

Neither silverfish nor fowl: the enigmatic Carboniferous *Carbotriplura kukalovae* Kluge, 1996 (Insecta: Carbotriplurida) is the putative fossil sister group of winged insects (Insecta: Pterygota)

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Abstract. We revise the type material of the enigmatic fossil insect *Carbotriplura kukalovae* Kluge, 1996 from the Pennsylvanian of the Czech Republic. Multiple errors in the original description are documented and corrected. *C. kukalovae* is regarded as a possible transitional fossil link between Zygentoma and Pterygota. Carbotriplurida is therefore elevated to ordinal rank and considered as putative fossil sister group of Pterygota. The paranotal theory of the origin of insect wings and the parachute theory of origin of insect flight are briefly discussed and further corroborated. *Testajapyx thomasi* from the Pennsylvanian of Mazon Creek is tentatively considered as Dermaptera rather than Diplura.

Introduction

Carbotriplura kukalovae Kluge, 1996 was originally considered as the nymph of a giant pterygote insect. Both adult and its putative nymph together were described as *Bojophlebia prokopi* Kukalová-Peck, 1985 in a single contribution by Kukalová-Peck (1985). The adult holotype and its alleged immature paratype were attributed to Ephemerida as the only representatives of a newly erected family Bojophlebiidae. Kukalová-Peck determined the two fossils as different life stages of a single species based on their shared primitive features, comparable size and simultaneous occurrence in the same geological layer (Kukalová-Peck, 1985). The deposits where the two specimens were found are located in the same geological horizon, geographically situated approximately 40 km apart from each other.

Kluge (1996) published a contribution on the nymph of *Bojophlebia*, in which he rejected Kukalová-Peck's attribution of the specimen to Ephemerida. He placed the fossil within the paraphyletic 'Thysanura' sensu Börner (1904), thus neglecting the closer relationship of Zygentoma to Pterygota (Hennig, 1969, 1981). Kluge (1996) established the new name *Carbotriplura kukalovae* and also erected a new genus *Carbotriplura*, new family Carbotripluridae and new suborder

Carbotriplurina for this fossil. The main reason for removing the specimen from Ephemerida was a different interpretation of its lateral thoracic and abdominal expansions. Kukalová-Peck (1985) considered them to represent thoracic wing pads and abdominal tracheal gills, whereas Kluge (1996) regarded all of them as nonarticulated laterotergal extensions. However, from his paper it is obvious that he based his assumptions solely on the study of the figures and photographs originally published by Kukalová-Peck (1985), rather than on a revision of the type material itself.

Bitsch & Nel (1999) regarded *C. kukalovae* as basal Zygentoma due to its flattened body. Rasnitsyn (2002a) considered *C. kukalovae* as 'either silverfish or immature winged insect' but refrained from a final assignment due to the poor knowledge of the fossil.

In a contribution on insect phylogeny, Willmann (2003a,b) briefly commented on *C. kukalovae*, suggesting the possibility that 'this insufficiently known taxon with long walking legs and very pronounced lobes (paranota) on all thoracic segments might represent the sister group of Pterygota'.

Grimaldi & Engel (2005) neither discussed Rasnitsyn's (2002a) nor Willmann's (2003a,b) suggestions, but only briefly remarked that '*Carbotriplura kukalovae* ... is likely a silverfish, and although its assignment to Zygentoma is tentative, its placement in a separate suborder of wingless insects is unjustified'.

Given the fact that this enigmatic fossil has stimulated so many controversial opinions regarding its characters and produced

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different views on its systematic position, it is surprising that no one has actually reinvestigated the original fossil material since its description by Kukalová-Peck (1985).

The main goal of the present study was the revision of the type material to check the validity of characters described by Kukalová-Peck (1985) and to determine the systematic position of *C. kukalovae* within insects. The revision of *Bojophlebia prokopi* will be treated in a separate contribution (Sroka *et al.*, in preparation).

Material and methods

The holotype of *Carbotriplura kukalovae* was found in the quarry 'Na Štilci' near Tlustice, Czech Republic, in tuffites of the Middle Pennsylvanian/Moscovian (Silesian, Westphalian C) (Kukalová-Peck, 1985). According to Prokop & Nel (2010), this deposit in the so-called Whetstone Horizon from the continental basins of the Bohemian massif represented a peat mire ecosystem with shallow lake that was gradually filled by re-deposited volcanic ashes from the Bolsovian of western Bohemia (Czech Republic). The Whetstone Horizon could be dated with the Ar/Ar method as 309 ± 3.7 Ma by Hess *et al.* (1985).

The holotype is deposited in the Museum of Czech Karst (Muzeum Českého krasu), Beroun, Czech Republic, catalogue number P 2670.

The specimen was studied under a stereomicroscope and photographed in different focal layers with a Nikon 60 mm f/2.8 G ED AF-S Micro lens on a Nikon D800E digital camera. It was entirely covered with a layer of ethanol to achieve a better contrast of the fossilized structures. In Adobe Photoshop CS6, focus stacks of photographs were subsequently merged to compound pictures. These were finally sharpened and adjusted in contrast and tonality.

Additionally, the software ACC Image Structure and Object Analyser 5.0 (SoFo Software, <http://acc-analyser.webzdarma.cz/>) was applied to selected RAW files. The ACC contrast algorithms optimize picture contrast and reveal even the finest underlying structural details in the fossil that might be overlooked otherwise.

All specifications of left and right body parts refer to the respective anatomical position, not to the position in the fossil.

Abbreviations used in figures: Abdominal segments are denoted in Roman numbers; segments of tarsi and maxillary palps are denoted in Arabic numbers; ce, cercus; cpd, coxopodite; mx, maxilla; pc, paracercus; pcl, pedicellus; sca, scapus; sty, stylus; ti, tibia.

Results

Redescription of the holotype of Carbotriplura kukalovae Kluge, 1996

The fossil (Fig. 1) is visible from its ventral side (see Discussion below). Although all three tagmata and three caudal filaments are preserved, the specimen is generally in rather poor condition. Triangular head laterally with large compound



Fig. 1. *Carbotriplura kukalovae* Kluge, 1996, holotype. Photograph of entire fossil, specimen is visible in ventral aspect.

eyes. Two filiform head appendages preserved. All thoracic segments with extended side lobes. Legs preserved to different extent: on all legs coxae, trochanters and basal parts of femora not preserved; left hind leg is almost entirely lost except for a femoral fragment; tarsus of right foreleg entirely missing, apical parts of tarsi in left fore- and both middle legs incomplete; only tarsus of right hind leg is complete except for one pretarsal claw probably broken off. Lateral lobes also present on abdominal segments I–IX. Abdomen with ten discernable segments. For measurements see Table 1.

Head

Head of triangular shape in dorsal view, large compound eyes protruding laterally (Fig. 2). Isolated left antennal fragment present, consisting of a broad and short scapus, followed by a thinner pedicellus of approximately same length, proximal part of thin flagellum, and minute isolated part of flagellum situated more distally. Basal part of scapus and attachment point to head capsule not visible. Short hairs distinguishable on scapus and pedicellus. Individual flagellomeres not discernible. Preserved part of flagellum as long as combined length of scapus and pedicellus. Mouthparts mostly not discernible, but fragment of right maxilla with attached maxillary palp visible. Right maxillary palp with five segments completely preserved, except that parts of second and third segment are broken off, so division between second and third segment is only discernible by presence of apical spines on segment two. Short hairs on first three segments visible. Fourth segment approximately as long as segment two, without visible hairs. Fifth segment shortest and

Table 1. Measurements of *Carbotriplura kukalovae* Kluge, 1996 (holotype).

Measurements	mm
Length of body excluding tail filaments	103.34
Length of head	11.84
Width of head	18.9
Length of maxillary palp	13.05
Length of antenna ^a	7.39
Length of prothorax	12.1
Width of prothorax	18.98
Length of mesothorax	18.13
Width of mesothorax	25.36
Length of metathorax	17.62
Width of metathorax	25.16
Length of right forefemur ^a	3.85
Length of right foretibia ^a	11.93
Length of left forefemur ^a	6.85
Length of left foretibia	15.13
Length of left foretarsus ^a	9.11
Length of right middle femur ^a	8.28
Length of right middle tibia	18.36
Length of right middle tarsus ^a	16.2
Length of left middle femur ^a	7.57
Length of left middle tibia	19.51
Length of left middle tarsus ^a	11.29
Length of right hind femur ^a	7.26
Length of right hind tibia	24.71
Length of right hind tarsus	19.29
Length of tarsal claw (right hind leg)	2.12
Length of left hind femur ^a	4.38
Length of abdomen	48.88
Width of abdomen (segment II)	25.92
Length of abdominal leglet (segment III)	4.94
Length of right cercus ^a	38.68
Length of left cercus ^a	36.33
Length of paracercus ^a	37.69

^aPreserved part.

