemur*	11.74
Length of left foretibia*	21.69
Length of left foretarsus*	13.91
Length of right middle femur*	10.53
Length of right middle tibia*	37.06
Length of right middle tarsus*	10.19
Length of left middle femur*	9.97
Length of left middle tibia*	25.70
Length of left middle tarsus*	14.03
Length of right hind femur*	22.82
Length of right hind tibia*	21.74
Length of left hind tibia*	9.30
Length of abdomen*	30.75
Width of abdomen (segment I)	14.17

*Preserved part.

Description

Head. Prognathous. Antennae not preserved. Mouth parts visible from ventral side (Fig. 2). The ventral closure of the mouth parts in insects is formed by the labium, so the most likely interpretation is given in Figure 2. The labium is enlarged and obscures most of the remaining mouth parts that are situated more dorsally. The two medioapical, paired, oval structures are interpreted here as large glossae (gl); laterodorsally to these the smaller paraglossae (pgl) are visible. The left paraglossa is only partly preserved. Posterior to glossae and paraglossae, a short prementum (prm) and postmentum (pm) follow. On its right side, the labium is somewhat distorted; in particular the postmentum is medially cracked and, together with the prementum, displaced and shifted anterolaterad. On the right side, a three-segmented labial palp (plb) inserts laterally at the prementum. The apical part of the corresponding left labial palp is not preserved, only the first segment is visible, but bent posteriorly. Basal part of right maxilla preserved (ca, st). Other mouth parts not visible.

Thorax. Division into pro-, meso- and metathorax clearly visible (Fig. 3). Prothorax smallest of all thoracic segments, meso- and metathorax of approximately same length. Prothoracic wings or paranota not present. The thoracic sterna show multiple sclerites, for which we here suggest a tentative homologization, based on a comparison with Recent mayflies (Tsui & Peters 1975).

Prothorax. With two sclerites that we interpret as basi- and furcasternum (bs1, fs1).

Mesothorax. With several discernible sclerites. Anterolaterally, the episternum extends to the basisternum (bs2). The episternum is divided into an anterior anepisternum (AES) and a posterior katepisternum (KES). The episterna are medially separated by the basisternum (bs2). Posteriorly to the basisternum, a large furcasternum (fs2) is present. The lateral parts of the furcasternum are bulged, forming a pair of furcasternal protuberances (fsp). Laterally of the furcasternum, an epimeron (EM) is visible.

Metathorax. With large, rectangular basisternum (bs3) and furcasternal protuberances as in mesosternum. In none of the three sterna could a separate spinasternum be identified.

Legs. Long and slender; probably mainly used for clinging to the vegetation (Fig. 1). For measurements see Table 1.

In all visible legs, femora, tibiae, and tarsomeres are at least partially preserved. Neither a separate patellar segment nor tarsal claws are visible in any of the preserved legs (Fig. 4). A small number of scattered spines in a row are discernable on the surface of femora and tibiae. Right foreleg almost completely preserved except for tarsus and

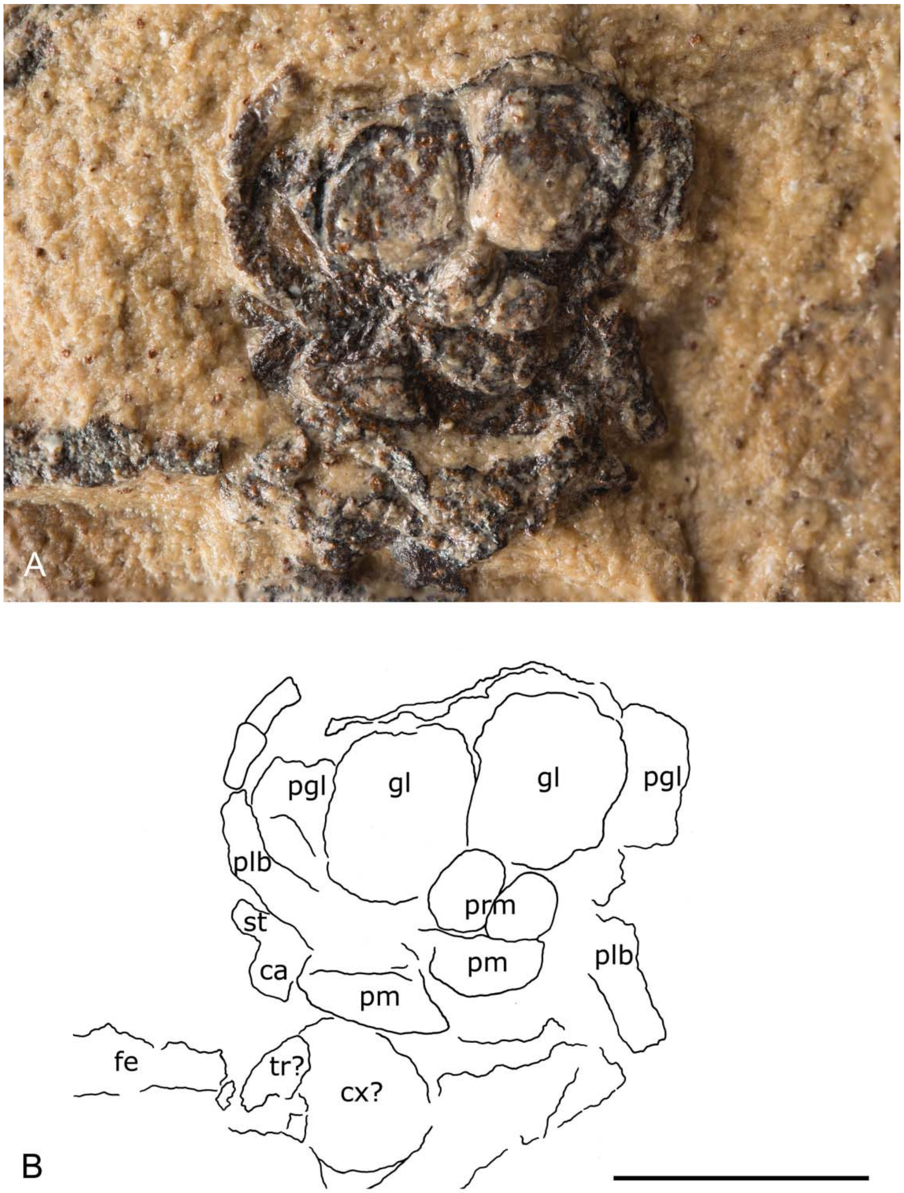

Figure 2. *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype, head (scale bar = 1 cm). **A,** photograph; **B,** line drawing.

first two basal leg segments (coxa and trochanter). Region of coxal insertion crushed, rounded sclerotized area may represent either crushed coxa or coxal cavity; laterally to it a deformed trochanter may be preserved (Fig. 3). Femur clearly visible, forming an acute angle with long tibia. First two tarsal segments and an isolated small tarsal fragment preserved (Fig. 4E). Definite number of tarsal segments cannot be determined with certainty, but two tarsal segments and the base of the third segment are clearly recognizable. However, the tarsus is not completely preserved. Tarsal claws not preserved.

Left foreleg only with distal part of femur, incomplete tibia, and isolated tarsal fragment with two tarsomeres preserved (Fig. 4F).

Right middle leg with fragmented coxa, distal part of femur, probably almost complete tibia, and isolated fragment with two partly preserved tarsomeres present (Fig. 4G).

Left middle leg with incomplete coxa, distal part of femur, proximal part of tibia, and isolated fragment with two to three partly preserved tarsomeres (Fig. 4H).

Right hind leg only with distorted coxa, distal part of femur, and proximal part of tibia visible.

Left hind leg almost completely missing except for possible coxa and isolated short tibial fragment.

Wings. Basal parts of right pair of wings and almost the entire left pair of wings except for their apices are

