Coxoplectoptera, a new fossil order of Palaeoptera (Arthropoda: Insecta), with comments on the phylogeny of the stem group of mayflies (Ephemeroptera)

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Abstract

Mickoleitia longimanus gen. et sp.n. is described from the Lower Cretaceous limestone of the Crato Formation in Brazil. It is attributed to a new family Mickoleitiidae and a new fossil insect order Coxoplectoptera within the palaeopterous Ephemerida, based on the presence of an elongated costal brace. This fossil insect exhibits a very peculiar combination of derived characters like specialized forelegs with strongly elongated, free coxae, single-clawed pretarsus, and distinctly skewed pterothorax as in dragonflies. On the other hand, several plesiomorphies are present that exclude this taxon from modern Ephemeroptera, namely large hind wings with widened anal area and numerous cross veins that separate the elongate costal brace from the costal margin. Fossil larvae described by Willmann as larval Cretereismatidae are herein attributed to Mickoleitiidae fam.n., based on the shared presence of broad hind wing buds with distinctly broadened anal area, wing bud venation similar to the adult holotype, and subchelate forelegs with elongate free coxae. These larvae are also highly autapomorphic in the structure of their abdominal gills and laterally flattened body with vertically oval section that is unique within Ephemerida. On the other hand they possess plesiomorphic lateral wing pads with pronounced articulation like Palaeozoic pterygote larvae, while wing pads in modern insects are always secondarily fused to the tergum. A similar fossil larva from the Jurassic of Transbaikals was earlier described as *Mesogenesia petersae* and classified within modern mayflies. It is herein attributed to Mickoleitiidae fam.n. Coxoplectoptera are recognized as putative sister group of modern Ephemeroptera based on the shared presence of only 7 pairs of abdominal gills, while Permoplectoptera still have retained 9 pairs of gills. The phylogenetic reclassification of the mayfly stem group by Willmann is critically discussed and modified.

Introduction

The Crato Formation from the Lower Cretaceous of northeast Brazil is one of the most important localities for fossil insects. In the last years, numerous surprising fossil insects have been discovered in the Crato limestones that greatly increased our knowledge of the insect fauna of the Cretaceous period (Martill et al. 2007). Herein we describe a very interesting new group of palaeopterous insects from this locality.

There are some peculiar fossil insect larvae not uncommonly reported from the Crato Formation. These fossils are well-known among the local brick workers under the vernacular name "abacaxi" (=ananas). They were first pictured and discussed by Bechly (2001: 47–49, fig. 36). Staniczek (2003b: 39) discussed their characters and considered them as stem group representatives of mayflies. A very well preserved specimen was also figured by Grimaldi & Engel (2005: fig. 6.13) as "unusual mayfly naiad". Willmann (2007) formally described a new stem group mayfly genus *Cretereisma* and new family Cretereismatidae, based on two adult specimens hosted in the collection of the State Museum of Natural History Stuttgart (SMNS). He attributed several specimens of the above-mentioned larvae to the same genus. Bechly (2007: fig. 11.90i-j) figured the holotype of *Mickoleitia longimanus* gen. et sp.n. and already then presumed that these larvae might rather belong to the latter than to *Cretereisma*.

Tshernova (1977) described a fossil larva from the Jurassic of Transbaikals as *Mesogenesia petersae* in the mayfly family Palingeniidae. Staniczek (2003b: 39) recognized its similarity and probable affinity to the "abacaxi" larvae from the Lower Cretaceous of Brazil. It is here formally attributed to Mickoleitiidae fam.n. and Coxoplectoptera ord.n.

Materials and Methods

The morphological terminology of Ephemeroptera follows Kluge (2004), and the taxonomy and phylogeny is expanded on Kluge (2004), Willmann (2007a,b) and Ogden et al. (2009). Fossil specimens were studied using a Leica M80 stereo microscope with 1.6 Plan Achromat lens, and drawings were made with a camera lucida. Photographs of fossils were taken with a Leica DFC490 digital macro camera on a Leica Z16 Macroscope, processed with Leica Application Suite 3.1.0 software for focus stacking, and subsequently enhanced with Adobe Photoshop CS3® image processing software.

Systematics

Coxoplectoptera ord.n.

Families: Only including the family Mickoleitiidae fam.n.

Diagnosis

Same as for family Mickoleitiidae.

Etymology

Name refers to the elongated coxae and the old ordinal name for mayflies, Plectoptera (not to be confused with Plecoptera).

Comment

According to Hennig (1966) the only objective criterion for the designation of hierarchical taxonomic ranks could be the age of origin of a taxon. Consequently sister groups always must have the same rank. A unique set of larval and imaginal autapomorphies, and the phylogenetic position as sister group of the order Ephemeroptera, justifies the erection of Coxoplectoptera as separate new insect order.

Mickoleitiidae fam.n.

Type genus

Mickoleitia gen.n. by present original designation.

Other Genera
Mesogenesia Tshernova, 1977, a fossil larva from the Jurassic of Transbaikalia.

Diagnosis

This family is distinguished by the following combination of characters:

Imagines: head with large compound eyes; skewed pterothorax with distinctly oblique interpleural sutures (convergence to Odonatoptera); forelegs with elongate, free coxae and a subchelate telopodite (autapomorphy); pretarsi each single-clawed (autapomorphy); wing venation with intercalary veins (incl. IR1 and IR2) (synapomorphy with Odonatoptera and Panephemeroptera within Hydropalaeoptera); wing venation with curved costal brace that crosses ScP (synapomorphy with Ephemeroptera); costal brace elongate, not arcular, and not fused with costal margin but connected to costal margin by several cross veins (symplesiomorphy with Permoplectoptera incl. Cretereismatidae); vein MA not curved towards RP (plesiomorphy that excludes a position within Syntonopteroidea); hind wing with widened cubito-anal area; abdominal structures not preserved, but probably the adults had three terminal filaments like Permoplectoptera and Ephemeroptera.