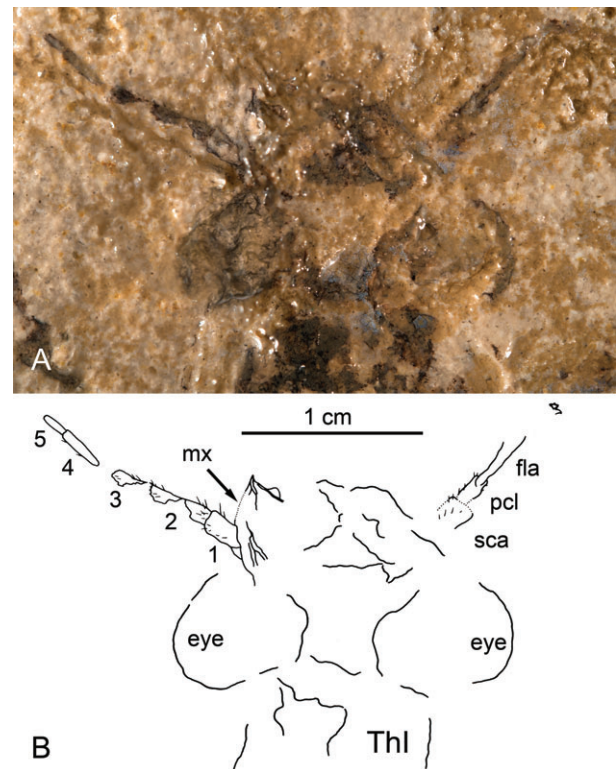
thinnest. General shape of head and anteriorly directed maxilla indicates a prognathous condition in *C. kukalovae*.

Thorax

All three thoracic segments with large, rounded outlines of flat paranotal lobes (Fig. 3). Paired paranotal lobes together as wide as notum itself. No tracheation, venation or articulation visible at all. Prothorax significantly shorter and narrower than meso- and metathorax. Paranota well-developed, flattened and laterally extended, so that they appear as distinct from notum. Posterior margins of pro- and mesothoracic paranota overlapping anterior margin of succeeding paranotum (for details see Discussion). Sternites centrally with apparent traces of heavy sclerotization, possibly representing coxal cavities.

Legs

All legs very long and slender. Numerous short spines present on all podomeres. Coxae and trochanteres not preserved, visible

**Fig. 2.** *Carbotriplura kukalovae*, holotype, head. Left antenna and right maxilla with maxillary palp preserved, (A) photograph, (B) line drawing.

podomeres include only femora, tibiae and tarsi on both fore-, middle and right hind leg (Fig. 1). Femora thickest of all podomeres, basal parts of femora not preserved. Tibiae longest of podomeres, even longer than tarsi (Fig. 4A). Tibia probably rectangular in cross-section, equipped with highly sclerotized longitudinal ridges bearing rows of stout bristles. Exact number of tarsomeres difficult to discern, two possible interpretations are given in Fig. 4D, E. First tarsomere elongated, followed by possibly another four or even possibly up to eight additional tarsomeres on right middle (Fig. 4C) and hind leg (Fig. 4A, B). So either a five-segmented tarsus or even secondarily multi-segmented tarsomeres were present. Tarsi of other legs incomplete (see Figs 1, 3). Right hind leg with single preserved pretarsal claw (Fig. 4A, B). From its lateral point of insertion it seems obvious that legs were each equipped with double tarsal claws.

Abdomen

Abdomen with nine large pairs of extended, plate-like paraterga dorso-laterally on segments I–IX (Fig. 5). Not preserved are paratergal lobes on right side of segments VIII–IX and on left side of segments I and III. No articulation between tergites and paratergal lobes visible, paratergal lobes without any traces of tracheation. Anterior margin of each lobe thickened and basally in line with anterior margin of respective



Fig. 3. *Carbotriplura kukalovae*, holotype, photograph of thorax with lateral paranota. Black arrows point to overlapping of thoracic segments in ventral view. White arrows point to basal abrasions of legs.

abdominal segment. Lobes apically rounded and directed posteriorly, thus overlapping the succeeding paratergal lobe. Sternal borders in between abdominal segments hardly visible.

Single abdominal leglet reasonably well preserved on left side, originating from the hind margin of segment III (Figs 5, 6A, B). Leglet probably composed of basal coxopodite and terminal stylus, terminal claws not visible. Eversible coxal vesicles not present or not preserved. Possible remains of leglets also visible on the right hind margin of segments II–III and on left hind margin of segment IV (Fig. 7, arrows). Gonostyli on abdominal segment IX not preserved (Fig. 8). Cerci and paracercus directed backwards, thin, annulated, covered evenly with short hairs, without rows of swimming bristles (Figs 8, 9). All caudal filaments apically broken off.

Discussion

Preservation in dorsal or ventral aspect?

Kukalová-Peck (1985) considered the specimen of *C. kukalovae* to be visible from its ventral side, probably

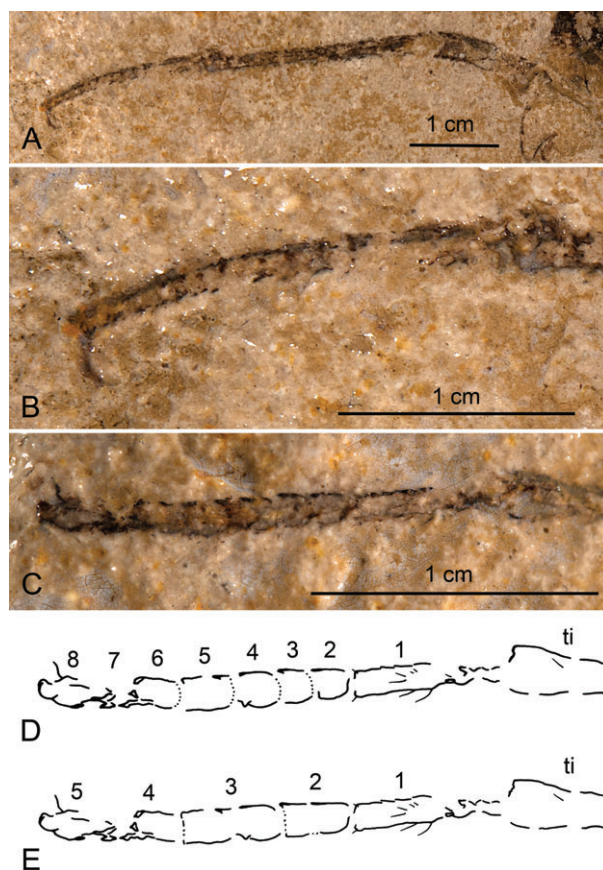


Fig. 4. *Carbotriplura kukalovae*, holotype, photographs of right hind leg (A), right meta- (B) and mesotarsus (C), two alternative interpretations of segmentation in right mesotarsus (D, E).

based on the presence of an abdominal leglet. However, some aspects give the impression that the specimen is actually viewed dorsally. Because the orientation of the fossil is important for the correct interpretation of various morphological structures, we investigated this issue more closely.

At first sight the thoracic paranota seem to overlap the femora, as the lateral margins of the thoracic segments are always well visible, and the proximal leg parts seem to be hidden beneath the paranotal lobes. This would rather point to the dorsal aspect of the specimen. However, in our view the basal parts of the legs were probably abraded when the specimen was detached from its counterpart (which is not verifiable, because no counterpart is preserved). In some legs, these basal abrasions are obvious (Fig. 3, white arrows). Notwithstanding the arrangement of the legs, other clues also indicate that the fossil is not visible from its dorsal aspect.

In all known arthropods with plate-like extensions, the preceding segment always overlaps the following one. In *C. kukalovae*, the posterior part of each paratergium is always overlapped by the anterior margin of the subsequent one (Fig. 3, black arrows). This pattern of overlapping on both thoracic and abdominal segments clearly points to the visibility of the fossil from its ventral aspect. Moreover, the evident visibility



Fig. 5. *Carbotriplura kukalovae*, holotype, photograph of abdomen. Arrows point to abdominal side lobes.

of at least one abdominal leglet also supports this assumption. Taking all these considerations into account, we conclude that the fossil is visible from its ventral side.

Comparison of characters mentioned in the original description with our own observations

Prior to any consideration on the systematic placement of *C. kukalovae*, it is necessary to reconsider and discuss several of its characters as described by Kukalová-Peck (1985). Below we repeat several of Kukalová-Peck's observations and interpretations in quote marks, with page indication in brackets, followed by our own reasoning.