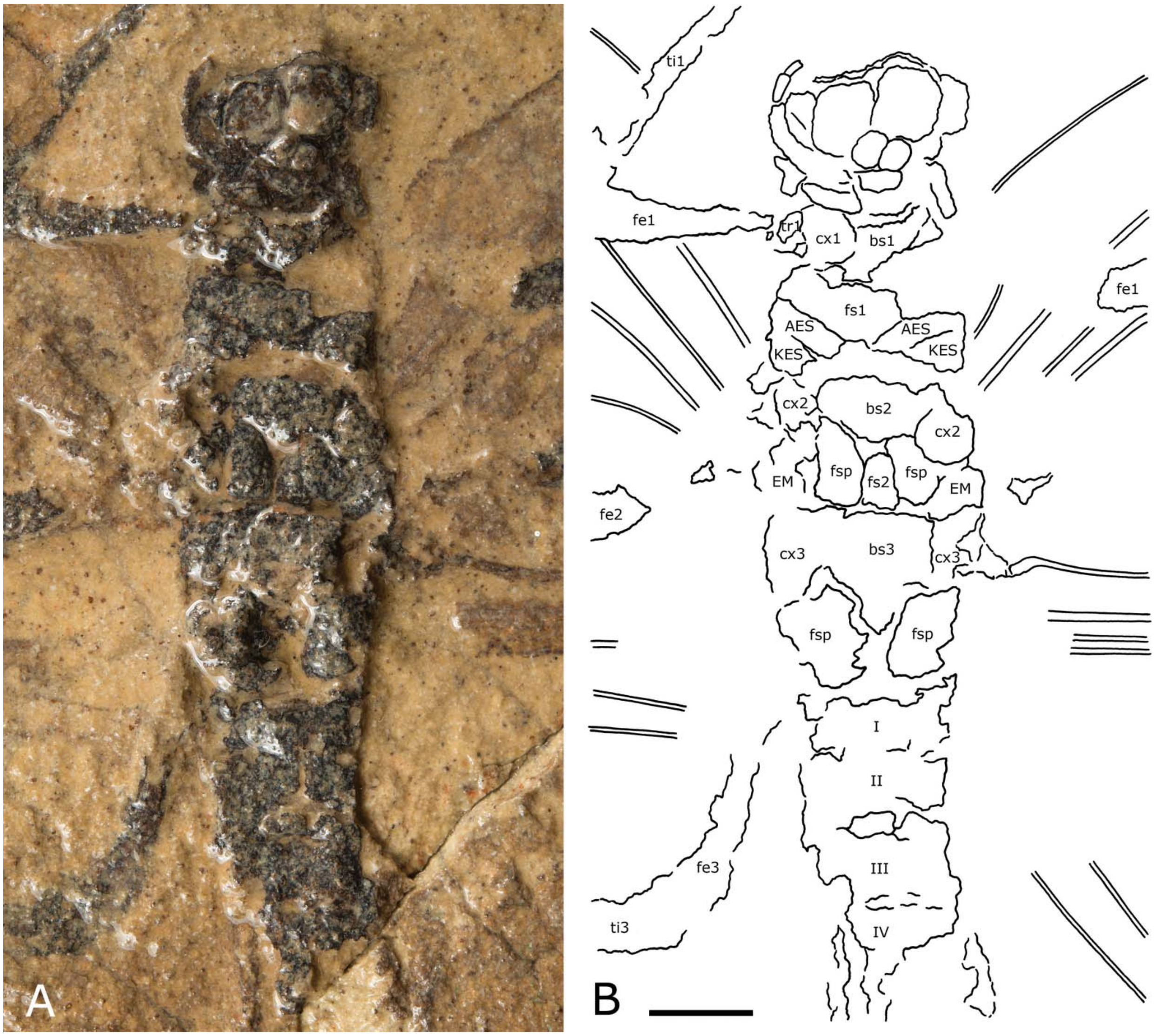

Figure 3. *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype, body (scale bar = 1 cm). **A,** photograph; **B,** line drawing.

preserved (Figs 1, 5, 6). Generally, most of the principal venation pattern is preserved on the specimen, although some veins are only fragmentary. Cross-veins are barely visible except for the basal part of costal, subcostal, and radial field in the left forewing (Fig. 7).

We frequently noticed red, green and yellow colour pigments on the fossil (e.g. see Fig. 10), mostly along the main wing veins, which appear to be remains of wax crayon marks that had been applied directly onto the wing to mark longitudinal veins, cross-veins and intercalary veins.

Left forewing (Figs 1, 5, 7, 8)**.** Oval in shape, basally narrower than hind wing. Costal margin seems to be slightly serrated. Costal brace (ScA *sensu* Kukalová-Peck) absent. Costal field basally relatively broad. C preserved almost at entire length, except for some minor interruptions, wing tip, and most basal part. ScP very thick and long, approximately parallel to C and not shortened, distally approaching C, probably ending near apex. In the proximal half of preserved wing, RA and RP running very close to each other with strongly pigmented wing membrane preserved between these veins (Figs 5, 7). Apical part of wing in the area of RA and RP is very poorly preserved. Thus, it cannot be verified if RP is branched and if IR1 and IR2 are present or not.

MA basally directly fused with RP. No basal vein connection present between MA and MP (Fig. 8). At mid-length of wing, the bifurcation of MA into MA1 and MA2 is not preserved, but apically two convex veins and one concave vein can be distinguished that most probably represent the two branches of MA and in between one intercalary vein IMA.

MP basally approximated to RP, further distally MP diverges from RP and is forked into MP1 and MP2,

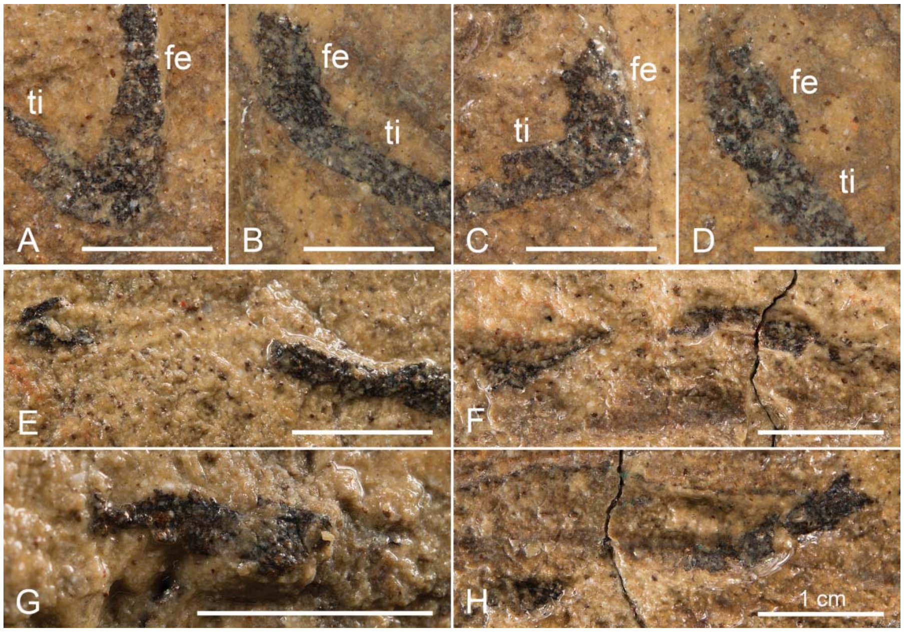

Figure 4. *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype, detailed photographs of legs (scale bars = 1 cm). **A–D,** femuro-tibial joints of **A,** right foreleg, **B,** left foreleg, **C,** right middle leg and **D,** left middle leg. **E–H,** preserved tarsomeres in **E,** right foreleg, **F,** left foreleg, **G,** right middle leg and **H,** left middle leg.

approximately at a length of 9.1 cm from the wing base. One intercalary vein IMP present between MP1 and MP2. An apparent vein closely parallel to MP2, which might be misinterpreted as a branch of CuA, is actually only an irregular crack that continues far beyond the area of the wing even right into the hind wing.

CuA basally not preserved, only two isolated positive veins visible between MP2 and CuP1 that most probably represent CuA1 and CuA2. There is no indication whether CuA is basally isolated, attached to MP, or attached to CuP. The concave stem of CuP bifurcates basally into CuP1 and CuP2. CuP2 is completely preserved, whereas CuP1 is only visible as distal isolated vein fragment. Between CuP1 and CuP2, an intercalary vein ICuP is preserved in the posterior half of wing. Bases of R, M and Cu are very poorly preserved; possible fusions in that region are not excluded.

Anal veins mostly not preserved, only faint traces may indicate the possible presence of three preserved anal veins.

Left hind wing (Figs 1, 6, 9)**.** Basally broader but not much shorter than forewing. C preserved only as a small fragment originating from wing base. C without row of spines. Costal brace (ScA *sensu* Kukalová-Peck) not visible, most probably absent. ScP basally thickened, continuing up to wing apex. RA and RP basally running parallel and close to each other. RA not branched, entirely preserved except for a short distance in the basal third of wing. RP furcated into RP1+2 and RP3+4 in the apical third of wing, approximately 9.4 cm from wing base. RP1+2 further divided into RP1 and RP2 subapically from wing tip. Possible bifurcation of RP3+4 not visible, as only a short fragment of this vein is preserved. No IR2 and IR1 visible between RP1+2 and RP3+4 and between RP1 and RP2 respectively.

Basal stems of M, Cu and anal veins not preserved. MA basally connected to RP in the basal third of preserved wing. MA probably branched into MA1 and MA2 directly below first RP furcation, but MA2 is only faintly preserved. MP branched into MP1+2 and MP3+4 at half length of wing, about 7.4 cm from the wing base; MP3+4 posteriorly further divided into MP3 and MP4. Possible bifurcation of MP1+2 not visible, as posterior part of hind wing is missing.

Stem of Cu not preserved. CuA hardly discernible, traces of two convex veins near the wing hind margin between MP4 and CuP may represent CuA1 and CuA2. In between these faintly preserved branches of CuA, a prominent concave ICuA is present. Two further prominent concave veins represent CuP1 and CuP2 that are basally confluent, although an actual bifurcation is not preserved, but can be inferred from the course of the two branches.

Large anal fan present with at least 15 alternating convex and concave anal veins. Only posterior parts of these veins well visible, their bases and branching pattern mostly not preserved. Jugal veins are not to be expected, as they only occur as synapomorphy in Phalloneoptera (Paraneoptera + Holometabola) (Hamilton 1972), and thus do not belong to the ground plan of Pterygota (*contra* Kukalová-Peck 1983).