Larvae: body subcylindrical, taller than wide and laterally flattened, with vertically oval body section, which is unique within Ephemerida. This autapomorphic "gammarid"-like habitus is clearly not an artefact of preservation, because the fossil insects of the Crato Formation are generally preserved three-dimensionally without diagenetic compression. Furthermore, one specimen is preserved in dorsal view (Fig. 26). Head with frontomedial triangular process between compound eyes (autapomorphy); antennae very long (plesiomorphy); pronotum strongly sclerotized and with rugose pilosities;

legs with enlarged, free coxae; forelegs usually held in a subchelate position; femur-tibia joint of fore- and mid legs directed anteriorly, femur-tibia joint of hind legs directed posteriorly (opposite posture of mid and hind legs, autapomorphy), pretarsi each with single claw (synapomorphy with Ephemeroptera); lateral wing pads with pronounced articulation (symplesiomorphy with Permoplectoptera); hind wing pads with distinctly bulged posterobasal margin, suggesting a widened anal area of the adult wing (symplesiomorphy with Syntonopteroidea); seven pairs of abdominal gills (synapomorphy with Ephemeroptera) that are developed as elongate, lobe-like structures directed ventrally (autapomorphy); three caudal filaments (plesiomorphy) that are curled upwards.

Mickoleitia gen.n.

Type species

Mickoleitia longimanus gen. et sp.n. by present original designation.

Diagnosis

See diagnosis of family. The putative larvae are distinguished from *Mesogenesia* by the elongate and slender forefemur, compared to the distinctly broadened forefemur with dense inner setation (Kluge 2004: 365) of *Mesogenesia*. Furthermore, the larvae differ in the setation of terminal filaments (paracercus and cerci each with a dense row of setae on both sides in *Mickoleitia*, but in *Mesogenesia* cerci only with setae on inner sides), and in the structure of tarsal claws (simple in *Mickoleitia*, with tooth in *Mesogenesia*). The shape of abdominal gills may also be different in the two genera (elongate lobes in *Mickoleitia*, ovoid plates with strong costae in *Mesogenesia* according to its original description, but according to Kluge (pers. commun. 2011) not sufficiently preserved to draw any conclusion at all).

Etymology

Named in honour of German entomologist Dr Gerhard Mickoleit (Eberhard-Karls-Universität Tübingen), who was among the first proponents of Willi Hennig's Phylogenetic Systematics, and as a university teacher shaped numerous German biologists, including AHS and GB.

Remark

A putative second species of the same genus is represented by a specimen (Fig. 1) in the private collection of Mr Masayuki Murata in Kyoto, Japan. It shares the elongate free forecoxa, the rear position of the wings, the primitive type of costal brace and the broad hind wings with *Mickoleitia longimanus* sp.n., but is only of about half the size (hind wing length, 14.7 mm). We refrain from formally describing and naming this new species because the only known specimen is not deposited in a public museum collection.
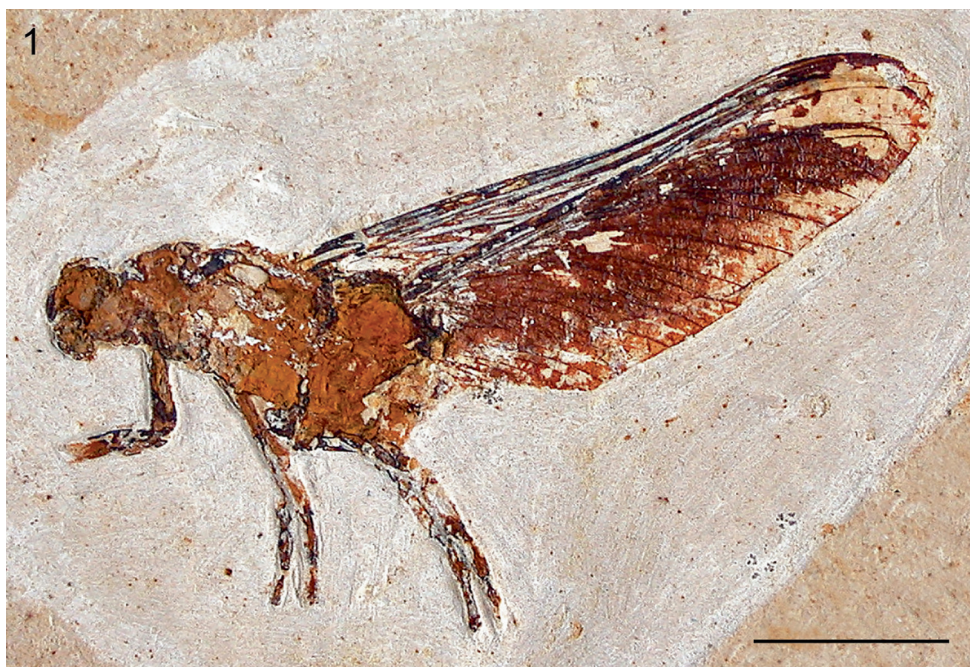
Fig. 1. *Mickoleitia* sp., specimen without number in coll. Masayuki Murata, Kyoto, Japan. Unnamed smaller species. Scale bar=5 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

Mickoleitia longimanus **sp.n. (Figs 2–13)**

2007 undescribed stemgroup mayfly (Bechly, p. 392, fig. 11.90i-j).

*Diagnosis*

See diagnosis of family and genus.

Etymology

The species epithet *longimanus* (Latin for long hand) is treated as noun in apposition, referring to the elongate forelegs.