Antennae and mouthparts

'Antennae similar to syntonopterid nymphs, longer and thicker than in protereismatid nymphs; mouthparts powerful, well sclerotized' (p. 936)

Both filiform head appendages visible in the fossil were considered by Kukalová-Peck (1985) to be antennae. In any

case, the head appendages definitely do not consist of nine or ten segments as depicted by Kukalová-Peck (p. 937, fig. 4), but there are only up to five segments identifiable (Fig. 2B). Moreover, the basal segments of left and right appendage show significant differences in position, size and proportions (see also measurements in Table 1). These substantial differences arguably do not allow an interpretation of the two as representing the same pair of head appendages. Generally, the antenna in true insects (*Ectognatha sensu* Hennig, 1981) is made up of scapus, pedicellus and a thin, multi-segmented flagellum with a larger number of short segments. The elongated segments of the right appendage in *C. kukalovae* thus look very different from antennal segments one would expect in a silverfish or early pterygote insect. Instead, in their general appearance they rather resemble those of a maxillary palp. In addition, the right appendage clearly inserts sublaterally at a pointed mouth part, which consequently can only be interpreted as maxilla. Insect mandibles do not exhibit palps, their labium looks different with labial palps that generally have three or fewer segments. In the right maxillary palp, pieces of segments 2 and 3 are partly broken off, indicating segment borders only by apical spines on segment 2. Thus we conclude that the maxillary palp in *C. kukalovae* is made up of five segments, which would correspond to the ground plan condition in insects.

The other, isolated filiform appendage is positioned more dorsally than the right maxillary palp and probably represents the basal part of the left antenna. Apart from the different size proportions, this is also supported by the telescopic interlocking of the segment joints, which is especially well visible between second and third antennal segment. Consequently, we interpret the visible remains as scapus, pedicellus and basal part of antennal flagellum (see Fig. 2B).

It might seem curious that only the left antenna and the right maxillary palp are preserved, but the absence of a preserved left maxilla makes the presence of an isolated maxillary palp on the left side unlikely. We thus consider this an artefact of preservation.

In any case the statement by Kukalová-Peck that the antennae are similar to antennae of syntonopterid nymphs is invalid: The only two fossil insect nymphs that have been attributed to Syntonopteridae are *Lithoneura piecko* and *L. clayesi* described by Kukalová-Peck (1985). However, Carpenter (1987) considered the attribution of these two fossil nymphs to Syntonopteridae to be very questionable, and Kluge (2004) regarded them as Hexapoda incertae sedis.

Thorax

'Three pairs of wings equally shaped' (p. 936)

Kukalová-Peck interpreted the lateral tergal extensions of the thoracic segments as wings [sic!] or winglets, which could have been influenced by the interpretation of the specimen as nymph of *Bojophlebia prokopi*. However, in our view it is impossible to maintain this assumption. Instead, these lobes are simply

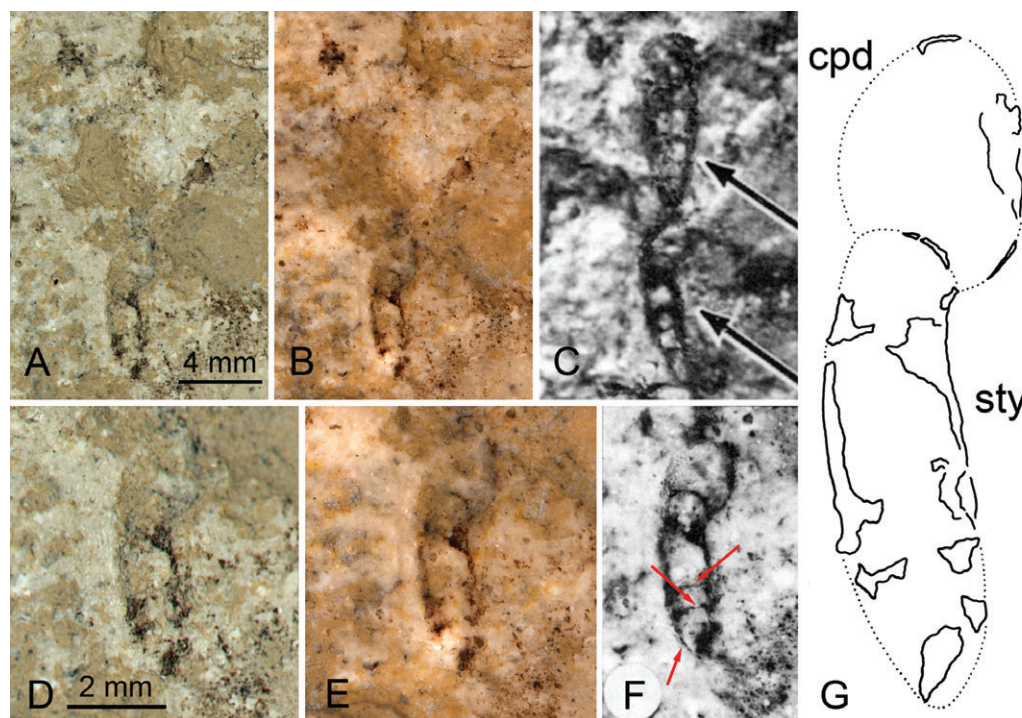


Fig. 6. *Carbotriplura kukalovae*, holotype, (A–G) right abdominal leglet on segment III, (A–C) in overview and (D–G) in detail, (A, D) photographed in dry condition, (B, E) photographed under a layer of ethanol, (C) scanned detail from original print of fig. 6A in Kukalová-Peck (1985) showing an additionally inserted leglet on segment II, (F) scanned original print of fig. 6B in Kukalová-Peck (1985), original figure numbering replaced and arrows added to highlight modifications obviously applied to photograph (see also Discussion on leglets), (G) line drawing illustrating our interpretation of abdominal leglets being composed of basal coxopodite (cpd) and apical stylus (sty). Figure 6C, F © 2008 Canadian Science Publishing or its licensors, reproduced with permission.

lateral, rigid extensions of the thoracic nota (Fig. 3). They neither bear visible traces of venation nor a basal articulation, nor are their tips orientated caudally as in protereismatid nymphs and other early mayflies, or in any known pterygote insect nymphs. Wing pads of Paleozoic nymphal Ephemeroidea such as Prottereismatidae formed large, postero-laterally protruding extensions, considerably exceeding the caudal border of the respective thoracic segment (Carpenter, 1992). Anything similar is entirely missing in *C. kukalovae*; lateral thoracic extensions here look completely different.

Moreover, even if these extensions were wing pads despite their different shape and lack of venation, they would still be of a very small size compared to the overall body size. Such a ratio of nymphal body size to wing pad size is present in the earliest instars only. Considering the size of the specimen (more than 10 cm without caudal filaments), we do not assume that it could be an early instar nymph. Therefore, we concur with Kluge (1996) and consider these structures as thoracic paranota.

Legs

‘four legs’ (p.936); ‘The patella is separated from the tibia by a suture’ (p. 944); ‘Legs ... with femur short, basitarsus, tarsus, and posttarsus longer, and patello-tibia the longest

part of each leg; double posttarsal claws present’ (p. 936); ‘Metathoracic leg, tibia, basitarsus, tarsus with 4 subsegments and large posttarsus’ (p. 939).

Kukalová-Peck (1985) explicitly mentions only four preserved legs in the specimen. However it becomes obvious even from her own photographs that there are actually all six legs at least partly preserved.

Many taxa of modern mayfly nymphs exhibit a superficial, oblique, so-called tibio-patellar suture in the basal part of the tibia. This suture was occasionally interpreted as a remnant of a fusion of patella and tibia (for details see Kluge, 2004). However, in our view neither a separate patella nor any trace of a tibio-patellar suture is visible on any leg of *C. kukalovae* (Figs 1, 4A). Kukalová-Peck even described a separate patellar leg segment in the leg of *Bojophlebia prokopi* (adult) and took this as further evidence in favour of an attribution to Ephemeroidea (but see Sroka *et al.*, in preparation).

Kukalová-Peck described the femora as short, but as the basal leg segments (coxa and trochanter) as well as the basal parts of the femora are not preserved in the specimen, we cannot conclude on the definite length of the femora.