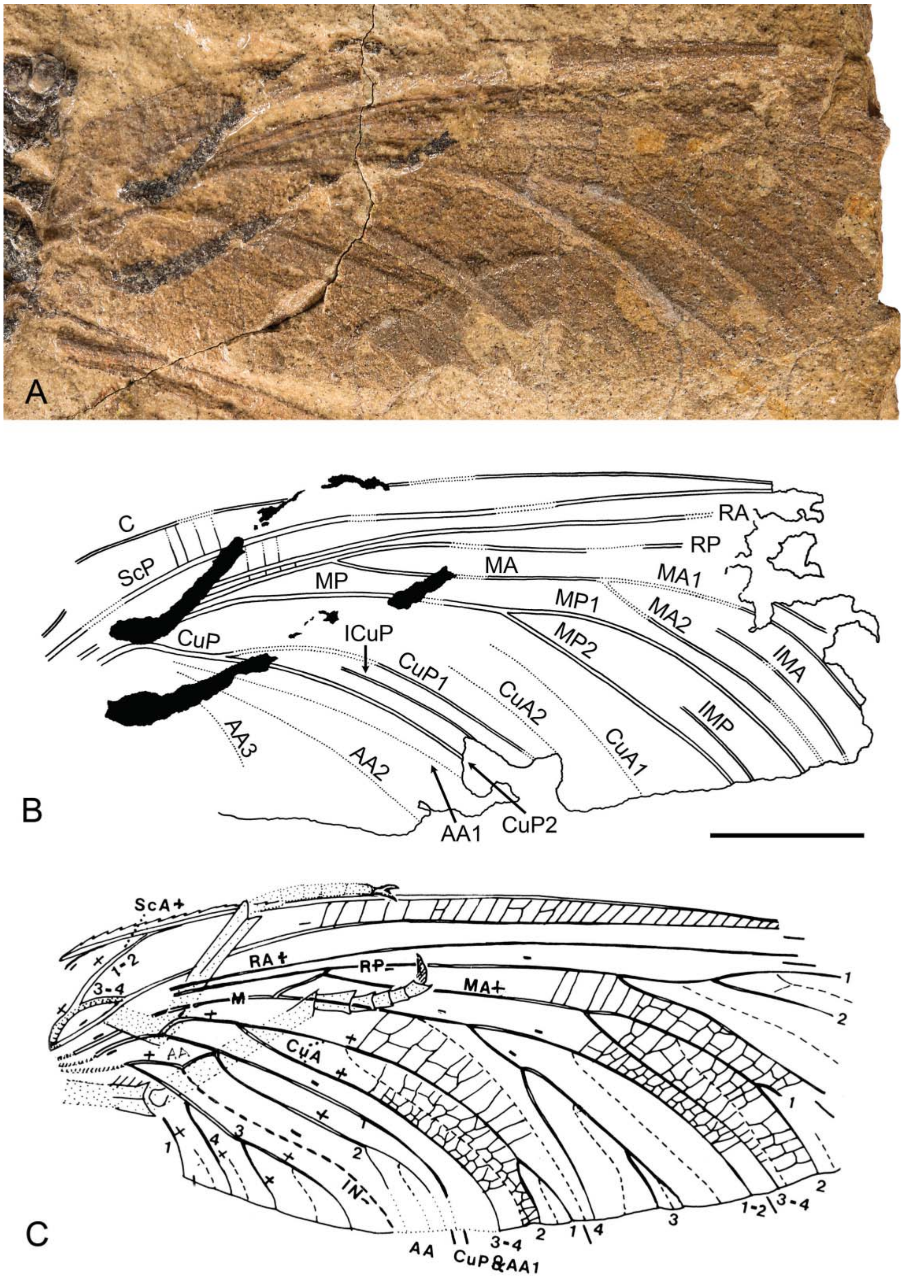

Figure 5. *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype, left forewing (scale bar = 3 cm). **A,** photograph; **B,** line drawing; **C,** detail of Kukalová-Peck (1985, fig. 2; © 2008 Canadian Science Publishing or its licensors, reproduced with permission).

Abdomen. For measurements see Table 1. Abdominal segments I–IV fully preserved, segment V distorted, remaining segments almost entirely lost, only small fragments visible (Figs 1, 3). Genitalia and caudal filaments not preserved.

Remarks on characters of *Bojophlebia prokopi* mentioned in the original description

Prior to any consideration on the systematic placement of *Bojophlebia prokopi*, it is necessary to reconsider and discuss several of the characters described and depicted by Kukalová-Peck (1985). Below we repeat in italics several of Kukalová-Peck's observations and interpretations (as stated in her description and depicted in her fig. 2), followed by our own observations and comments.

Head. "*Head probably with relatively long and thick antennae, large protruding eyes, and functional chewing mouthparts*" (Kukalová-Peck 1985, p. 936 and fig. 2, p. 935).

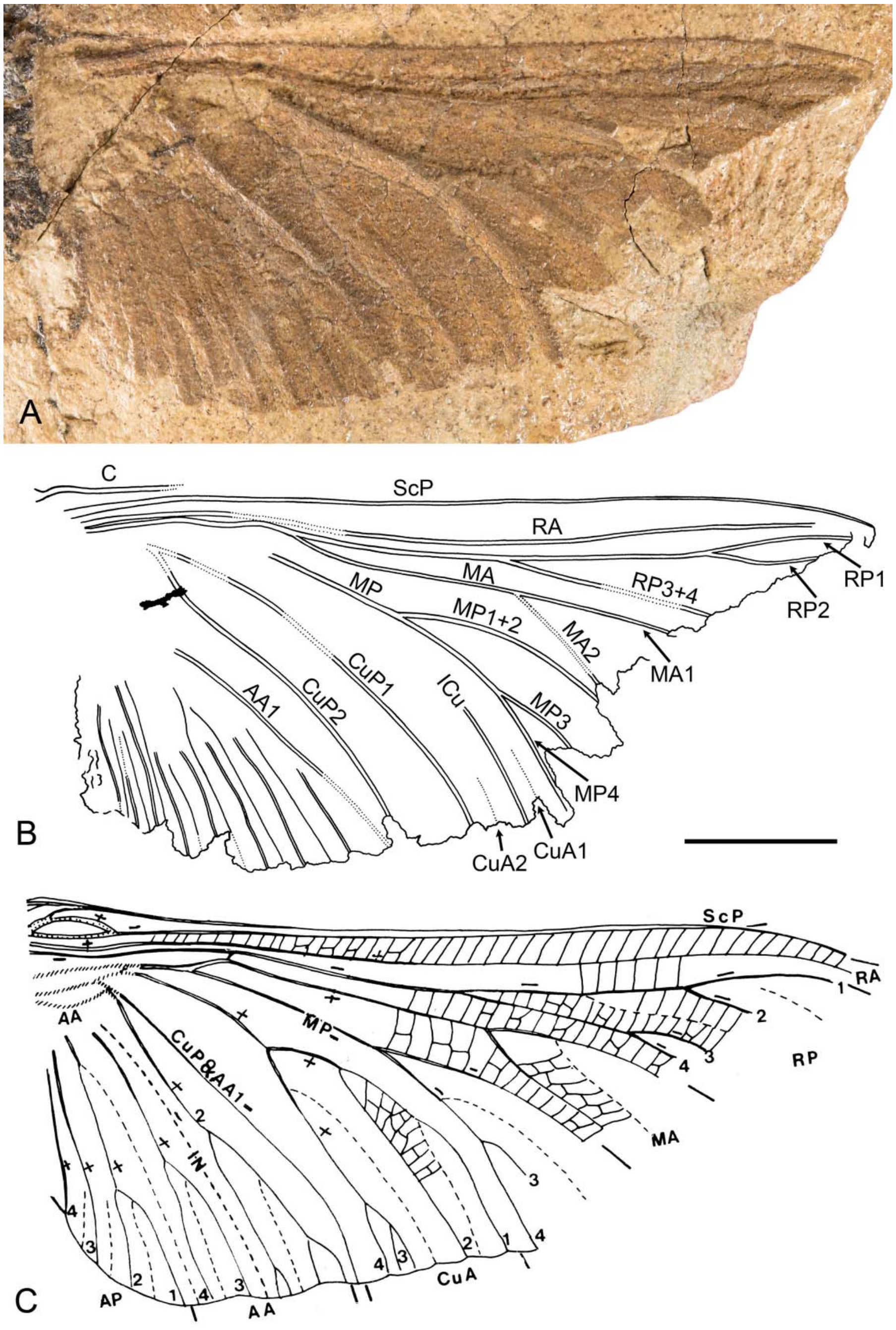

Figure 6. *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype, left hind wing (scale bar = 3 cm). **A,** photograph; **B,** line drawing; **C,** detail of Kukalová-Peck (1985, fig. 2; © 2008 Canadian Science Publishing or its licensors, reproduced with permission).

Neither eyes nor antennae are visible or preserved in the specimen. Kukalová-Peck (1985) herself stated in the species description that these structures are actually not preserved in *Bojophlebia prokopi.* In a footnote to the generic description she revealed that she only assumed the respective character states according to their (also assumed?) occurrence in the putative related Syntonopteridae. However, in his revision of the family Syntonopteridae Carpenter (1987, p. 385) mentioned that "Antennae, mouthparts, legs, and cerci (are) unknown".

Only a schematic drawing of the general body structure of *B. prokopi* was provided by Kukalová-Peck (1985), and we consider the head as drawn to be inaccurate, since several important features are missing, such as the right labial palp and the labium itself, which are clearly visible in the fossil (see Fig. 2).

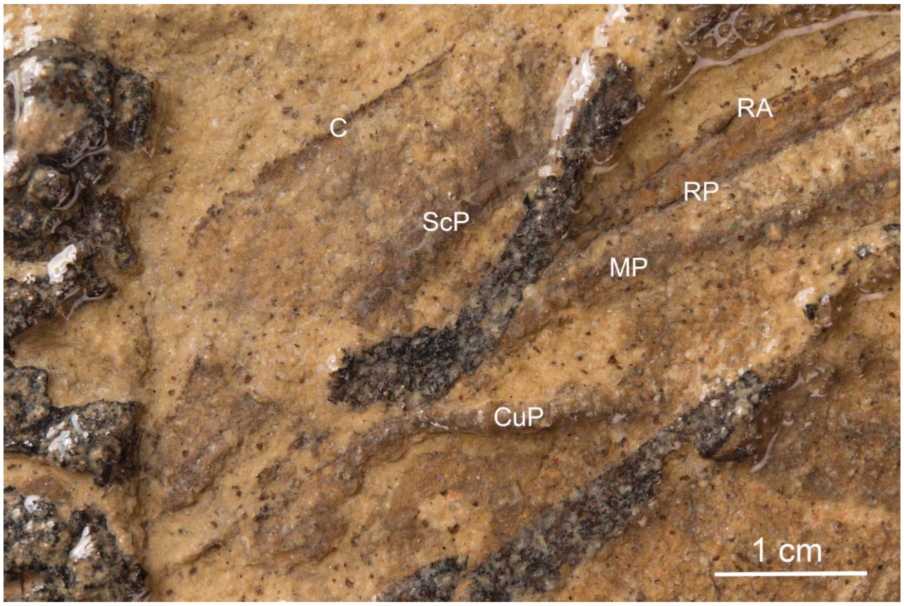

Figure 7. *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype, basal part of left forewing (scale bar = 1 cm), photograph.