Description

Holotype. Adult winged insect embedded in lateral position on the same plate with a juvenile fish of the genus *Dastilbe* (Teleostei: Chanidae). For measurements see Table 1. *Head* (Figs 6 and 7) well sclerotized, with pronounced vertex, but reduced gena, as prominent lateral eyes cover most of the lateral and ventrolateral area of head. Labial palps with 3 segments; first segment longest, second segment shorter and thickest, third segment spoon-like. Antennae and other mouth parts not preserved or not clearly distinguishable. Thorax with all three thoracic segments skewed so that ventral parts of
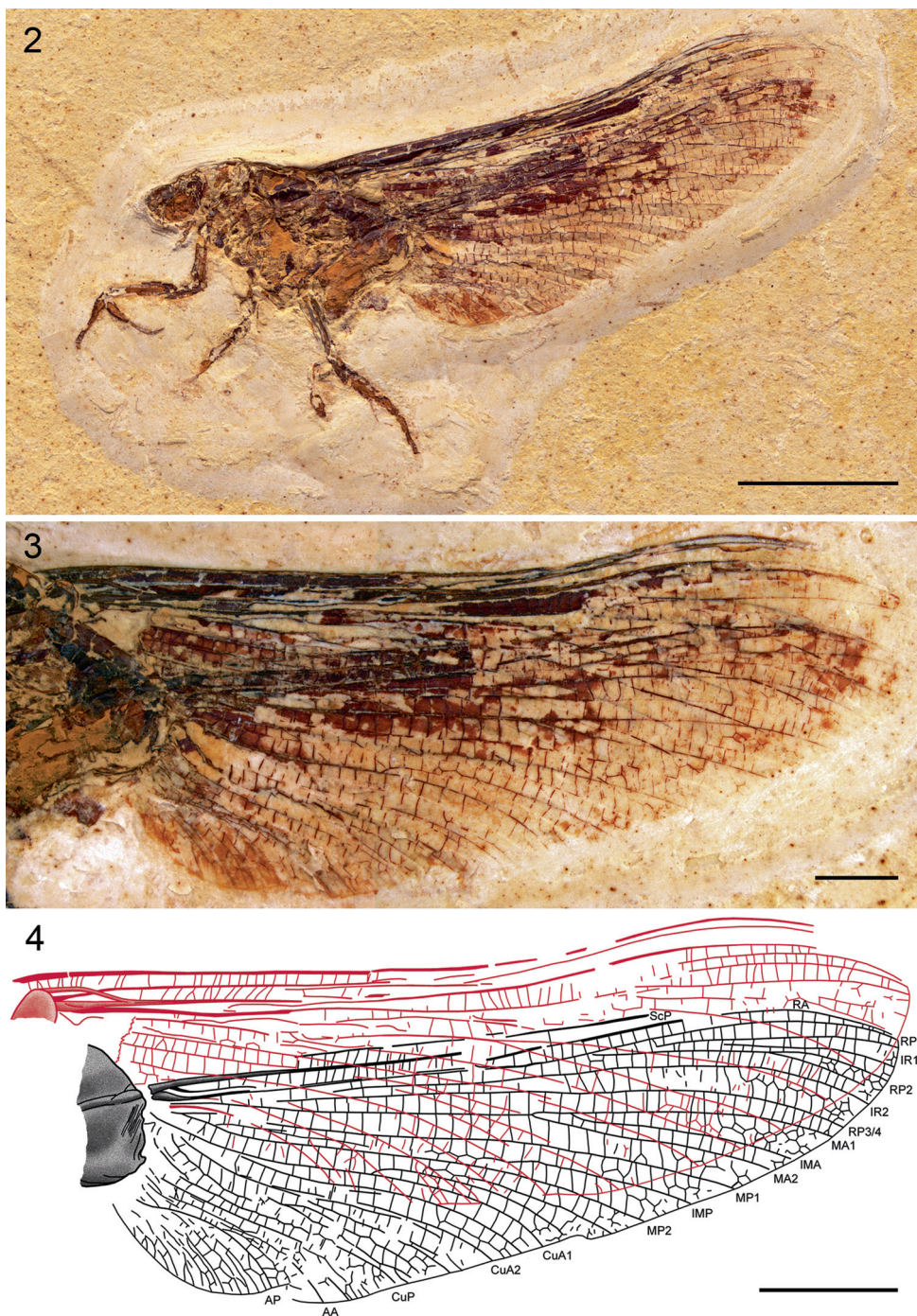