We concur with Kukalová-Peck that in all preserved tarsi there is a long first tarsal segment (basitarsus) present. It is more difficult to judge the number of remaining tarsal segments (tarsus

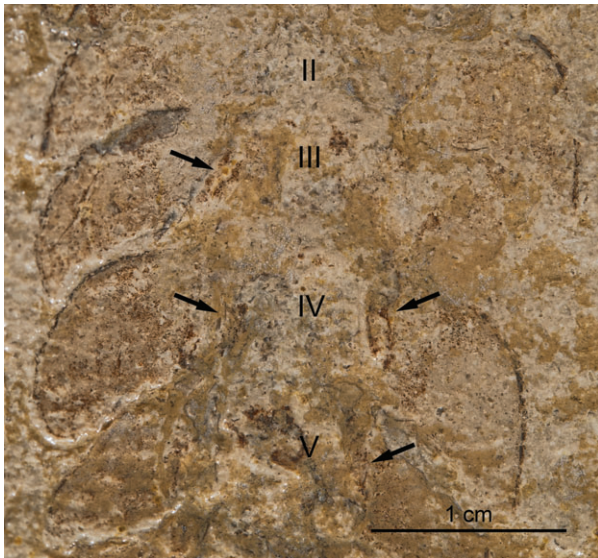


Fig. 7. *Carbotriplura kukalovae*, holotype, photograph of middle part of abdomen with optimized contrast to enhance all remains of leglets (indicated by arrows).

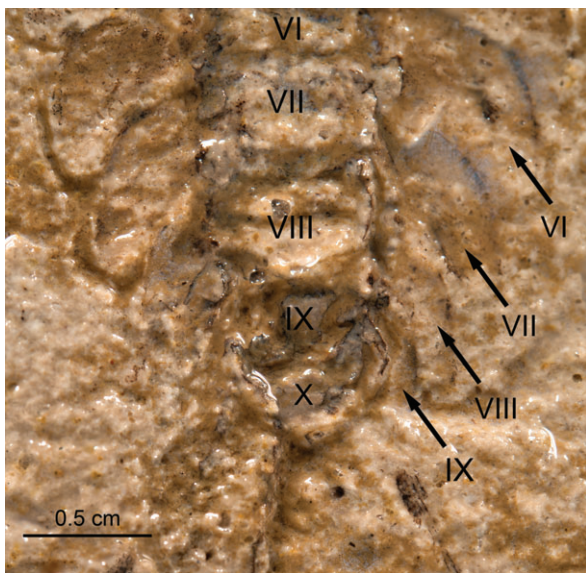


Fig. 8. *Carbotriplura kukalovae*, holotype, photograph of posterior part of abdomen (with missing claspers).

sensu Kukalová-Peck, 1985). Kukalová-Peck described and figured another four short segments (see p. 937, fig. 4), which would account for a five-segmented tarsus. Actually, from what can be seen in the fossil one might even conclude on a much higher number of successive short tarsomeres. However, even the best preserved tarsus of the right middle leg is inconclusive and could be interpreted both ways (Fig. 4C–E). Segmentation of other tarsi is even less obvious, but the tarsi of right hind leg might also indicate the presence of multiple segments (Fig. 4A, B). This would be an unusual feature, as the number

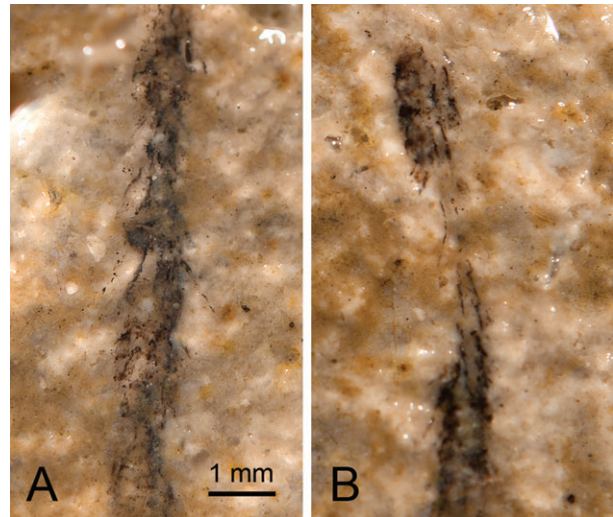


Fig. 9. *Carbotriplura kukalovae*, holotype, photograph, setation of cerci.

of tarsal segments in the ground plan of insects is five, with frequent reductions in subordinate taxa, so a multisegmented condition in *C. kukalovae* would have to be regarded as autapomorphic.

Within Arthropoda, only few examples of multisegmented tarsi have been recognized, usually connected with a specific function (see Nel *et al.*, 2004; Delclòs *et al.*, 2008). If *C. kukalovae* indeed had multisegmented tarsi, these may have facilitated climbing in the vegetation (together with very long legs in general).

Kukalová-Peck described and figured double claws (posttarsus sensu Kukalová-Peck) in left foreleg, right middle and hind leg (p. 937, fig. 4). Actually only one single claw is visible in the right hind leg (Fig. 4A, B) of the specimen. As the point of insertion on the apical tarsal segment is clearly not centred, we indeed assume that a corresponding second claw was present, but it is not preserved.

Abdomen

‘9 pairs of broad leaflike, veined tracheal gills’ (p. 936)

Contrary to Kukalová-Peck (1985), the preserved structures do not allow an interpretation of the abdominal lateral extensions as tracheal gills. Neither is there visible any tracheation nor trace of basal articulation between lobes and central part of abdomen present. The side lobes are much thinner than the rest of the body and basally extend along the entire length of the respective abdominal segments. Kluge (1996) took this as evidence against the interpretation of these side lobes as tracheal gills. In modern mayflies, the latter generally insert with a pointed articulation at the hind margin of the respective segment. However, in Coxoptera, the fossil sister group of modern mayflies, the styliform gills also extend along the

entire length of the respective abdominal segments, but they are already clearly articulated and movable (Staniczek *et al.*, 2011).

Obviously the ventral parts of the central body in *C. kukalovae* have been partly abraded, so especially in the posterior half of abdomen the lateral sternal margins of the central body are cut through, giving the impression of a division between central body and paraterga. However, this must not be confused with a proper articulation. Each paratergum is seamlessly connected with the tergum along its entire length, with no lateral abdominal margin visible in the anterior half of the abdomen.

Probably the most convincing evidence in favour of non-movable paraterga is the correlation of the position of these structures with the bending of the abdomen. The paraterga along the convex side of the bent body are distally spread, whereas the paraterga along the concave side are crowded and overlapping. This phenomenon is to be expected when the structures are nonmovable paraterga, although no such correlation is to be expected in the case of movable articulated gills.

Considering all available evidence, we concur with Kluge (1996) that there is no reliable proof to consider the abdominal side lobes of *C. kukalovae* as movable tracheal gills.

‘9 pairs of abdominal legs (telopodites) composed of probably 7 segments; 9th pair of legs changed into claspers, terminated in all probability by double claws’ (p. 936)

Kukalová-Peck in her description mentions nine [sic!] pairs of ventral abdominal leglets, each leglet composed of probably seven [sic!] segments. As she claims the leglets of the ninth segment to be developed as claspers, this would point to a pair of unaltered leglets in abdominal segments I–VIII.

However, in her own line drawing (p. 937: fig. 4) she figures just six styliform pairs of leglets on the posterior borders of abdominal segments II–VII, plus a pair of claspers attached to abdominal segment IX. In one of her photographs (p. 937: fig. 6A) that, according to Kukalová-Peck, was taken ‘with oblique lighting’, arrows point to three successive leglets on the left side of segments II–IV. In another photograph (p. 937: fig. 5), there is only a single leglet clearly visible on the left side of segment III. Finally, in a highly magnified photograph (p. 937: fig. 6B), this leglet seems to be divided into at least five segments.

We thoroughly scrutinized the specimen under different lighting both in dry condition and submerged under a layer of ethanol to verify Kukalová-Peck’s description and photographs, but we were not able to confirm her findings in most respects. Gonopodal claspers are actually not discernible on the fossil at all (Fig. 8); in fact, there is no evidence for any male or female modification in the genital segments, probably due to the poor preservation of the specimen.

We were only able to verify the presence of a single styliform leglet on the left posterior margin of abdominal segment III (Fig. 6A, B, D, E). In our view this leglet is only composed of two segments, namely a rounded coxopodite and an elongated stylus. Although it is likely that abdominal leglets were present in more than one abdominal segment (possible faint remnants of additional leglets may also be present on segments II and

IV, see arrows in Fig. 7), the poor preservation of the specimen does not provide further evidence on this.