Thorax. "*prothoracic wings present as veined lateral lobes*" (Kukalová-Peck 1985, generic description, body of adult, p. 936).

There are no lateral projections of the prothorax visible (Figs 1, 3). Kukalová-Peck herself did not even depict 'prothoracic wings' in her own figure (p. 935, fig. 2). However, the thoracic sternal structures depicted there were in general congruent with our own observations, but she did not include the depicted characters in her text.

Legs. "*legs probably long and comparatively stout; patello-tibia longer and femur shorter than basitarsus, tarsus and posttarsus combined; tarsus with four subsegments*" (Kukalová-Peck 1985, generic description, p. 936 and fig. 2, p. 935).

The presence of a separate patellar segment in *Bojophlebia prokopi* is not substantiated (Fig. 4A–D). Kukalová-Peck only depicted a separate patella in the right foreleg. A superficial view might indeed suggest a short patellar segment (Fig. 4A). However, the corresponding left foreleg (Fig. 4B), which is visible in ventral aspect, does not support this assumption. If a true patella were present, a respective segment border between patella and tibia would also be visible from ventrally in the left foreleg. Its absence leads us to assume that the alleged tibio-patellar border in the right foreleg is instead the result of a crack in the fossil rather than true segmentation. In all other preserved legs there is also no indication for a separate patella or even a superficial tibio-patellar suture as present only in extant mayflies (see Kluge 2004).

Kukalová-Peck (1985) referred to the presence of a 'posttarsus' (generally referred to as pretarsus) but did not mention the number of tarsal claws in the text. However, two tarsal claws on the left foreleg are shown in her figure 2. Rasnitsyn (2002) postulated the presence of single tarsal claw in *B. prokopi* as a putative apomorphy of Bojophlebiidae. In fact, in none of the legs are tarsal claws preserved (Fig. 4E–H). In the right middle leg, the most distal preserved tarsal fragment resembles a claw in shape (Fig. 4G). However, as this fragment clearly bears spines we can definitely exclude its interpretation as claw.

Wings. "*low arched and forked subcostal brace ScA+*" (Kukalová-Peck 1985, family diagnosis, p. 934); "*subcostal brace forming low broad arch, ScA+ forked, ScA1–2 fusing with costal margin, ScA3–4 fusing with ScP*" (Kukalová-Peck 1985, generic description, p. 936).

Such a brace is actually visible neither in the bases of forewings (Fig. 7) nor the hind wings (Fig. 9). Although the posterior part of the costal field in the left forewing is somewhat distorted, its anterior part is sufficiently preserved to suggest strongly that there is no costal brace present at all. The costal field of the hind wing is very small and contains no traces of an arched vein as depicted by Kukalová-Peck. An alleged basal crossvein in the costal field (Fig. 9A) is an artefact, which becomes obvious under different illumination (Fig. 9B). Thus we consider a costal brace in *Bojophlebia prokopi* to be absent.

"*MA vein … is arched towards but not fused with the RP vein*" (Kukalová-Peck 1985, family diagnosis, p. 934; generic description, p. 936).

The basal attachment of MA to RP is actually visible in both left fore- and hind wings (Figs 8, 10). MA approaches RP at an angle that clearly implies a common stem, and MA is not visible anywhere between basal RP

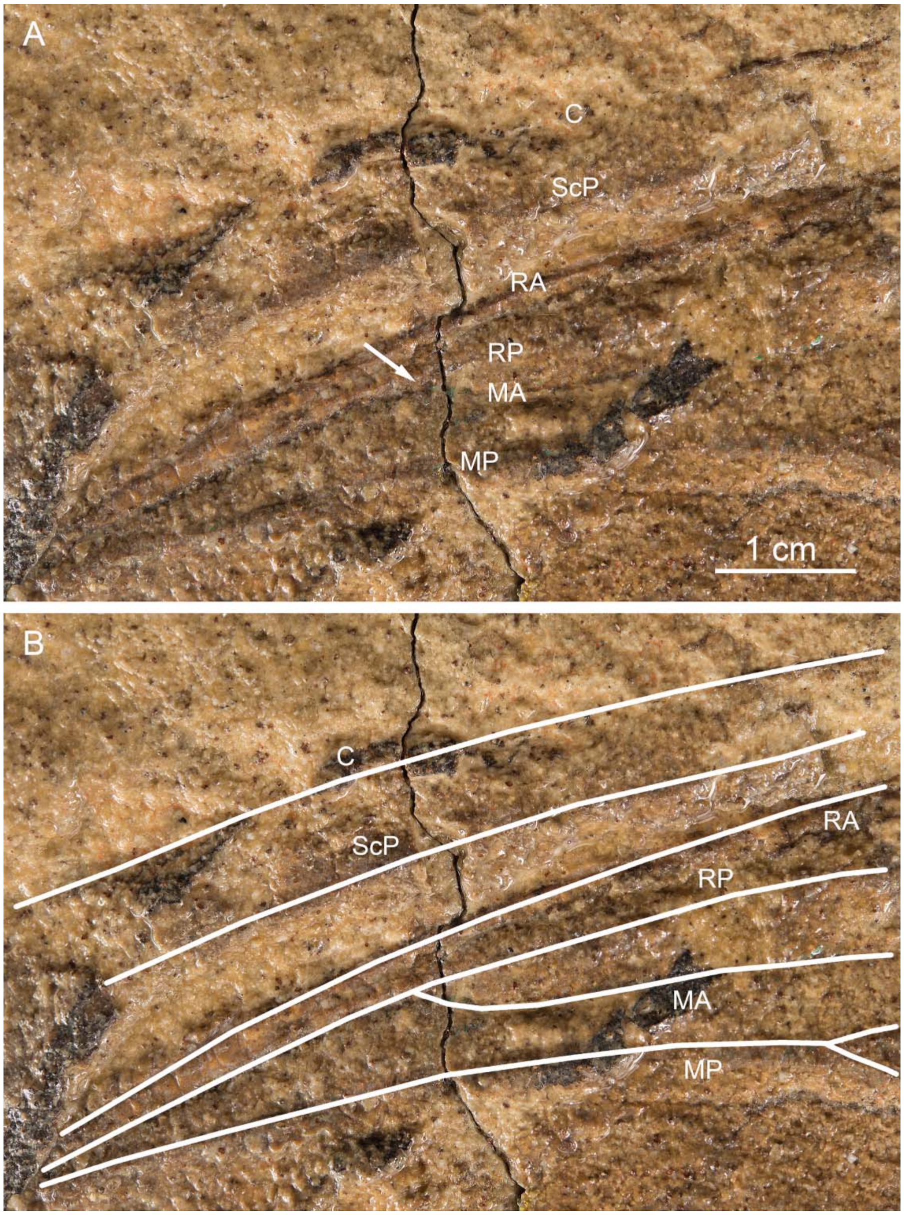

Figure 8. *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype, photograph of left forewing (scale bar = 1 cm). **A,** showing basal fusion of MA and RP (indicated by an arrow); **B,** with overlay drawing of venation.

and MP, even though the wing cuticle in that area is preserved (dark colour) and neighbouring veins (RP and MP) are clearly visible. In our view, there is a direct connection of both veins, which does not involve a strut as suggested by Kukalová-Peck. Additionally, she depicted an oblique veinal connection between the alleged strut and MP. However, this is also not visible in the specimen.

"*CuA not fused to M but connected with M by a strut*" (Kukalová-Peck 1985, family diagnosis, p. 934).

The strut is actually not discernible on the specimen. In the left forewing, the proximal part of CuA is not visible at all; only distal parts can be tracked near the posterior wing margin. Additionally, the entire area of the supposed basal connection between CuP (CuP and AA1 in Kukalová-Peck's interpretation, but see below), CuA, and M is obscured by the left foreleg (Fig. 7). Nevertheless, CuP basally is bent just posterior of the foreleg fragment, thus one might assume a connection to CuA (and possibly to M) in that region. However, in all other wings, CuA is also not preserved in its proximal part. Therefore, any possible connection to M is only speculative.

At least for the hind wing, Kukalová-Peck (1985) indicated basal parts of CuP, CuA and M by dashed lines (including CuA−M strut, see Fig. 6), which implies that such a connection was only a presumption. But also the entire hind wing CuA stem, bifurcation of CuA, and

CuA2 as drawn by Kukalová-Peck (1985) are erroneous, because the corresponding structures in the fossil clearly are just patterns of cracks as is easily visible by their very irregular course. Nearly identical cracks can also be observed outside of the fossil.

"*AA1 completely fused with CuP in both fore and hind wings*" (Kukalová-Peck 1985, family diagnosis, p. 934).

The wing sector around the veins CuP and AA1 is actually not preserved as depicted by Kukalová-Peck (1985). Branching pattern and possible braces between the veins posterior to CuP are not visible on any wing (see Figs 5, 6), and there is no evidence for a fusion of CuP and AA1. Prokop *et al.* (2010) already doubted this fusion even on the basis of the original figure of the wing venation.

"*AA2 diverging from CuP in an arch*" (Kukalová-Peck 1985, family diagnosis, p. 934).