Figs 2–4. *Mickoleitia longimanus* sp.n., holotype SMNS 66550. (2) Lateral view, scale bar=10 mm; (3) wings (photographed with alcohol cover), scale bar=3 mm; (4) wing venation (red: forewing, black: hind wing), scale bar=5 mm.
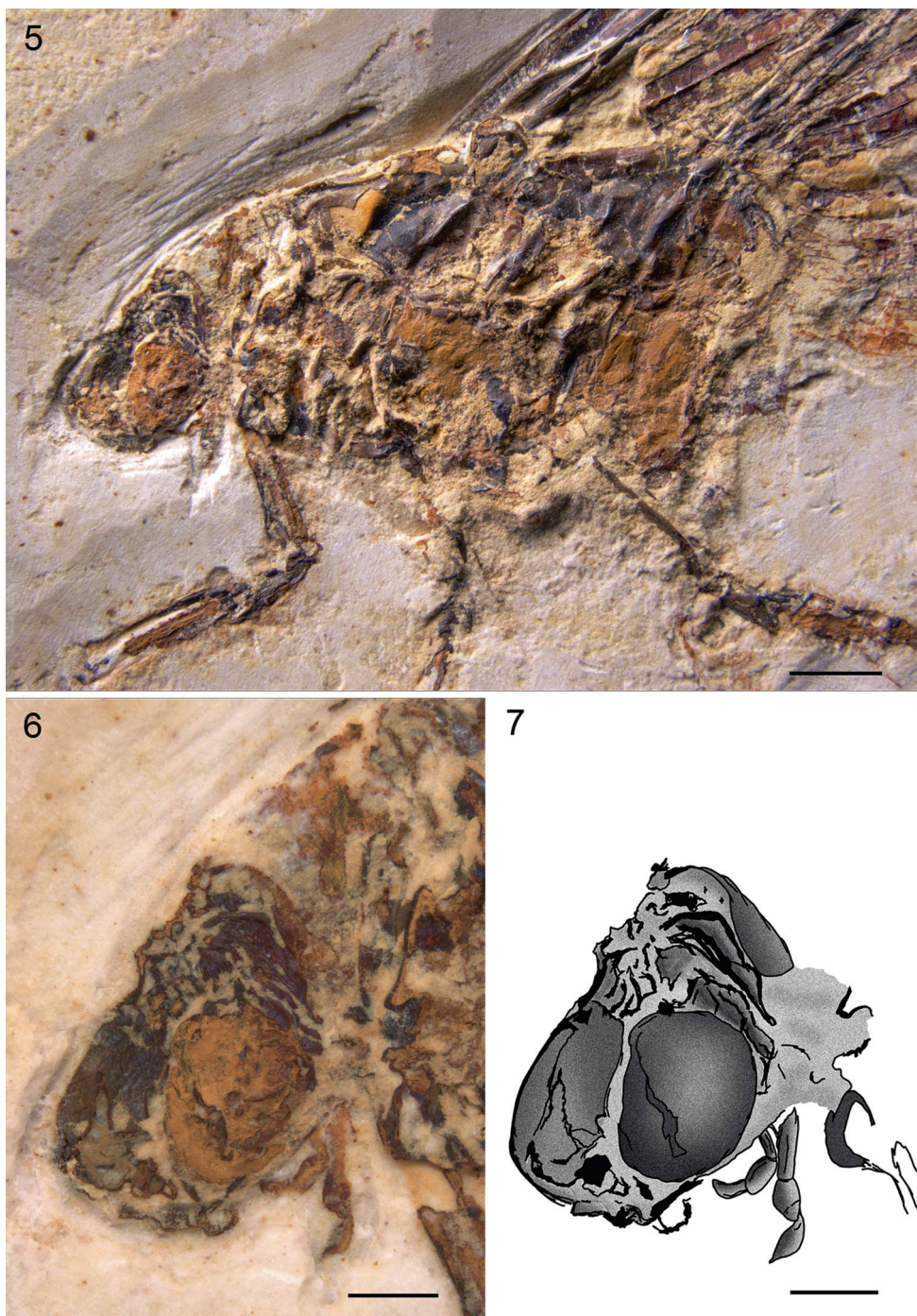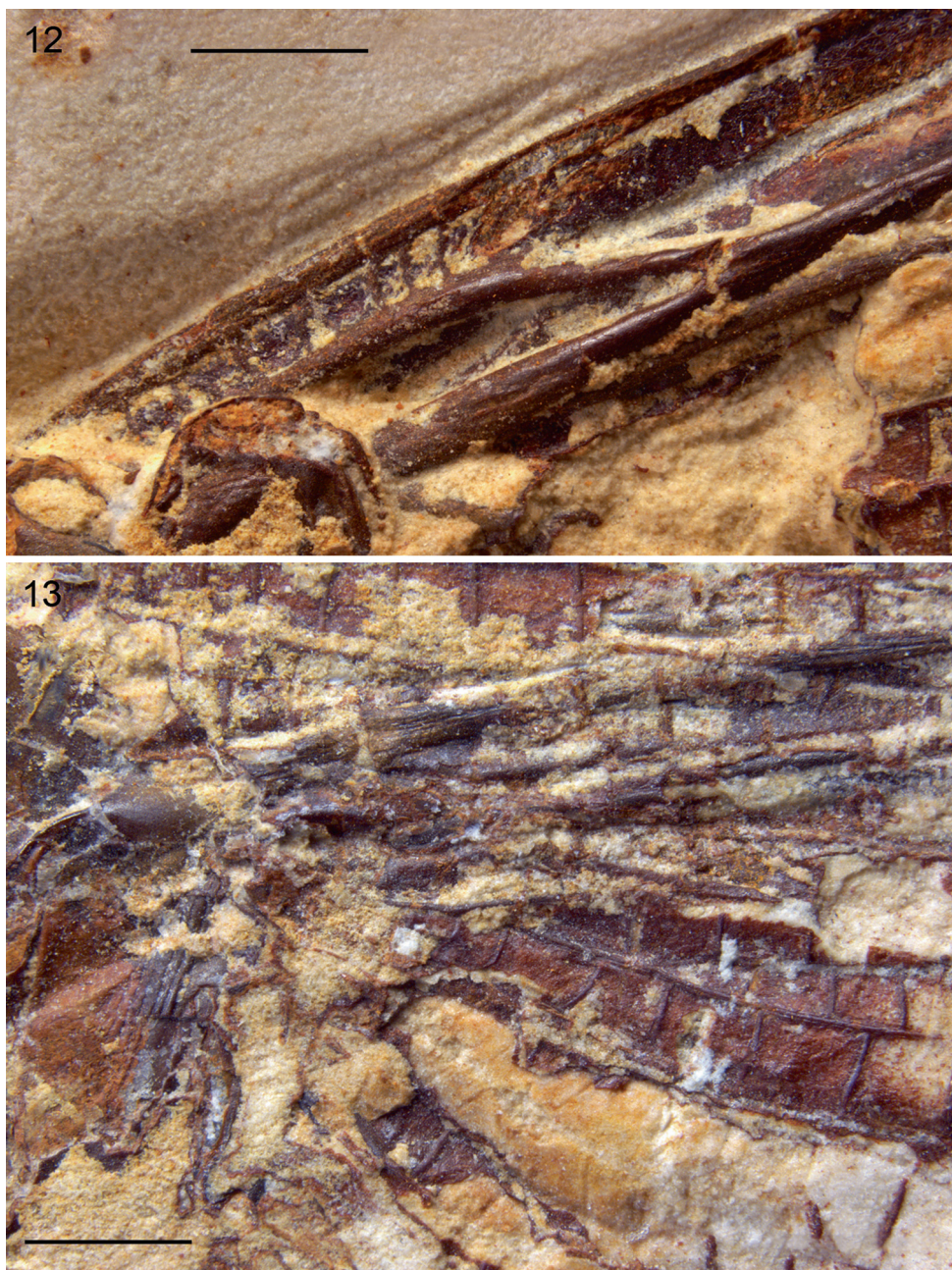
Figs 5–7. *Mickoleitia longimanus* sp.n., holotype SMNS 66550. (5) Head and thorax, scale bar=2 mm; (6) head (photographed with alcohol cover), scale bar=1 mm; (7) head, scale bar=1 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise
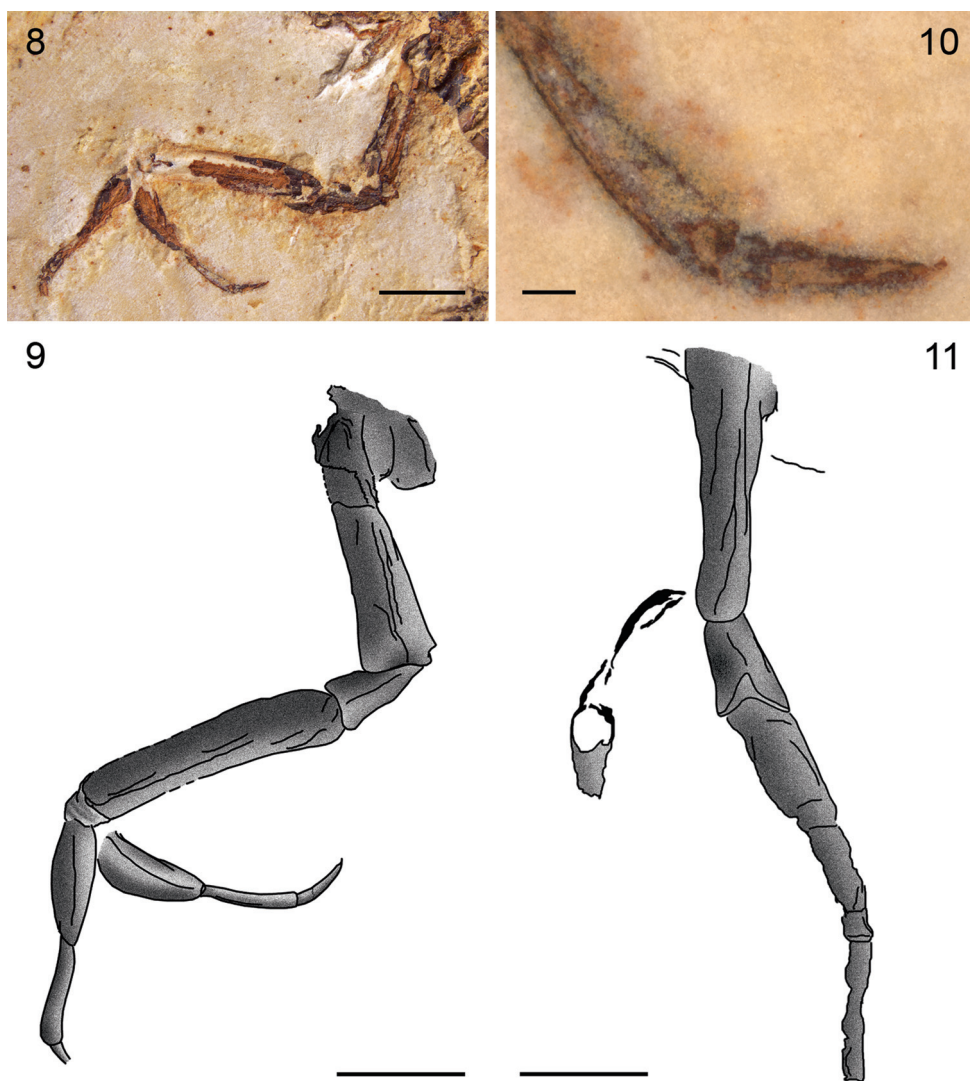
Figs 8–11. *Mickoleitia longimanus* sp.n., holotype SMNS 66550. (8) Forelegs, scale bar=2 mm; (9) forelegs, scale bar=2 mm; (10) foreleg claw, scale bar=0.2 mm; (11) hind legs, scale bar=2 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