When we compared the actual fossil and our own photographs thereof with the figures in Kukalová-Peck (1985), we were extremely puzzled how such a different impression could be achieved that would indeed point to the presence of several multi-segmented leglets, as we were not able to reproduce it. By looking more closely at her photographs in an original printed copy of the publication (not a photocopy), we came to the conclusion that some parts in these photographs seem to be artificially altered, probably by using a retouching pen, in order to ‘highlight’ or ‘enhance’ the assumed structures in question. We compared our own photographs of the preserved leglet III in dry condition (6A, D) and under ethanol (6B, E) with a detail of the originally published photographs 6A and 6B by Kukalová-Peck (1985), here reproduced as Fig. 6C, F. In our view it is obvious that in Kukalová-Peck’s original figures additional lines of pigments were added onto the photographs, as the colour and general structure of these added lines clearly deviate from the remaining structures in the fossil. In Fig. 6F this results in the effect of a segmented stylus. Also in her fig. 6A, the outlines of all putative leglets on segments II–V most likely were drawn by a retouching pen or similar device. In our view this is quite obvious when we compare a detail of that photograph showing the alleged presence of leglet II (reproduced here as Fig. 6C) to our own Fig. 6A, B. Even if this was done with the best intentions by Kukalová-Peck to enhance structures, of which she was convinced were present, this is not proper scientific practice and should not have been done, or at least should have been clearly indicated in her description or in her figure captions. So at best we can take Kukalová-Peck’s published photographs as interpretations of her theories but not as primary sources of information.

In extant primarily apterygote hexapods (Diplura, Archaeognatha and Zygentoma), various abdominal sterna are equipped with paired appendages. These appendages are mostly interpreted as remnants of abdominal legs (Klass & Kristensen, 2001; Klass, 2009; Bitsch, 2012). Each appendage is generally composed of a plate-like coxopodite (coxite), often fused with sternite. At its posterior end it medially bears an eversible coxal sac and laterally a stylus. In *Tricholepidion gertschi*, the putative sister group to all other Zygentoma, these abdominal leglets are still present on abdominal segments II–IX (Wygodzinsky, 1961).

Whereas in extant adult Pterygota these abdominal leglets are assumed to be lost or modified (Klass & Kristensen, 2001), they are obviously still present in *C. kukalovae*, although we do not know their definite number. The only well-preserved coxopodite in *C. kukalovae* is not plate-like, but instead rather short and rounded (Fig. 6D–G; cpd). The presence of eversible coxal sacs cannot be confirmed, but this may be due to the poor condition of *C. kukalovae*. Like in fossil Monura (see Bechly & Stockar, 2011) and in modern Archaeognatha and Zygentoma, the attached stylus is unsegmented and without claw. Segmented abdominal styli were repeatedly reported by Kukalová-Peck in various Paleozoic insects (Kukalová-Peck, 1987, 1991), but in a re-investigation of Geraridae (Orthoptera) it was concluded that these were artefacts (Béthoux & Briggs, 2008). As in our

case the presence of segmentation in the abdominal styli of *C. kukalovae* could not be confirmed, there remain increasing doubts on the segmented nature of the styli as earlier described by Kukalová-Peck in various Paleozoic taxa.

‘paracercus longer than cerci’ (p. 936)

Kukalová-Peck assumes the paracercus to be longer than the cerci. However, the apical ends of both cerci are clearly broken off, so there is no definite conclusion on the length ratio between cercus and paracercus possible.

In her fig. 4, Kukalová-Peck figured cerci and paracercus basally isolated from the terminal abdomen. In our view, right cercus and paracercus are basally clearly attached to the tenth abdominal segment (see Fig. 8).

Concluding remarks on the original description by Kukalová-Peck

It becomes obvious from the preceding paragraphs that Kukalová-Peck’s original descriptions seriously suffer from erroneous observations, over-interpretation, or even tampering with structures in order to fit her theories. As several other authors in their revisions of fossils described by Kukalová-Peck basically came to the same conclusions (Carpenter, 1987; Rasnitsyn & Novokshonov, 1997; Willmann, 1999; Béthoux & Briggs, 2008; Bechly & Stockar, 2011; Sroka *et al.*, in preparation), it will be necessary to re-investigate other Palaeozoic taxa also and their alleged peculiar morphology described by Kukalová-Peck.

A notable example is the case of *Testajapyx thomasi*, which was described as a Carboniferous dipluran by Kukalová-Peck (1987), based on a fossil from the Pennsylvanian of Mazon Creek in the private collection of Thomas Testa. Grimaldi & Engel (2005) already mentioned reservations concerning its attribution to Diplura, due to its poor preservation. According to the photos in the original description, we strongly doubt the presence of abdominal leglets and eversible vesicles, the number of ten abdominal segments, and entognathous mouth parts. There are only two groups of insects with cerci modified as forceps, namely japygid Diplura and Dermaptera. Indeed, several characters of *T. thomasi* rather suggest an attribution to Dermaptera: large size; head prognathous without ocelli; legs with three tarsomeres; abdominal terga 8–10 fused (as in female Dermaptera); cerci developed as forceps. This tentative hypothesis would imply that *T. thomasi* is a female wingless earwig that is more derived than stem group Dermaptera from the Early Permian (Protelytroptera, e.g. Protelytridae) or even Jurassic–Cretaceous (Archidermaptera, e.g. Protodiplatyidae), which still possess ocelli, five tarsomeres and filamentous cerci (Willmann, 2003b). However, the presence of advanced Dermaptera in the Carboniferous is not unlikely considering the recent description of various lineages of Holometabola of the same age (Kirejtshuk & Nel, 2013; Nel *et al.*, 2013). Of course the long ghost lineage of more derived dermapterans for the Permian and Triassic

would be remarkable, but may be explained by the fact that earwigs are very scarce in the fossil record anyway (Zhao *et al.*, 2010).

It should be mentioned that the museum of Czech Karst and with it the stored holotype fossil of *C. kukalovae* was affected by a flood in 2002, but according to the curator the only alteration consists in a very thin overlay of light-brownish sediment (Š. Rak, personal communication), which also can be seen in our figures. This reduces the contrast of some parts of the fossil. However, the profound differences between our observations and the published figures of Kukalová-Peck cannot be reasonably explained with subsequent degradation of the fossil. Additionally, the application of ACC software to make underlying structures more clearly visible also points to the fact that some of the alleged styli in Kukalová-Peck’s figures have never been present in the fossil.

The systematic position of *C. kukalovae*

Why C. kukalovae is not a bristletail or silverfish

Carbotriplura kukalovae easily can be attributed to Insecta due to its segmented tarsi, pretarsus with (assumed) double claw, and presence of a long paracercus. It is more difficult to judge its position regarding bristletails (Archaeognatha) and silverfish (Zygentoma), as it only shares plesiomorphic characters with these taxa, namely the lack of wings and presence of abdominal leglets in addition to the characters mentioned above.

In contrast to Archaeognatha, the complex eyes of *C. kukalovae* are well separated and not medially fused. Furthermore, the maxillary palp in *C. kukalovae* is smaller, five-segmented, and lacks a triangular process on its first segment, which is present in the first segment of the long, seven-segmented maxillary palp of Archaeognatha (Sturm & Machida, 2001).

Although the general morphology of *C. kukalovae* is what one would tentatively associate with a ‘primitive’ dicondylous insect, it is not easy to find apomorphies that clearly would define it as a member of Dicondylia. Most characters that are generally accepted as apomorphies of Dicondylia are not preserved in *C. kukalovae*, such as, for example, the dicondylous mandible, epistomal suture, complete postoccipital suture or medial fusion of anterior tentorial arms (see Willmann, 2003a,b). However, there are two characters that point to *C. kukalovae* as a taxon within Dicondylia: The maxillary palps are greatly reduced in length compared to the thoracic legs, and in the ground plan of Dicondylia there is most probably a five-segmented tarsus present (Kristensen, 1991). Although the precise number of tarsal segments in *C. kukalovae* cannot be exactly determined, it certainly had at least five segments (see Fig. 4 and description).

Based on its unique appearance, Kluge (1996) erected a new suborder within Zygentoma to accommodate *C. kukalovae*. However, whereas *C. kukalovae* most probably can be included in Dicondylia, it differs from Zygentoma in several important aspects: In contrast to all Zygentoma, the lateral compound eyes

in *C. kukalovae* are not reduced in size, but instead are large and protruding. Additionally, coxae and femora in silverfish are very broad and flattened; the coxae directed posteriorly, the femora are short, fitting into a coxal concavity, which is regarded as autapomorphy of Zygentoma by Willmann (2003a,b). The legs of *C. kukalovae* look very different, with slender femora and largely elongated tibiae. Moreover, the position of the legs does not indicate the presence of enlarged coxae. If large coxae were present in *C. kukalovae*, the position of the preserved parts of femora should be far more posterior.