The basal part of AA1 and AA2 is not preserved on any wing of the holotype (Figs 7, 9). Therefore, this character

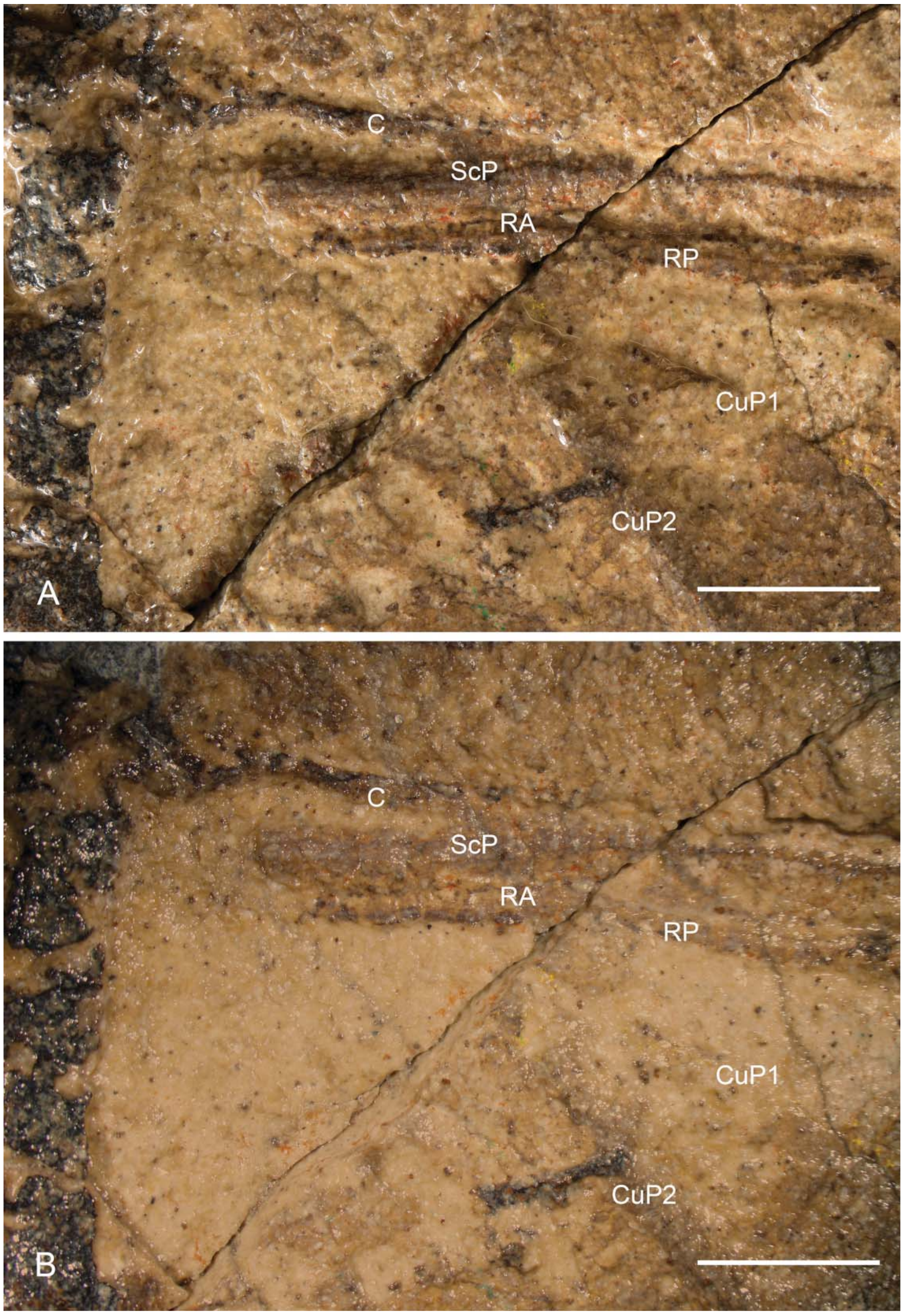

Figure 9. *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype, basal part of left hind wing (scale bars = 1 cm). **A, B,** photographs under different illumination.

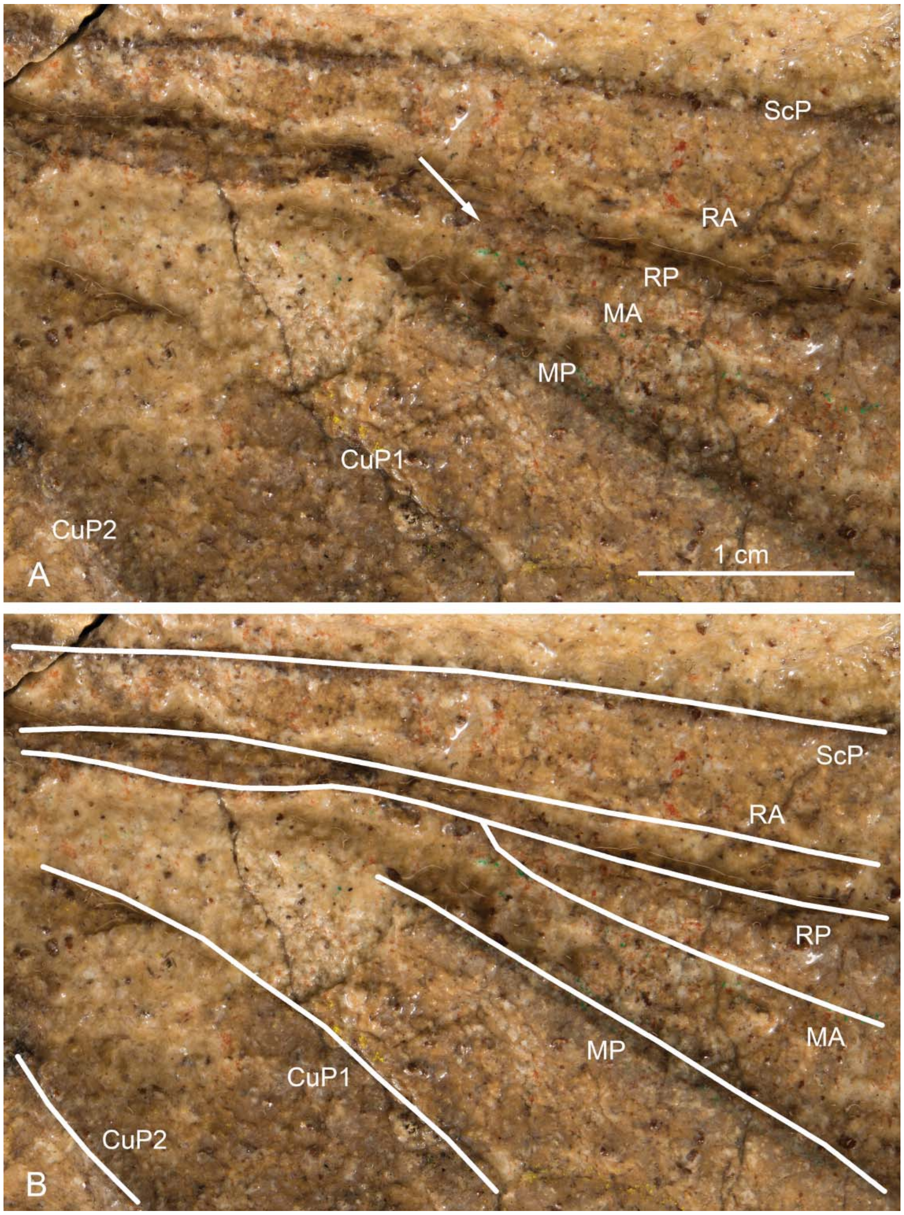

Figure 10. *Bojophlebia prokopi* Kukalová-Peck, 1985, holotype, photograph of left hind wing (scale bar = 1 cm). **A,** showing basal fusion of MA and RP (indicated by an arrow); **B,** with overlay drawing of venation.

cannot be verified. There is no evidence for an anal brace in *Bojophlebia prokopi*, which was used by Kukalová-Peck (1985), along with the costal brace, as important characters for the attribution of this fossil taxon to Hydropalaeoptera and Ephemerida. An anal brace is only developed in basal Odonatoptera, but not in fossil or extant mayflies. Consequently, an anal brace can no longer be considered as a ground plan character of Hydropalaeoptera.

"*richer branching of almost all veins*" (Kukalová-Peck 1985, family diagnosis, p. 934).

There is no evidence for an unusually high degree of vein branching in the preserved venational pattern of *Bojophlebia prokopi*. The alleged repeated branching pattern into four branches cannot be confirmed with the possible exception of MP in the hind wing. There may be more vein branches in the distal wing regions, but these areas are almost not preserved at all.

"*presence of irregular, weak, anastomosed crossveins and archedictyon*" (Kukalová-Peck 1985, family diagnosis, p. 934).

Cross-veins are actually barely visible. In basal fields between C, Sc, RA and RP, an alternating pattern of some stripes of lighter coloration is apparent, which might indicate cross-veins. There is no trace of an archedictyon on any wing. Irregular patterns that were apparently interpreted by Kukalová-Peck (1985) as archedictyon clearly represent structures of the rock matrix that are also visible outside of the wing area.

Abdomen. "*abdomen with two segments*" (Kukalová-Peck 1985, species description, p. 936, but see also fig. 2, p. 935); "*cerci and paracercus probably with short hair, cerci shorter than paracercus*" (Kukalová-Peck 1985, generic description, p. 936).

There are not just two abdominal segments present as described by Kukalová-Peck, but actually the first four segments are complete and the fifth segment is partially preserved. Shape and dimensions of the preserved abdominal segments also differ strongly from the drawing of Kukalová-Peck (1985), which appears to be very schematic in this respect. The statement in the generic description regarding the terminal filaments again is a mere assumption by Kukalová-Peck that is not supported by any evidence (see Fig. 1).

Concluding remarks

It is obvious from the preceding paragraphs that Kukalová-Peck's original description suffers from erroneous observations and over-interpretations. This finding is reinforced by the fact that other authors in their revisions of fossils described by Kukalová-Peck found similar shortcomings (Carpenter 1987; Rasnitsyn & Novokshonov 1997; Willmann 1999; Béthoux & Briggs 2008; Staniczek *et al.* 2014). Several phylogenetically relevant character states that were documented in the original description turned out either not to be present in the actual fossil specimen at all, or to have a different state than that described. Hence, the conclusions suggested by Kukalová-Peck for the phylogenetic affinities of *Bojophlebia prokopi* and the evolution of early mayflies are unsubstantiated.