thorax are further brought forward (as in dragonflies). Legs (Figs 8–10) long and slender, forelegs held in subchelate position with femur and tibia strongly bent to each other, coxa free, slender, and extremely elongated, almost as long as femur, trochanter short, tibia thicker and shorter than femur, distally tapering, tarsus slender, not segmented, pretarsus with long, slender claw, leg proportions of preserved mid- and hind leg segments similar to proportions in foreleg. Wings apparently held vertically above the abdomen in "palaeopterous" wing position and mostly superimposed. Corrugation of longitudinal veins reveals that only the anterobasal part of right forewing and basal fourth of left hind wing are visible, while distally parts of left forewing and right hind

Figs 12–13. *Mickoleitia longimanus* sp.n., holotype SMNS 66550. (12) Right forewing, costal brace, scale bar=1 mm; (13) hind wing base, scale bar=1 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

Table 1. Measurements of *Mickoleitia longimanus* sp.n. (holotype)

Measurement	(mm)
Length of head	3.56
Height of head	2.45
Length of labial (?) palp	1.60
Length of thorax	11.20
Height of thorax	7.45
Length of right forewing	28.95
Length of left hind wing	28.05
Width of left hind wing	8.50
Length of costal brace, right forewing	3.50
Length of left foreleg	14.03
Length of forecoxa	3.94
Length of foretrochanter	1.57
Length of forefemur	4.17
Length of foretibia	2.08
Length of foretarsus	1.61
Length of foreclaw	0.66
Length of mid coxa	3.24
Length of mid trochanter	1.41
Length of mid femur*	3.04
Length of hind coxa	3.76
Length of hind trochanter	1.57
Length of hind femur	4.02
Length of hind tibia	2.59

*Preserved part.

wing are superimposed. Wing venation in some parts is obviously abraded and hard to distinguish. Forewings: right forewing with elongate costal brace that is well separated from costa by ten cross veins. Subcosta (ScP) apparently not shortened and reaching wing apex, costal and subcostal field basally with numerous cross veins, distally cross veins obviously abraded. Radius anterior (RA) not branched. Radius posterior (RP) and Media anterior (MA) branched, remaining veins in forewing difficult to distinguish due to superposition. Hind wings: costa (C) and basal part of left hind wing not preserved, only short medial part of ScP preserved of wing. RA not branched. RP branched, with long intercalary veins (IR) distally. MA branched at two thirds of wing length, long intercalary vein (IMA) basally attached to MA1. Media posterior basally branched, long intercalary vein (IMP) basally attached to MP2. Two intercalary veins present between MP2 and Cubitus anterior (CuA). CuA branched into CuA1 and CuA2 with an intercalary vein inbetween; Cubitus posterior (CuP) apparently not branched. Anal area strongly developed with numerous anal veins (AA, AP). Abdomen not preserved.

Type material

Holotype SMNS 66550 (old no. I81) is deposited in the collection of the Staatliches Museum für Naturkunde Stuttgart, Germany. Type locality: Chapada do Araripe,

vicinity of Nova Olinda, southern Céara, northeast Brazil. Type stratum and age: Lower Cretaceous, Late Aptian, Nova Olinda Member of the Crato Formation (Martill & Heimhofer, 2007).