Other putative autapomorphies of Zygentoma cannot be judged in *C. kukalovae*, as these characters, such as four-segmented labial palp, absence of superlinguae, or dorsal hooked articulation of cerci (Koch, 2003), are not preserved.

Klass (2009) regarded many of the putative autapomorphies of Zygentoma as possible ground plan characters of Dicondylia, especially the peculiar leg arrangement of Zygentoma (for a detailed discussion on other apomorphies of Zygentoma, see Klass, 2009). In our view this leg arrangement is rather an adaptation in soil-dwelling insects that enables them to move fast over the ground. Thus we concur with Willmann (2003a,b), who regards this peculiar leg arrangement as an autapomorphic character of Zygentoma. However, there are even more characters previously not considered that suggest the exclusion of *C. kukalovae* from Zygentoma: In many silverfish the cerci are held erect and almost rectangular to the longitudinal body axis. This certainly applies not only for Lepismatidae, but also for the relic silverfish *Tricholepidion gertschi* (see photo 5.5 by H. Sturm, p. 151 in Grimaldi & Engel, 2005), the putative sister group to all other Zygentoma (Kristensen, 1991; Koch, 2003). Moreover, throughout Zygentoma the cerci are covered with characteristic, long, tactile, movable hairs that respond to sudden changes in air flow (own observation). Both of these characters are not present in *C. kukalovae* that has posteriorly directed cerci equipped only with short bristles.

Although all these differences are plesiomorphies that would only exclude *C. kukalovae* from the crown group of Zygentoma, we also describe several putative synapomorphies with Pterygota (see below).

Why *C. kukalovae* is not a pterygote nymph

Pterygota is a well-established monophyletic taxon (Kristensen, 1991). The predominant feature of Pterygota – namely wings on the meso- and metathoracic segments – is obviously not present in *C. kukalovae*. In many Paleozoic pterygote nymphs (especially of palaeopterous basal pterygotes) there are articulated wing pads present (Carpenter, 1992), which may represent the plesiomorphic state, because modern Hydropalaeoptera (mayflies and odonates) have nonarticulated wing pads like all fossil and modern Neoptera. Also in all fossil and modern pterygote nymphs the wing pads are either curved posteriorly or bent posteriorly, whereas the thoracic paranota of *C. kukalovae* are rectangular along the margins of the thoracic segments. Consequently, in our view the thoracic extensions in *C. kukalovae* do not represent wing pads due to

their different shape and lack of any articulation or venation. Moreover, the interpretation of the rather small thoracic side lobes as emergent wing pads would imply that *C. kukalovae* represents a rather early instar nymph, which would have to be much smaller even for a *Meganeura*-sized adult. According to Kukalová-Peck (1978), wing pads in Paleozoic insect nymphs were growing gradually in posterolateral direction throughout larval development. Even if we assume a positive allometric growth of wing pads like in modern mayfly nymphs (Maxwell & Benson, 1963; de Paula Paciencia *et al.*, 2012), this specimen with an extraordinary body length of already 10 cm (!) excluding terminal filaments would need to develop into an adult much larger than any other Paleozoic insect discovered so far. Therefore, we regard it as highly unlikely that *C. kukalovae* represents a pterygote nymph as suggested by Rasnitsyn (2002a). He regarded *C. kukalovae* as 'either silverfish or immature winged insect' but refrained from a final assignment based on the poor knowledge of the fossil. The preservation of the abdomen does not allow any conclusion about the presence or absence of functional genitalia, so that this character cannot be used to establish a status as nymph or adult. A pedomorphic origin of *C. kukalovae* cannot be excluded, but we consider this as highly unlikely.

Rasnitsyn (2002a: fig. 61) also published a photograph of a pterygote fossil nymph from Grés à Voltzia, Middle Triassic of the Vosges, France, with apparent wing pads and laterally extended abdominal laterotergal extensions, which reminded Rasnitsyn of *C. kukalovae*. This Triassic fossil was later formally described by Sinitshenkova *et al.* (2005) as *Vogesonympha ludovici*. Sinitshenkova *et al.* (2005) noted its similarity to *C. kukalovae*, but also realized some significant differences: the abdominal lateral extensions in *V. ludovici* do not extend to segments VIII–X, its lateral extensions of meso- and metathorax resemble typical wing pads of pterygote insects, and its size is much smaller compared to *C. kukalovae*. As a consequence, Sinitshenkova *et al.* (2005) attributed *V. ludovici* to Pterygota incertae sedis.

Why *C. kukalovae* rather represents the sister group of Pterygota

There are five putative synapomorphies that indicate a sister-group relationship between *C. kukalovae* and Pterygota, as already proposed by Willmann (2003a,b):

- 1 In *C. kukalovae*, meso- and metathoracic segments are enlarged in size compared to the prothorax and first abdominal segment, whereas in Archaeognatha only the mesothorax and in Zygentoma the prothorax are autapomorphically enlarged. Thoracic paranota are well developed, flat and laterally expanded. In Archaeognatha and many Zygentoma the thoracic side lobes are ventro-laterally curved. An enlarged meso- and metathorax with laterally expanded and flat paranota thus could be interpreted as apomorphic and an important preadaptation for the acquisition of wings.

- 2 Additionally, laterally extended abdominal paratergal lobes as in *C. kukalovae* are not present in silverfish or any other primarily wingless insects, but might actually be homologues of the abdominal gills present in mayfly nymphs (Staniczek *et al.*, 2011). We thus consider it likely that in the ground plan of Pterygota there are also abdominal paraterga present. Further evidence for this assumption can be found in the abdominal lobes that are also present in *Vogesonympha ludovici* described by Sinitshenkova *et al.* (2005), the undescribed Mazon Creek fossil featured in Fig. 10, and many Paleozoic nymphs of Palaeodictyoptera (Wootton, 1972) and Polyneoptera (Garwood *et al.*, 2012). Abdominal paraterga might thus account for a shared derived condition in *C. kukalovae* + Pterygota. Tergal expansions are also present in the abdominal segments of Archaeognatha (Bitsch, 1973), but these are directed ventro-medially, enclosing the sides of the abdomen.
- 3 In *C. kukalovae*, the abdominal coxopodites are no more plate-like than they are in the remaining apterygote insects, but reduced to small, conical structures (Fig. 6D–G; cpd). Consequently, this reduction can also be assumed for the ground plan of *C. kukalovae* + Pterygota, with subsequent loss of styli and fusion of coxopodites with sterna in the pregenital abdominal segments of Pterygota.
- 4 Compared to the relatively short legs with short femora, tibiae and tarsi in Collembola, Protura, Diplura, Archaeognatha and Zygentoma, the very long legs with elongated femora, tibiae and tarsi of *C. kukalovae* and most pterygote insects (e.g. the very basal Ephemeroptera) probably represent a derived condition.
- 5 Finally, the enlarged lateral compound eyes might represent a further synapomorphy of *C. kukalovae* + Pterygota, although it is also possible that this character state was already present in the ground plan of Insecta. The large and medially fused compound eyes of Recent Archaeognatha could suggest the latter hypothesis, but their fossil sister group (Monura) has smaller and medially separated eyes (Bechly & Stockar, 2011), which rather suggests that the eye configuration in Archaeognatha is an autapomorphy.

Objections might be raised that the above-mentioned five synapomorphies are not very strong evidence for a sister relationship. However, weak evidence would only be critical if and only if stronger evidence could reasonably be expected from an early transitional form between Zygentoma and Pterygota at all, which is obviously not the case. The fossil shows all characters that we should expect from such an early transitional form, and even corresponds very well to published theoretical reconstructions of such forms (Rasnitsyn, 2002b: 82, fig. 72; Grimaldi & Engel, 2005: 159, fig. 6.2.a). An abductive Inference to the Best Explanation (*sensu* Lipton, 1991) of all the available evidence therefore clearly favours the presented hypothesis, which is of course also the most parsimonious interpretation of the character distribution.

Consequently, we elevate the former suborder Carbotriplurina to ordinal rank as distinct order Carbotriplurida, and suggest that this order is best considered as the fossil sister group of



Fig. 10. Unnamed Mazon Creek fossil exhibiting similar arrangement of abdominal paraterga as *Carbotriplura kukalovae*. Photograph without scale.

Pterygota, and as a phylogenetic link between Zygentoma and Pterygota.