Phylogenetic affinities of *Bojophlebia prokopi*

Hennigian phylogenetic systematics

Contrary to a common misconception, traditional Hennigian phylogenetic systematics does not involve a 'manual' but rather a 'mental' analysis of character patterns (Bechly 2000). This includes a careful description and comparison of the characters, as well as a weighting of their phylogenetic relevance based on reasonable estimations of their probability for homoplasy. Complex and rare derived character states are weighted higher than simple and often independently evolved character states.

Like computer cladistics, Hennigian phylogenetic systematics relies on the principle of parsimony ('Occam's razor'). However, it does not agree with computer cladistics that the principle of parsimony is exhausted by the procedure of minimizing the number of character transformations, but also considers the plausibility of the implied homology hypotheses and evolutionary transitions. This rejection of always preferring the shortest trees is right in the spirit of Einstein's famous quote 'Everything should be made as simple as possible, but not simpler'.

Character polarities are established by an a priori outgroup comparison (to be distinguished from a posteriori outgroup rooting in computer cladistics), for which representatives are preferably selected from several basal lineages of taxa that are certainly outside the group in study but nevertheless closely related. This does not involve the logical fallacy of circular reasoning, but an abductive inference of the best explanation that was called 'mutual enlightenment' by Willi Hennig and that resembles the methodology of the hermeneutic spiral. Ground plans are reconstructed by inferring all relevant plesiomorphic and apomorphic character states for the most recent common ancestor of a clade using the same procedure of outgroup comparison.

Our study of *Bojophlebia* allows a revised diagnosis for the family Bojophlebiidae: very large size with a wing span of nearly 40 cm (autapomorphy); forewing with large basal costal field (plesiomorphy); costal brace absent in both wings (plesiomorphy); ScP very thick (autapomorphy); ScP and RA very long, nearly reaching apex (plesiomorphy); RA and RP closely parallel, but remaining separated basally (plesiomorphy); MA attached to RP without anterior connection of MA to MP (autapomorphy, convergent with Ephemerida and higher Odonatoptera); CuP branched (plesiomorphy, except for a possible reversal in Miracopteridae); MA, MP, CuA, CuP with intercalaries developed as triadic branchings (synapomorphy with Hydropalaeoptera, otherwise only present as a convergence in the hind wing of the highly aberrant palaeodictyopteran *Lodetiella magnifica* Béthoux *et al*., 2007), thus as dichotomous branching of a main longitudinal vein that is bracketing a long and straight intercalary vein of opposite corrugation; hind wing base broader than in forewing, with large anal field (anal fan) composed of alternating concave and convex veins (plesiomorphy); glossae developed as enlarged plates (autapomorphy). The polarity of these characters is based on an outgroup comparison with the ground patterns as exhibited by the most basal lineages of Ephemerida, Odonatoptera, Palaeodictyopterida and Neoptera.

A remarkable feature of *Bojophlebia* is the presence of a very thick ScP compared to RA. In most pterygote taxa, RA is the thickest vein in the wing. This unique autapomorphy could suggest a different scheme of wing articulation in *Bojophlebia*, which is unfortunately not preserved in the single known fossil.

Even though the most distal parts of the wings are not preserved, the veins ScP and RA most probably reached close to the wing apex. This character was mentioned by Kluge & Sinitshenkova (2002) as one of the diagnostic characters of Ephemerida, but it seems instead to be a symplesiomorphy because it is also present in some basal Palaeodictyoptera (e.g. Megaptilidae, Eugereonidae and Spilapteridae).

Thus, most of the characters that can be reliably observed on *Bojophlebia* are either unique autapomorphies, or plesiomorphies and homoplasies that are present in various unrelated pterygote lineages. All of these characters are not suitable when attempting to resolve the phylogenetic affinities of *Bojophlebia*.

However, several characters at least allow the exclusion of some higher taxa. The presence of a branched MP in both wings excludes a position within Odonatoptera, where MP is always single (Bechly 1996). The absence of sucking-piercing mouth parts excludes a position within Palaeodictyopterida, where mouth parts always look very different, even in species with a short haustellum. The absence of the costal brace excludes a position in Panephemeroptera *sensu* Staniczek *et al.* (2011). Finally, the separated origins of RA and RP exclude a position within Neoptera. Of course, the absence of the diagnostic autapomorphies of the forementioned taxa would not exclude a sister-group position, but only exclude an in-group position.

Due to the poor preservation and the scarcity of useful characters, there is no general consensus in the available literature concerning the systematic position of *Bojophlebia*: Kukalová (1985) considered it as an early stem group mayfly, which was accepted by Grimaldi & Engel (2005), Willmann (2007b), Klass (2007) and Engel *et al.* (2013). Rasnitsyn (2002) classified *Bojophlebia* in the separate order Syntonopterida as sister group of true mayflies. Hubbard (1987) and Kluge (2004) considered it as Syntonopteroidea *incertae sedis*, and Prokop *et al.* (2010) as a Pterygota *incertae sedis*, while Staniczek *et al.* (2011) tentatively considered it as a Hydropalaeoptera *incertae sedis.*

There is no doubt that *Bojophlebia* has some phenetic similarity with other genera previously attributed to Syntonopteroidea. However, to resolve finally the question of its systematic position, two other issues must be addressed first: (1) are the higher taxa Syntonopteridae, Sytonopteroidea and Syntonopterida monophyletic; and (2) what are putative synapomorphies of the 'syntonopterid' genera with other taxa?

Below we evaluate previous diagnoses of Syntonopteridae given by different authors and provide a phylogenetic assessment in square brackets for each character.

The diagnosis of Synotonopteridae according to Carpenter (1987, p. 385) is: "Medium-sized to large insects [uninformative]. Fore wing (incompletely known): costal area relatively broad proximally, very narrow distally [symplesiomorphy]; R without branches [symplesiomorphy]; stem of RS independent of stem R [symplesiomorphy]; stem of MA either close to RS or coalesced with it for brief interval [symplesiomorphy, apomorphy of Hydropalaeoptera]; RS, MA, MP, and CUA with intercalary, triad branches [symplesiomorphy, apomorphy for Hydropalaeoptera]; cross veins numerous, but rarely branched [symplesiomorphy]. Hind wing: broader than fore wing basally [symplesiomorphy]; venation essentially as in fore wing, but slightly modified by wing shape [symplesiomorphy]. Body: little known [uninformative]. Pronotum apparently with small lateral lobes [symplesiomorphy, only known in *Lithoneura*, but refuted by Willmann 1999]. Antennae, mouthparts, legs, and cerci unknown [uninformative]."

The main diagnostic characters of Syntonopteridae according to Prokop *et al.* (2010) are: "wing corrugate [symplesiomorphy]; no archedictyon but a simple and relatively straight pattern of cross-veins between the longitudinal veins [also present in Odonatoptera and some Palaeodictyopterida (e.g. Breyeriidae)] [symplesiomorphy, apomorphy of Hydropalaeoptera]; CuP simple [symplesiomorphy, apomorphy of Euhydropalaeoptera]; MA with a strong anterior curve at its base, touching RP for a short distance [only a synapomorphy of *Lithoneura* + *Anglolithoneura*]; most anterior branch of AA with a strong curve ('zigzag') and touching CuP in one point [just a synapomorphy of *Lithoneura* + *Anglolithoneura*]."

Prokop & Nel (2011) featured an undescribed new genus and species, and stated the diagnosis of Syntonopteridae as: "a strong corrugation of the main longitudinal veins connected by mainly simple transverse crossveins also present in Odonatoptera and some Palaeodictyopterida (e.g., Breyeriidae) [symplesiomorphy], MA with a strong anterior curve at its base, shortly connected with RP distally [just a synapomorphy of *Lithoneura*, *Anglolithoneura*, and the undescribed genus and species]; CuA with a short terminal twigging [symplesiomorphy] and anal area with well-defined cell(s) [dubious character]."

Prokop *et al.* (2010) mentioned that the genera "*Syntonoptera*, *Lithoneura*, and *Anglolithoneura* are similar in wing morphology, and likely closely related as they also share several apomorphies". However, the four putative synapomorphies mentioned in the three preceding paragraphs (namely MA with a strong anterior curve at its base, touching RP for a short distance; most anterior branch of AA with a strong curve ('zigzag') and touching CuP in one point; characteristic concave vein between the two convex veins AA1+2 and AA3+4; and constriction of the area between the first and the second convex branches of AA, with a strong brace between them) are only visible in *Lithoneura* Carpenter, 1938 and *Anglolithoneura* Prokop *et al*., 2010, while the relevant area of the wing is not preserved at all in *Syntonoptera* Handlirsch, 1911.

Consequently, there are no known synapomorphic characters that could support the monophyly of Syntonopterida and Syntonopteroidea. *Bojophlebia* and *Syntonoptera* share only a general similarity in trivial or symplesiomorphic (e.g. triadic branchings) features with *Lithoneura* + *Anglolithoneura*.

We therefore here establish a new family – Lithoneuridae fam. nov. (type genus: *Lithoneura*; main diagnostic apomorphy: MA with conspicuous basal curve approximated or connected to RP) – for *Lithoneura* and

Anglolithoneura, and the undescribed genus and species featured by Prokop & Nel (2011). The family Miracopteridae has to be considered as closely related to Lithoneuridae, based on the shared constriction and concave vein between AA1+2 and AA3+4 (Prokop *et al.* 2010). We restrict the family Syntonopteridae to its type genus *Syntonoptera*.

The genus *Gallolithoneura* Garrouste *et al.*, 2009 is insufficiently preserved and is considered as a Hydropalaeoptera *incertae sedis*, which might belong to Syntonopteridae or Lithoneuridae, or even basal Ephemerida.

The genus *Aedoeophasma* Scudder, 1885, which was attributed to Syntonopteridae by Demoulin (1954), was considered by Prokop *et al.* (2010) as a Palaeoptera *incertae sedis*. However, its wing venation was incorrectly homologized by these authors in their figure 4. The side-light in the photo shows the corrugation of the main wing veins very well and proves that vein MA1+2 of Prokop *et al.* (2010) is a branched RP3+4, IMA is an intercalary between RP3 and RP4, MP1+2 is MA1, IMP is IMA, MP3+4 is MA2, and the area CuA and CuP is unclear and probably includes MP and IMP and or CuA. This new homology also fits much better with the fact that the holotype fossil is an apical wing fragment. The available characters allow an attribution of *Aedoeophasma* only to Hydropalaeoptera *incertae sedis*.