Description of the putative larvae of Mickoleitia (Figs 14–39)

Willmann (2007a) already provided a description of these larvae, mainly based on specimen no. SMNS 66673, which is here only briefly amended. Body length varies from 10 mm (smallest specimen no. SMNS 66605) to 32 mm (largest specimen no. SMNS 66673); of the 21 specimens studied, 6 are preserved in a dorsally bent posture (specimen nos 66548, 66549, 66599 and 66547 in coll. SMNS, and without no. in coll. SMF and coll. Murata), and only one specimen is preserved in dorsal aspect (specimen no. Z78 in coll. Pohl/WDC).

Entire larva heavily sclerotized. Head: vertex forming elevated plate bordered by prominent dorsolateral crests above eyes, frons with large, shovel-like medial projection (Figs 16 and 27), smaller medial projection also present on clypeus. Antenna: scape 3-times thicker than antennal flagellum, inserting lateral of frontal beak, pedicel 2-times thicker than flagellum, long, filiform flagellum with numerous segments, longer than length of head and thoracic segments together, often embedded in vertical position with distal end curled backwards. Mouthparts: labrum not clearly preserved or identifiable; the structure in Figs 27 and 28 might also be a mandibular mola rather than a labrum. Mandibles (Fig. 28) obviously each with rounded, long tusk produding anteriorly and crossing each other (similar to condition in larval Ephemeridae). Maxilla and hypopharynx not clearly visible. Labium (Fig. 28) elongated, with long post- and prementum (resembling the condition in larvae of Odonata). Thorax: prothorax with pronotum laterally extending to pleurae, covered with rugose pilosities, Legs: Femur-tibia joint of fore- and mid legs directed anteriorly, femur-tibia joint of hind legs directed posteriorly (opposite posture of mid and hind legs); forelegs held in subchelate position, same proportions of foreleg segments as in adults, coxae of forelegs free, slender, extremely elongated, coxae of mid- and hind legs elongated and extremely thickened, remaining leg segments of mid and hind legs thickened, but also shortened. Hind tibia with strong basal spur (Figs 29 and 33). All legs with unsegmented tarsus, pretarsus with single claw. Leg segments with extended patches of dense setal pores. Wing pads (visible in specimen nos SMNS 66547, 66549, 66603, 66673 and specimen no. 512 in coll. Murata) with pronounced articulation and flexion line, directed posterolaterad, in some specimens the convex longitudinal veins are visible (RA, IR1, IR2, IMP, and AA unbranched, MA and CuA branched); hind wing pad with distinctly bulged posterobasal margin (Figs 34 and 35). Abdomen heavily sclerotized, rugose, with 10 segments divided into tergal and sternal plates that are not fused to continuous abdominal rings (plesiomorphy), contrary to modern Ephemeroptera; large areas of terga and sterna with dense setal pore fields, first seven segments each with pair of lateral gills, gills inserting dorsolaterally at ventral border of abdominal tergites (if a bulged tergal margin is presupposed) or even on abdominal tergites (if a straight tergal margin is presupposed) (Figs 18 and 37), and directed ventrally; basal half of gill widened and strongly sclerotized, with pronounced dorsoventral fold; apical
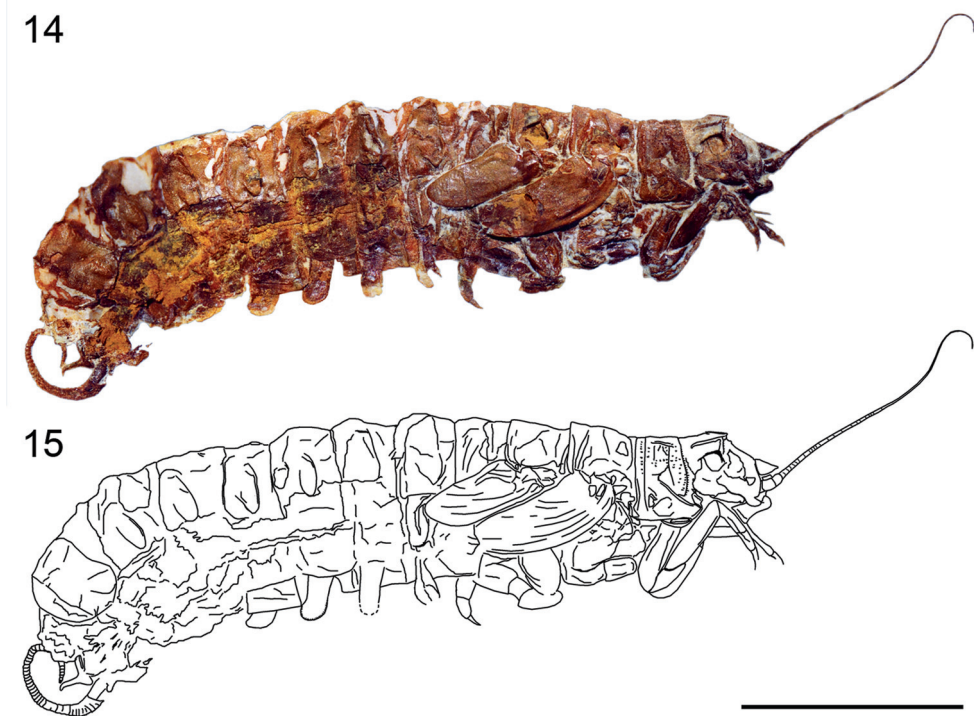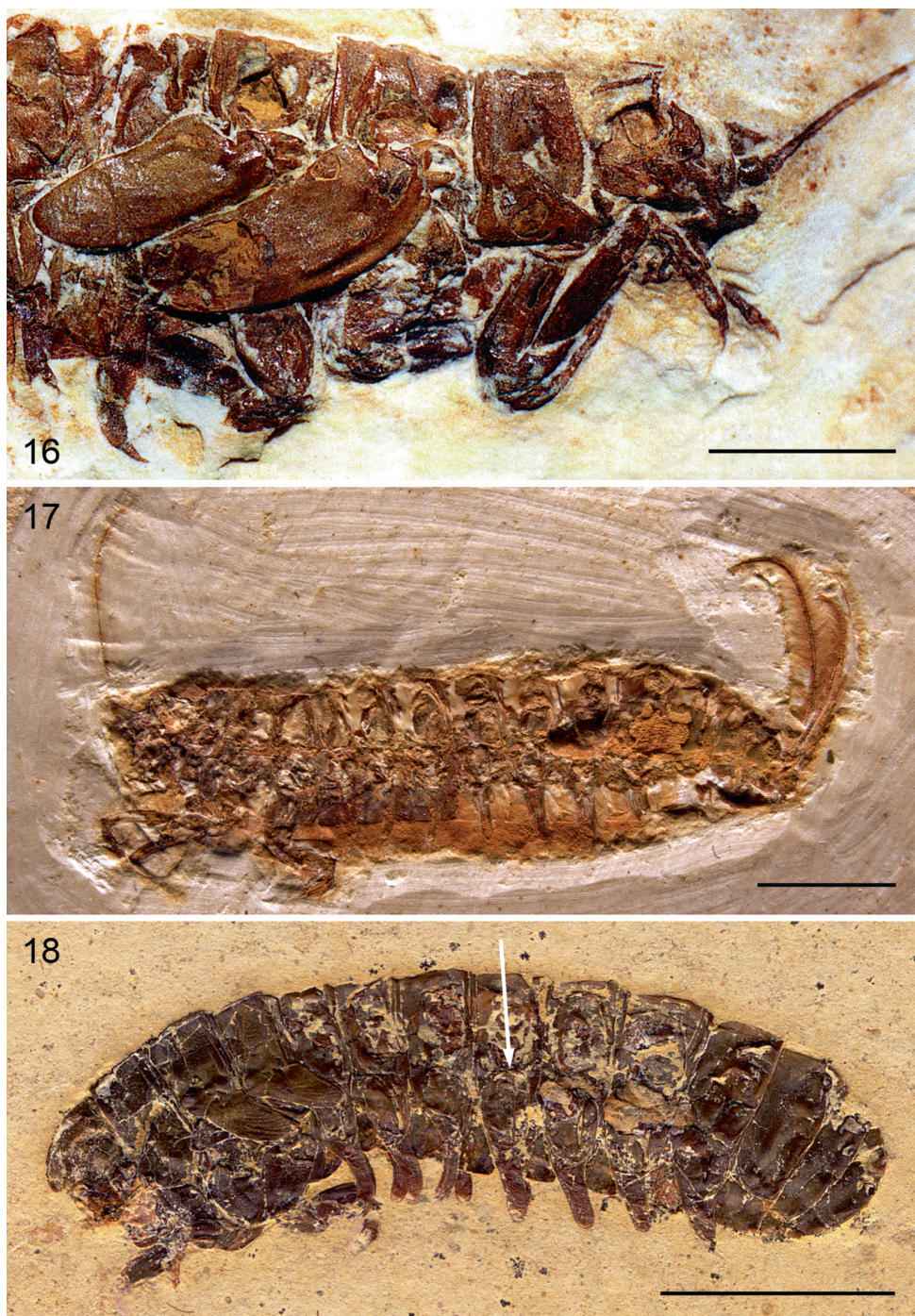
Figs 14–15. *Mickoleitia* sp., larva, no. 512 coll. Murata (note that only abdominal gills of left side are preserved). (14) Fossil digitally cut out, scale bar=5 mm; (15) drawing, scale bar=5 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