Other undescribed taxa potentially related to C. kukalovae

We have studied a photograph of a still undescribed Carboniferous fossil from the Mazon Creek locality (Fig. 10, housed in the collection of Carleton University, Ottawa), which exhibits striking similarity to *C. kukalovae*, although it possesses even larger abdominal and thoracic extensions. The thoracic side lobes seem to show some degree of venation and thus more resemble true wing pads than the paranota of *C. kukalovae*. We had no possibility of studying this peculiar Mazon Creek fossil itself, so we are not able to prove if it already represents a taxon with movable paraterga or even if it was a terrestrial or aquatic pterygote nymph with wing pads. However, its thoracic side lobes seem to be serially homologous with the abdominal ones. In our view these abdominal extensions resemble paraterga rather than abdominal gills as in Ephemera, as they seem to be attached along the entire sides of the abdominal segments I–IX and do not have a single-point articulation at the posterior side

margins of the respective segments (see especially abdominal segment I).

The next step in evolution of active flight must have resulted in a successive increase in size of the thoracic paranota as first stage for acquiring pterygote wings. Staniczek *et al.* (2011) presented new fossil evidence for a paranotal origin of thoracic wings and abdominal gills of mayfly nymphs, and suggested that these tergal structures became movable by the subsequent evolutionary origin of an articulation, which was facilitated by 'borrowing' regulatory genes from leg control regions (compare Niwa *et al.*, 2010).

Scenario for the evolution of flight

Carbotriplura kukalovae was originally considered to exhibit an aquatic lifestyle, but our reinvestigation revealed that there are no obvious aquatic adaptations present in this fossil. The deposit holds both aquatic and terrestrial taxa (Prokop & Nel, 2010) as well as fossilized remnants of vegetation possibly over 20 m in height (see Opluštil *et al.*, 2009). The presence of long legs with possibly multiple tarsal segmentation and large protruding eyes rather suggests that *C. kukalovae* had an arboreal, climbing lifestyle combined with diurnal activity.

Thoracic paranota may have aided in gliding manoeuvres to quickly change location or to escape predators in the canopy by controlled fall. Controlled aerial descent is a phenomenon much more widespread than previously known (Dudley & Yanoviak, 2011; Jusufi *et al.*, 2011). The latter requires an aerial righting reflex, which was probably adopted from a ubiquitous terrestrial righting reflex in insects (Dudley & Yanoviak, 2011; Jusufi *et al.*, 2011). Additionally, long antennae and tail filaments may have been useful as steering and control device during gliding in proto-ptyergotes (Hasenfuss, 2008). Ablation experiments in extant gliding archaeognaths also support this view (Yanoviak *et al.*, 2009). As demonstrated by Dudley & Yanoviak (2011), an arboreal lifestyle followed by the evolution of aerodynamic control of falling was the first step preceding powered flight. It comprises aerial righting and landing reflexes, parachuting, passive gliding and active flapping flight.

Thoracic paranota in *C. kukalovae* seem to be relatively small for effective gliding, but they are laterally more expanded than in any known apterygote insect. Recent arboreal bristletails exhibit considerable gliding capabilities even with less pronounced paranota (Yanoviak *et al.*, 2009). To control aerial descent, *C. kukalovae* could also use its abdominal paraterga, long legs and caudal filaments. The large size of *C. kukalovae* (10 cm) facilitates gliding and/or parachuting with such primordial paranotal airfoils, because according to Wootton & Ellington (1991), small and minimally movable paranota are aerodynamically much more efficient in larger sized insects. The relatively short and wide shape of paranota and paraterga is congruent with the best gliding efficiency according to the experiments made by Hasenfuss (2002) with thysanuroid models.

According to Rasnitsyn (2002b), who assumed short legs in proto-ptyergote gliders, long thoracic legs should be an obstacle

for 'pro-flight'. However, Hasenfuss (2002) found long legs to be useful for increasing drag in free fall, but forming an obstacle for gliding. Therefore, we suggest that *C. kukalovae* was a climbing insect that rather used a combination of drag (parachuting effect) and lift (gliding effect) to move to the ground or another plant at relatively steep angles. Long legs would give it several advantages: they facilitate comfortable climbing for instance along trunks of species of *Cordaites* or *Lepidodendron* that dominated the arboreal vegetation in the Carboniferous (Opluštil *et al.*, 2009). Upon landing within vegetation after an aerial descent, long outstretched legs would be able to grab vegetation and prevent the insect falling to the ground. Even when landing on the ground, long legs could work as shock absorbers minimizing damage.

The earliest fossil record of insects with fully developed wings in the lowermost Pennsylvanian and the absence of any putative proto-ptyergotes among Lower Devonian fossil arthropod assemblages imply that flying insects probably evolved between the Late Devonian and Early Carboniferous (Bradley *et al.*, 2009). Rasnitsyn (2002b, p. 82, fig. 72) and Grimaldi & Engel (2005, p. 159, fig. 6.2.a) each illustrated a hypothetical precursor of pterygote insects gliding from the vegetation using paranotal appendages. As already mentioned above, these theoretically reconstructed ancestors of pterygotes indeed show considerable similarity with *C. kukalovae*. The recent discovery of extant gliding bristletails (Dudley & Yanoviak, 2011) makes scenarios for the evolution of insect flight as the one suggested above even more likely. Proto-ptyergotes probably had an arboreal way of life and used gliding to escape from predators, which were already abundant in the Devonian and Carboniferous (Shear & Kukalová-Peck, 1990). Such an arboreal lifestyle agrees with palaeobotanical evidence, which documents the existence of complex arboreal ecosystems since the mid-Devonian (Stein *et al.*, 2012). Therefore, the evolution of arboreal proto-ptyergotes using paranotal appendages for gliding has to be considered as the most plausible explanation based on the available evidence.

Conclusions

Based on the reinvestigation of the type material of *Carbotriplura kukalovae*, we correct errors and over-interpretations in the original description of Kukalová-Peck (1985). We suggest the attribution of *C. kukalovae* to a separate apterygote order Carbotriplurida that is considered as sister group to Pterygota.