The same holds for an unnamed new genus and species of Syntonopteridae described by Prokop & Nel (2011) from the Middle Permian of France, which in our cladistic analyses is mostly resolved as sister group to Triblosobidae + Ephemerida.

Since a typical ephemerid costal brace is clearly present in *Lithoneura lameerei* Carpenter, 1938 (the corresponding wing base in *L. mirifica* Carpenter, 1944 and *Anglolithoneura* is not preserved), but other diagnostic apomorphies of Ephemerida are absent, we suggest a basal position of Lithoneuridae + Miracopteridae as sister group to Ephemerida within Panephemeroptera.

The triadic branching (at least of MA, MP, CuA and CuP) represents a unique and strong putative synapomorphy of all Hydropalaeoptera (including Bojophlebiidae, Syntonopteridae, Miracopteridae, Lithoneuridae, Triplosobidae, Ephemerida and Odonatoptera) because such a branching pattern is known in all basal Ephemerida and the most basal Odonatoptera (Eugeropteridae), while it is always absent from Palaeodictyopterida (except the aberrant genus *Lodetiella*) and Neoptera. The alternative assumption of a triadic branching pattern in the ground plan of Pterygota would represent a less parsimonious hypothesis.

The widely branched CuP of *Bojophlebia* is a striking plesiomorphy among pterygote insects that is otherwise only known from *Miracopteron* Novokshonov, 1993 (according to our cladistic study, the narrowly branched CuP of *Miracopteron* most probably is a reversal), many Palaeodictyopterida, and a few very ‘primitive’ extinct Polyneoptera (‘Protorthoptera’). Therefore, this plesiomorphy excludes a position in the clade that is formed by all Hydropalaeoptera, which share an apomorphic unbranched CuP (namely Triblosobidae, Syntonopteridae, Lithoneuridae, Ephemerida and Odonatoptera). We propose the new taxon Euhydropalaeoptera for this clade, and classify *Bojophlebia* as its sister group in a monotypic family Bojophlebiidae.

Syntonopteridae *sensu stricto* would have to be considered as belonging to Euhydropalaeoptera *incertae sedis* because it shares the unbranched CuP as a synapomorphy, but the triadic branching is symplesiomorphic, and a costal brace is not preserved, so that a closer relationship with Ephemerida cannot be documented. However, in our cladistic analyses Syntonopteridae resolved between Miracopteridae and Lithoneuridae as sister group of the latter, so that Syntonopteroidea could be monophyletic after all.

Apart from Syntonopteridae and Odonatoptera, other clades within Hydropalaeoptera that seem to lack a costal brace are represented by the Carboniferous family Triplosobidae, which was retransferred from Palaeodictyopterida to Hydropalaeoptera by Staniczek *et al.* (2011), and the Triassic mayfly families Litophlebiidae and Tintorinidae.

Affinities of *Litophlebia* Hubbard & Riek, 1977 and *Tintorina* Krzeminski & Lombardo, 2001 to *Bojophlebia* are highly unlikely because they are very dissimilar with no known synapomorphies, and Tintorinidae differs in the autapomorphic shortening of vein ScP. Based on several derived similarities in the wing venation, we concur with Krzeminski & Lombardo (2001) that Tintorinidae and Litophlebiidae are sister groups within the narrow-winged Permoplectoptera, and thus consider their shared absence of a costal brace as an apomorphic reversal within Ephemerida. This hypothesis is also strongly supported by our cladistic analysis and we suggest uniting the two families in a new superfamily Litophlebioidea superfam. nov.

Triplosobidae are characterized by a very strong costal margin constituted by two veins fused or connected (probably C and ScA), with a series of small spines along the anterior margin of both of them (Prokop & Nel 2009). Such spines are also present in Permian stem mayflies (Protereismatidae and Misthodotidae according to Willmann 2007b and Bechly unpublished). The same character state was reported for Odonatoptera by Bechly (1996) and for *Diaphanoptera* Brongniart, 1893 (Palaeodictyopterida) by Béthoux & Nel (2003), where these two veins diverged in the proximal part. The hypothetical presence of such an arrangement of the costal margin in *Bojophlebia* could eventually explain the abrupt step in the costal margin of the left forewing of the holotype. However, we have no direct proof of the presence of two veins in the costal margin of *Bojophlebia*. The wing venation of *Triplosoba* Handlirsch, 1906 strongly differs from

Bojophlebia in the arrangement of MA and RP in the hind wing, these two veins being widely separated in *Triplosoba* whereas in *Bojophlebia* they are connected. *Bojophlebia* also differs from *Triplosoba* in the shape of the hind wing (with a more developed anal area in *Bojophlebia*), and the branched CuP in both wings. Many additional characters cannot be compared since crucial wing regions (mainly stems of M, R and Cu) are too poorly preserved in *Bojophlebia*.

The Carboniferous genus *Thesoneura* Carpenter, 1944, which was considered as Hydropalaeoptera *incertae sedis* by Willmann (1999), was retransferred to Palaeodictyoptera by Staniczek *et al.* (2011). This position is also strongly corroborated by our cladistic analysis.

The RA and RP veins remain separated until the wing base in Bojophlebiidae and Eugeropteridae (Odonatoptera). These two veins are developed as a double-barrelled structure up to the wing base in Lithoneuridae and Odonatoptera (except Eugeropteridae), and are basally fused only in Triplosobida and Ephemerida. This suggests that Hydropalaeoptera is the sister group of all other pterygote insects because Palaeodictyopterida and Neoptera share a reduction of the terminal filament (epiproct) and a long common stem of RA and RP, which only separate in the distal half of the wing. Willmann (1999) earlier suggested these putative synapomorphies. We propose redefining Neopterygota Crampton, 1924 to accommodate the monophylum Palaeodictyopterida + Neoptera. Consequently, the taxon Palaeoptera *s.l.* is rejected by us as a paraphyletic group.

All of these phylogenetic inferences have been tested through an extensive cladistic analysis that basically confirmed the results of our Hennigian study. Thus, we here present the first profound phylogenetic tree of fossil palaeopterous insects (Fig. 11), including all putative stem group mayflies as well as several subgroups of Palaeodictyoptera and the other three orders of Palaeodictyopterida, which can serve as a basis for further phylogenetic studies and the development of evolutionary scenarios for basal pterygote insects.

Computer-assisted cladistic analysis

For the cladistic study two data matrices were assembled with the Nexus Data Editor NDE 0.5.0 (http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html). The first data matrix included 34 higher taxa (and a hypothetical ur-pterygote) and 66 characters, which were coded as assumed ground plan states for these higher taxa (inferred with the traditional Hennigian method described above). The use of reconstructed ground plans of higher taxa allows a better polarization of the characters, because obvious autapomorphies and reductions of individual species can be eliminated, by comparison of representatives of different species that are close to the base of the taxon. Furthermore, the data matrix can be more complete because fragmentary data from different species can be united. The two original Nexus data matrices (including detailed descriptions of all characters, their states, and comments about the selection of taxa etc.), two data matrices in TNT (tree analysis using new technology) format, and three trees as screen shots in the lossless portable network graphics (PNG) format are available in the Online Supplementary Material.

The second data matrix included 35 species (32 fossil species, two Recent mayfly species, and a hypothetical pterygote ancestor) and 66 characters. The most completely preserved species were selected for each fossil taxon, and missing character states were partly supplemented by information from congeneric or confamilial species, as documented in the Supplemental Material. The use of species as terminal taxa has the advantage of greater objectivity as it excludes potential bias and errors in reconstructed ground plans. The hypothetical pterygote ancestor (hypanc) (compare Bryant 1997) was coded based on a conceptual reconstruction of the ground plan by including either those states that are common in the main subclades (Palaeodictyopterida, Neoptera, Ephemeroptera and Odonata), or states that are obviously plesiomorphic based on general evolutionary considerations (e.g. a smoothly curved course of the main longitudinal veins with branching is certainly plesiomorphic compared to sharply bent or kinked courses or simple veins without branching, or unfused veins are plesiomorphic compared to fused ones).

Even though the enigmatic Palaeozoic family Paoliidae has previously been suggested to represent the stem group of all other pterygote insects (Prokop *et al.* 2012), we did not include it in our study because the most recent phylogenetic re-evaluation of this family by Prokop *et al.* (2014) revealed that it is the sister group of Dictyoptera. Furthermore, no species of paoliids are documented by sufficiently well preserved fossils that allow for a reasonably complete coding of the characters as many crucial character states are unknown (mouth parts, tarsi, genitalia, etc.).