half thinner, styliform, and much weaker sclerotized than remaining body, with slightly thickened and annulated cord-like margins. Terminal appendages: lateral pair of cerci and a medial paracercus present and developed as filaments, usually preserved in upright position, apical half bent anteriorly. Paracercus slightly shorter than cerci and equipped with a dense row of long setae on each lateral side, cerci longer and equipped with a dense row of long setae on lateral and medial side (Figs 26 and 39).
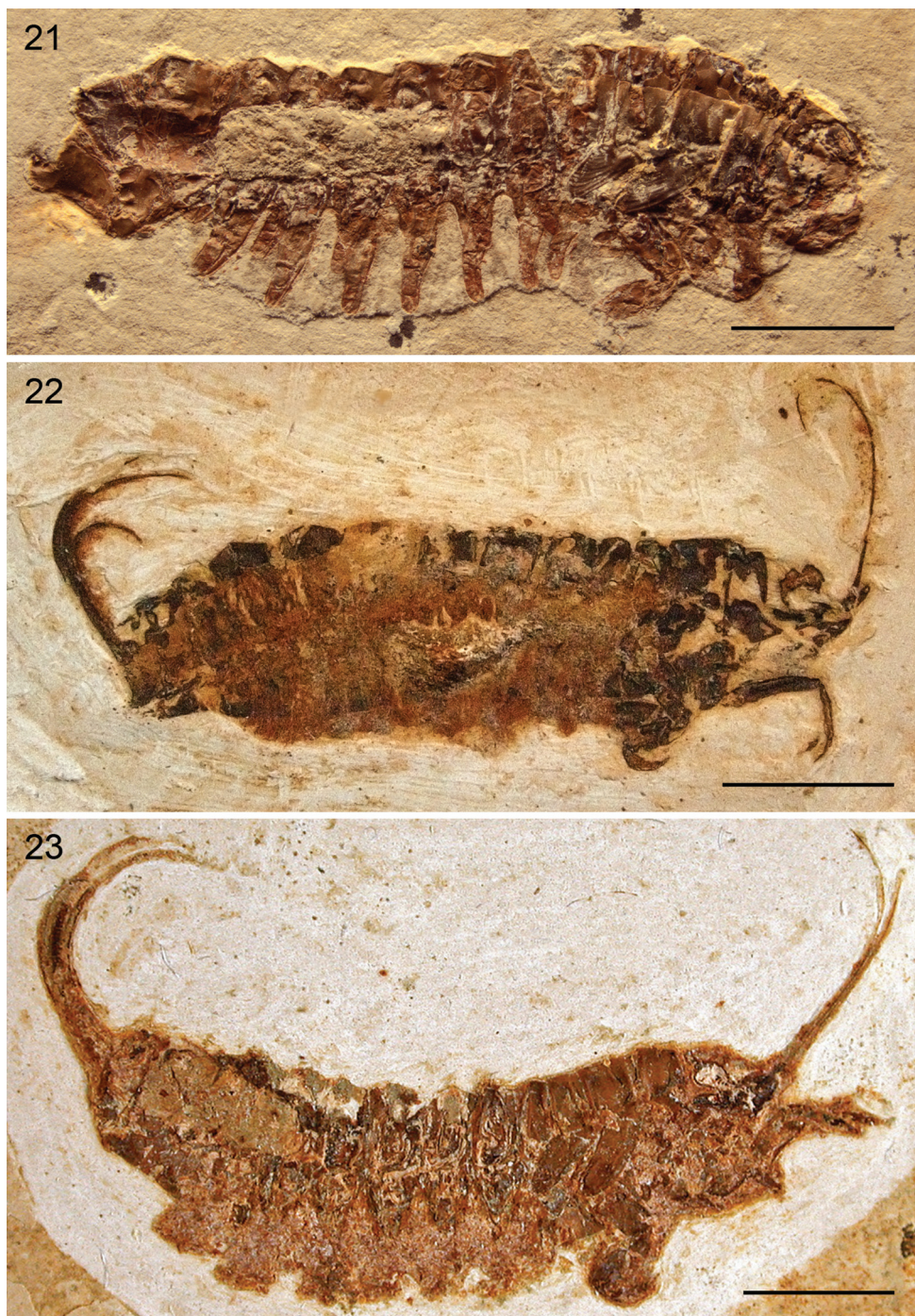
Specimens