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References

- Bechly, G. & Stockar, R. (2011) The first Mesozoic record of the extinct apterygote insect genus *Dasyleptus* (Insecta: Archaeognatha: Monura: Dasyleptidae) from the Triassic of Monte San Giorgio (Switzerland). *Palaeodiversity*, **4**, 23–37.
- Béthoux, O. & Briggs, D.E.G. (2008) How *Gerarus* lost its head: stem-group Orthoptera and Paraneoptera revisited. *Systematic Entomology*, **33**, 529–547.
- Bitsch, J. (1973) Morphologie abdominale des machilides (Insecta Thysanura). I. – Squelette et musculature des segments pré-génitaux. *Annales des Sciences Naturelles Zoologie et Biologie Animale*, **12**, 173–200.
- Bitsch, J. (2012) The controversial origin of the abdominal appendage-like processes in immature insects: are they true segmental appendages or secondary outgrowths? (Arthropoda Hexapoda). *Journal of Morphology*, **273**, 919–931.
- Bitsch, J. & Nel, A. (1999) Morphology and classification of the extinct Archaeognatha and related taxa (Hexapoda). *Annales de la Société Entomologique de France*, **35**, 17–29.
- Börner, C. (1904) Zur Systematik der Hexapoden. *Zoologischer Anzeiger*, **27**, 511–533.
- Bradley, T.J., Briscoe, A.D., Brady, S.G. *et al.* (2009) Episodes in insect evolution. *Integrative and Comparative Biology*, **49**, 590–606.
- Carpenter, F.M. (1987) Review of the extinct family Syntonopteridae (order uncertain). *Psyche*, **94**, 373–388.
- Carpenter, F.M. (1992) Order Ephemeroptera. *Treatise on Invertebrate Paleontology. Part R. The Geological Arthropoda 4, Vol. 3: Superclass Hexapoda*, pp. 19–26. Society of America and The University of Kansas, Boulder, Colorado, and Lawrence, Kansas.
- Delclòs, X., Nel, A., Azar, D., Bechly, G., Dunlop, J.A., Engel, M.S. & Heads, S.W. (2008) The enigmatic Mesozoic insect taxon Chresmodidae (Polyneoptera): new palaeobiological and phylogenetic data, with the description of a new species from the Lower Cretaceous of Brazil. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, **247**, 353–381.
- Dudley, R. & Yanoviak, S.P. (2011) Animal aloft: the origins of aerial behavior and flight. *Integrative and Comparative Biology*, **51**, 926–936.
- Garwood, R., Ross, A., Sotty, D., Chabard, D., Charbonnier, S., Sutton, M. & Withers, P.J. (2012) Tomographic reconstructions of neopterous Carboniferous insect nymphs. *PLoS One*, **7**, 1–10 (e45779).
- Grimaldi, D. & Engel, M.S. (2005) *Evolution of the Insects*. Cambridge University Press, Cambridge, U.K.
- Hasenfuss, I. (2002) A possible evolutionary pathway to insect flight starting from lepidisomatid organization. *Journal of Zoological Systematics and Evolutionary Research*, **40**, 65–81.
- Hasenfuss, I. (2008) The evolutionary pathway to insect flight: a tentative reconstruction. *Arthropod Systematics & Phylogeny*, **66**, 19–35.
- Hennig, W. (1969) *Die Stammesgeschichte der Insekten*. Waldemar Kramer, Frankfurt am Main.
- Hennig, W. (1981) *Insect Phylogeny*. Wiley, Chichester.
- Hess, J.C., Lippolt, H.J., Holub, V.M. & Pešek, J. (1985) Isotopic ages of two Westphalian C tuffs – a contribution to the Upper Carboniferous time scale. *Terra Cognita*, **5**, 236–237.
- Jusufi, A., Zeng, Y., Full, R.J. & Dudley, R. (2011) Aerial righting reflexes in flightless animals. *Integrative and Comparative Biology*, **51**, 937–943.
- Kirejtshuk, A.G. & Nel, A. (2013) Skleroptera, a new order of holometabolous insects (Insecta) from the Carboniferous. *Zoosystematica Rossica*, **22**, 247–257.
- Klass, K.-D. (2009) A critical review of current data and hypotheses on hexapod phylogeny. *Proceedings of the Arthropodan Embryological Society of Japan*, **43**, 3–22.
- Klass, K.-D. & Kristensen, N.P. (2001) The ground plan and affinities of hexapods: recent progress and open problems. *Annales de la Société Entomologique de France*, **37**, 265–298.
- Kluge, N.J. (1996) A new suborder of Thysanura for the Carboniferous insect originally described as larva of *Bojophlebia*, with comments on characters of the orders Thysanura and Ephemeroptera. *Zoosystematica Rossica*, **4**, 71–75.
- Kluge, N.J. (2004) *The Phylogenetic System of Ephemeroptera*. Kluwer Academic, Dordrecht.
- Koch, M. (2003) Towards a phylogenetic system of the Zygentoma. Proceedings of the 1st Dresden Meeting on Insect Phylogeny: “Phylogenetic Relationships within the Insect Orders” (Dresden, September 19–21, 2003), pp. 122–125. *Entomologische Abhandlungen*, **61**, 119–172.
- Kristensen, N.P. (1991) Phylogeny of extant hexapods. *The Insects of Australia*, 2nd edn, pp. 125–140. CSIRO/Melbourne University Press, Carlton.
- Kukalová-Peck, J. (1978) Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. *Journal of Morphology*, **156**, 53–126.
- 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.
- Kukalová-Peck, J. (1987) New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta). *Canadian Journal of Zoology*, **65**, 2327–2345.
- Kukalová-Peck, J. (1991) Fossil History and the Evolution of Hexapod Structures. *The Insects of Australia*, 2nd ed. pp. 141–179. CSIRO/Melbourne University Press, Carlton.
- Lipton, P. (1991) *Inference to the Best Explanation*. Routledge, New York, New York.
- Maxwell, G.R. & Benson, A. (1963) Wing pad and tergite growth of mayfly nymphs in winter. *American Midland Naturalist*, **69**, 224–230.
- Nel, A., Azar, D., Martinez-Delclòs, X. & Makhoul, E. (2004) A new Upper Cretaceous species of *Chresmoda* from Lebanon – a latest representative of Chresmodidae (Insecta: Polyneoptera inc. sed.): first record of homeotic mutations in the fossil record of insects. *European Journal of Entomology*, **101**, 145–151.
- Nel, A., Roques, P., Nel, P. *et al.* (2013) The earliest known holometabolous insecta. *Nature*, **503**, 257–261.
- Niwa, N., Akimoto-Kato, A., Niimi, T., Tojo, K., Machida, R. & Hayashi, S. (2010) Evolutionary origin of the insect wing via integration of two developmental modules. *Evolution & Development*, **12**, 168–176.
- Opluštil, S., Pšenička, J., Libertín, M., Bashforth, A.R., Šimůnek, Z., Drábková, J. & Dašková, J. (2009) A Middle Pennsylvanian

- (Bolsovian) peat-forming forest preserved in situ in volcanic ash of the Whetstone Horizon in the Radnice Basin, Czech Republic. *Review of Palaeobotany and Palynology*, **155**, 234–274.
- de Paula Paciencia, G., da Conceição Bispo, P. & Sanches Cortezzi, S. (2012) Allometric growth of two species of Ephemeroptera from Neotropical mountains streams. *Annales de Limnologie – International Journal of Limnology*, **48**, 145–150.
- Prokop, J. & Nel, A. (2010) New griffenfly, *Bohemiatus elegans* from the Late Carboniferous of western Bohemia in the Czech Republic (Odonoptera: Meganisoptera: Meganeuridae). *Annales de la Société Entomologique de France*, **46**, 183–188.
- Rasnitsyn, A.P. (2002a) 2.1. Subclass Lepismatona Latreille, 1804. The wingless insects (= Thysanura Latreille 1796, s.l.). *History of Insects* (ed. by A.P. Rasnitsyn and D.L.J. Quicke), pp. 69–74. Kluwer Academic, Dordrecht.
- Rasnitsyn, A.P. (2002b) 2.2. Subclass Scarabaeona Laicharting, 1781. The winged insects (= Pterygota Lang, 1888). *History of Insects* (ed. by A.P. Rasnitsyn and D.L.J. Quicke), pp. 75–85. Kluwer Academic, Dordrecht.
- Rasnitsyn, A.P. & Novokshonov, V.G. (1997) On the morphology of *Uralia maculata* (Insecta: Diaphanopterida) from the Early Permian (Kungurian) of Ural (Russia). *Entomologica Scandinavica*, **28**, 27–38.
- Shear, W.A. & Kukalová-Peck, J. (1990) The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Canadian Journal of Zoology*, **68**, 1807–1834.
- Sinitshenkova, N.D., Marchal-Papier, F., Grauvogel-Stamm, L. & Gall, J.-C. (2005) The Ephemeroidea (Insecta) from the Grès à Voltzia (early Middle Triassic) of the Vosges (NE France). *Paläontologische Zeitschrift*, **79**, 377–397.
- Staniczek, A.H., Bechly, G. & Godunko, R.J. (2011) Coxopteroptera, a new fossil order of Palaeoptera (Arthropoda: Insecta), with comments on the phylogeny of the stem group of mayflies (Ephemeroptera). *Insect Systematics & Evolution*, **42**, 101–138.
- Stein, W.E., Berry, C.M., VanAller Hernick, L. & Mannolini, F. (2012) Surprisingly complex community discovered in the mid-Devonian fossil forest at Gilboa. *Nature*, **483**, 78–81.
- Sturm, H. & Machida, R. (2001) Archaeognatha. *Handbook of Zoology, Vol. 4: Arthropoda: Insecta* (ed. by N.P. Kristensen and R. Beutel). Walter de Gruyter, Berlin.
- Willmann, R. (1999) The Upper Carboniferous *Lithoneura lameerei* (Insecta, Ephemeroptera?). *Paläontologische Zeitschrift*, **73**, 289–302.
- Willmann, R. (2003a) *Die phylogenetischen Beziehungen der Insecta: Offene Fragen und Probleme, Verhandlungen Westdeutscher Entomologentag 2001*. Löbbecke-Museum, Düsseldorf.
- Willmann, R. (2003b) Phylogenese und System der Insecta. *Lehrbuch der speziellen Zoologie, begründet von A. Kaestner, Band I: Wirbellose Tiere. Teil 5: Insecta*, Bd. **1/5**, 2. Auflage edn (ed. by H.H. Dathe), pp. 1–65. Spektrum Akademischer, Heidelberg.
- Wootton, R.J. (1972) Nymphs of Palaeodictyoptera (Insecta) from the Westphalian of England. *Palaeontology*, **15**, 662–675.
- Wootton, R.J. & Ellington, C.P. (1991) Biomechanics and the origin of insect flight. *Biomechanics in Evolution* (ed. by J.M.V. Rayner and R.J. Wootton), pp. 91–112. Cambridge University Press, Cambridge, U.K.
- Wygodzinsky, P. (1961) On a surviving representative of the Lepidotrichidae (Thysanura). *Annals of the Entomological Society of America*, **54**, 621–627.
- Yanoviak, S.P., Kaspari, M. & Dudley, R. (2009) Gliding hexapods and the origins of insect aerial behavior. *Biology Letters*, **5**, 510–512.
- Zhao, J., Zhao, Y., Shih, C., Ren, D. & Wang, Y. (2010) Transitional fossil earwigs – a missing link in Dermaptera evolution. *BMC Evolutionary Biology*, **10**, 1–10.

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