Both data matrices were converted from a NEXUS to a TNT format with Mesquite v. 2.75 (Maddison & Maddison 2011). The cladistic analysis was performed with TNT v. 1.1 (Goloboff *et al.* 2008). The first data matrix was analysed with the New Technology search option and the standard parameters for Sect. Search/Ratchet/Drift/Tree-fusing, which resulted in seven shortest trees of length 192 (consistency index CI = 0.474, retention index RI = 0.731) from which a majority rule consensus tree (cut 50) was calculated. The second data matrix was analysed with the standard options and parameters of the New Technology search and resulted in a single shortest tree of length 214 (CI = 0.430, RI = 0.711), which formed the basis for the phylogenetic tree shown in Figure 11, which mostly agrees with the results of the Hennigian phylogenetic analysis described above. An alternative search with the Traditional search algorithm

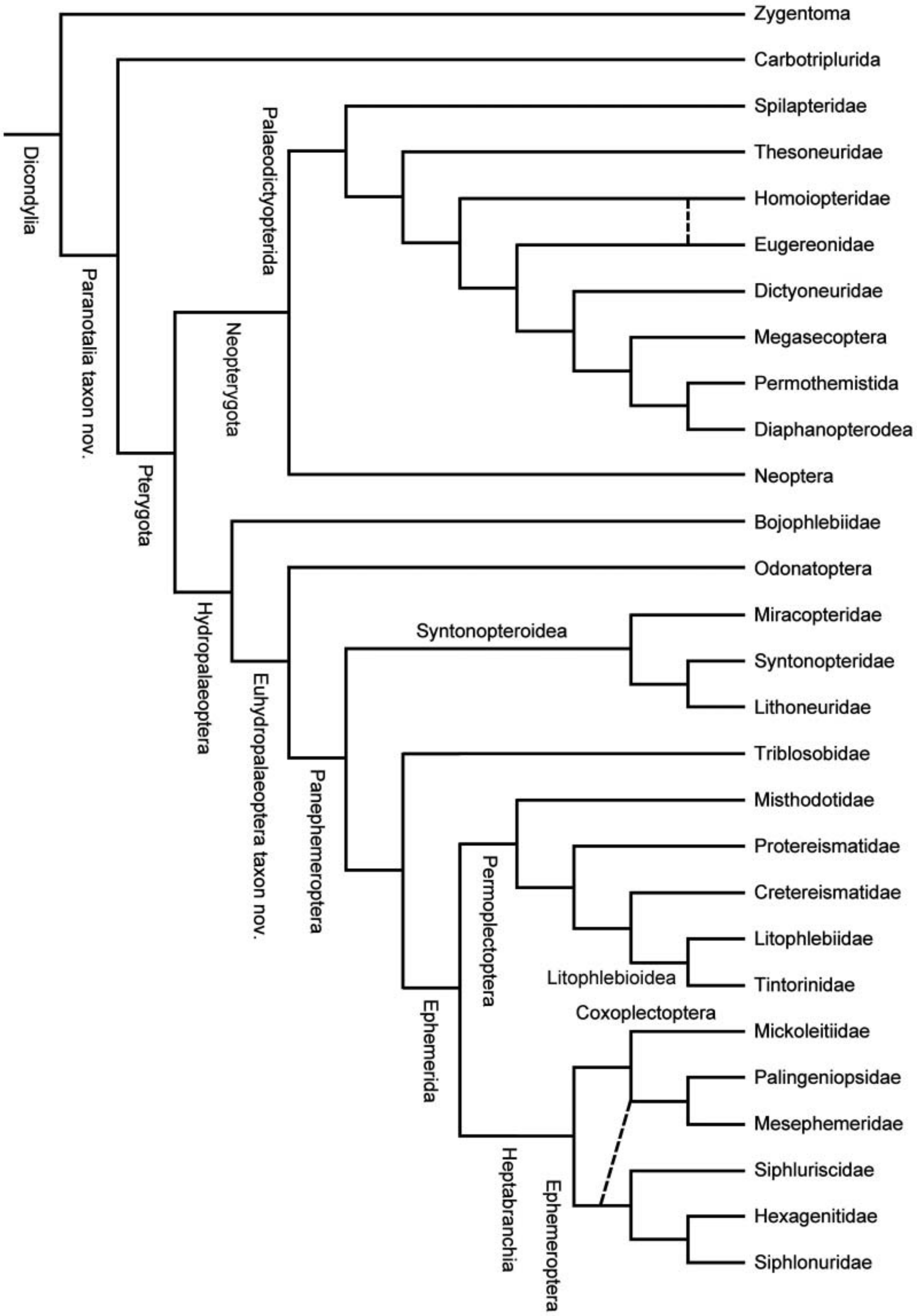

Figure 11. Phylogenetic tree of palaeopterous insects. Based on cladistic study for which the two data matrices and three trees are available in the Supplemental Material.

resulted in 50 shortest trees of length 214 (CI = 0.430, RI = 0.711), from which a majority rule consensus (cut 50) was calculated that was less resolved but did not conflict significantly with the first analysis. In all analyses the silverfish *Tricholepidion gertschi* was used as outgroup, and the rooting was improved by including *Carbotriplura kukalovae*, the putative sister group of winged insects (Staniczek *et al.* 2014), and a hypothetical pterygote ancestor (ground plan states again inferred with the Hennigian method described above). Removal of the hypothetical pterygote ancestor resulted in a less resolved consensus tree but again not in significantly conflicting topologies. No characters were weighted and no constraints were imposed in any of the cladistic analyses.

The main differences with our Hennigian analysis above are the recovery of Syntonopteridae as the sister group of Lithoneuridae, and *Gallolithoneura* as the sister group of Odonatoptera (represented by Eugeropteridae), which are both only very weakly supported by homoplastic characters.

The relatively low consistency index of all our cladistic analyses is due to homoplasy mainly in the wing venational characters and numerous unknown character states in the fossil taxa, which makes the tree topology sensitive to changes of included taxa and characters. This explains the few differences in tree topology of the two datasets. Unfortunately, this is a general problem that will persist because stronger character sets such as internal morphology or genetic data will remain unavailable for fossil taxa, which are mostly documented by, often fragmentary and isolated, wings. However, the CIs of both cladograms is far from being bad; Klassen *et al.* (1991, fig. 6) demonstrated that the statistical support of the CI value strongly correlates with the number of taxa, so that a CI of 0.43 is highly statistically significant for a data matrix with 35 taxa, while it would be low for a matrix with much fewer than 10 taxa.

List of main synapomorphies for the most important nodes

Generally, only characters from the data matrix are included, even though many more characters support recent crown groups such as Pterygota, Neoptera, Odonatoptera and Ephemeroptera. For the four newly proposed taxa (Paranotalia, Neopterygota, Euhydropalaeoptera and Litophlebioidea) we include other known evidence that supports their monophyly. These nodes are named because each reflects an important step in the early evolution of pterygote insects. Furthermore, they are supported by several synapomorphies without convincing conflicting evidence.

Paranotalia taxon nov. Laterally expanded paraterga on thorax and abdomen. Further putative synapomorphies were suggested by Staniczek *et al.* (2014): meso- and metathorax enlarged; abdominal coxopodites reduced; long legs with elongated femora, tibiae, and tarsi; large compound eyes (maybe rather a symplesiomorphy).

Pterygota. Articulated wings on meso- and metathorax.

Neopteragota sens. nov. Larval and adult terminal filum reduced; long common stem of RA and RP.

Palaeodictyopterida. Labium and labrum form beak with stylet-like hypopharynx, mandibles, and maxillae; labial palps reduced (one-segmented or absent); adult cerci much longer than body.

Megasecoptera + Permothemistida + Diaphanopteroidea. Forewing costal field not very large and broad; archaedictyon reduced.

Permothemistida + Diaphanopteroidea. Only three tarsomeres; undulation of ScP and RA near wing base; cross venation strongly reduced.

Neoptera. Subimaginal stages reduced; neopterous wing folding with second muscle on third axillary sclerite; costal spines reduced; RA with oblique veinlets near wing apex.

Hydropalaeoptera. MA approximated or fused to RP; RP, MA, MP, CuA, and CuP with triadic branchings (convergent to *Lodetiella*), incl. IR1 and IR2; pectinate branching of RP1 reduced; archaedictyon reduced.

Bojophlebiidae. Gigantic size (wing span 40 cm); glossae are enlarged plates; ScP thicker than RA.

Euhydropalaeoptera taxon nov. CuP unbranched (reversed in Miracopteridae); hind wing with connection between AA and CuP (anal brace); aquatic larvae (maybe rather a convergence because the aquatic adaptations like gills are not homologous). This taxon is also well supported by further wing venational characters (e.g. Ax0 of odonates is probably homologous to the costal brace of mayflies according to Bechly 1996), secondarily stiffened wing articulation (Willkommen 2009), head characters (Blanke *et al.* 2012, 2013), and several modern phylogenomic studies (Hovmöller *et al.* 2002; Kjer *et al.* 2006; Regier *et al.* 2010; Ishiwata *et al.* 2011; Thomas *et al.* 2013), including first results from the 1KITE project (Misof *et al.* 2014). It must be noted that some of the morphological characters (e.g. bristle-like antennae) that were suggested by Hennig (1981) and/or Kukalová-Peck (1983, 1985, 1991) in favour of a monophyletic (Hydro)Palaeoptera are erroneous and refuted by the fossil evidence (e.g. long antennae in Palaeozoic stem odonates and mayflies).

Odonatoptera. MP simple.

Panephemeroptera. At least a small costal brace; CuA basally curved and touching stem of M.

Syntonopteroidea. Constriction and concave vein IN between AA1+2 and AA3+4 (ambiguous because not preserved in Syntonopteridae).

Triblosobida + Ephemerida. Wing span much less than 10 cm; costal field not very large and broad; anal area of hind wing only slightly wider than in forewing; ScP reaches apex.

Triplosobida. MA and CuA simple.

Ephemerida. Costal brace elongate; MP-fork basal of CuA-fork; both wings with curved veinal arch, from which CuP and anal veins seem to originate.

Permoplectoptera. RP2 asymmetrically branched.

Litophlebioidea stat. nov. Costal brace reduced; RP seems to originate on MA; CuA, CuP, and anal veins very short (anal field largely reduced).

Heptabranchia. Larvae with abdominal gills only segments 1−7 (gills on 8 and 9 reduced); larvae only one tarsal segment with single claw; costal spines reduced.

Ephemeroptera. Forewing triangular; hind wing shortened (maximum half length of forewing); veinal arch, from which CuP and anal veins seem to originate, is more strongly curved.

Conclusions

A redescription of the giant Carboniferous pterygote *Bojophlebia prokopi* has revealed several shortcomings and errors in the original description by Kukalová-Peck (1985), which are here corrected. *B. prokopi* is shown not to be a stem mayfly. A revised phylogenetic position for this taxon in the stem group of Hydropalaeoptera is suggested and corroborated by a cladistic study of fossil and extant palaeopterous insects.

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Supplemental material

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