Twelve specimens, nos SMNS 66547, 66548 (L74), 66599, 66600, 66601, 66602 (H54), 66603, 66604 (H52), 66605, 66673, 66674 and 66675, deposited in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS) in Germany; contrary to Willmann (2007a: 160) specimen SMNS 66549 is not a larva of the same taxon, but a setous larva with comb-like spines on mouth parts and tarsi, the latter apparently with double claws; specimen no. MB.I.2028 at the Museum für Naturkunde (MNB, Berlin, Germany); two specimens with unknown collection number (one with old no. Q23) at Naturmuseum Senckenberg (SMF, Frankfurt am Main, Germany); specimen of unknown collection number at American Museum of Natural History (AMNH, New York, NY, USA); three specimens nos 43, Z13 and /78 in coll.

Figs 16–18. *Mickoleitia* sp., larva. (16) no. 512 coll. Murata, head, legs, and wing pads, scale bar=2 mm. (17) Specimen SMNS 66604, scale bar=5 mm; (18) specimen SMNS 66673, arrow points to the tergal origin of the abdominal gills, scale bar=10 mm.
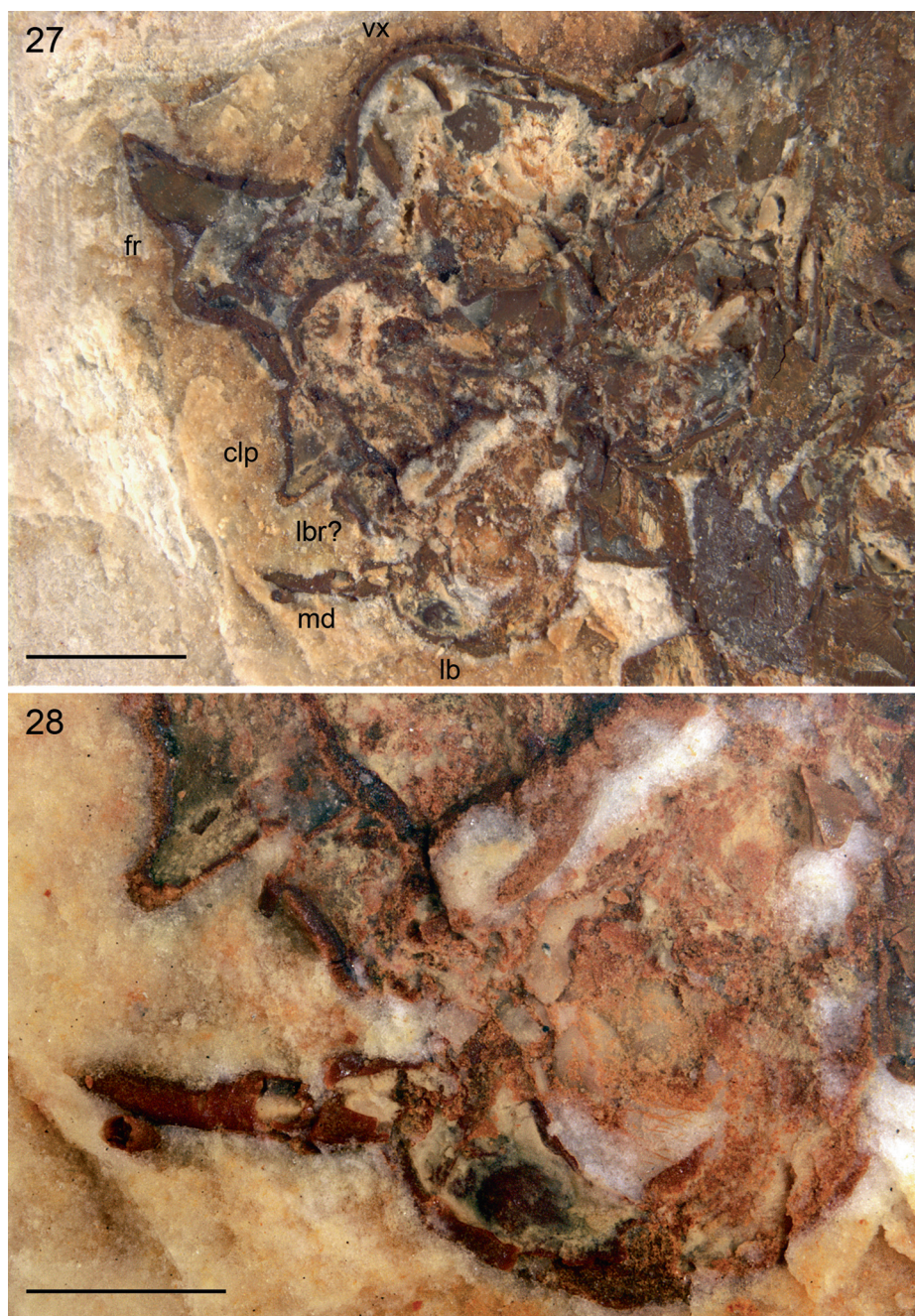
Figs 19–20. *Mickoleitia* sp., larva. (19) Specimen SMNS 66599, (photographed with alcohol cover), scale bar=2 mm; (20) specimen SMNS 66547, scale bar=5 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise
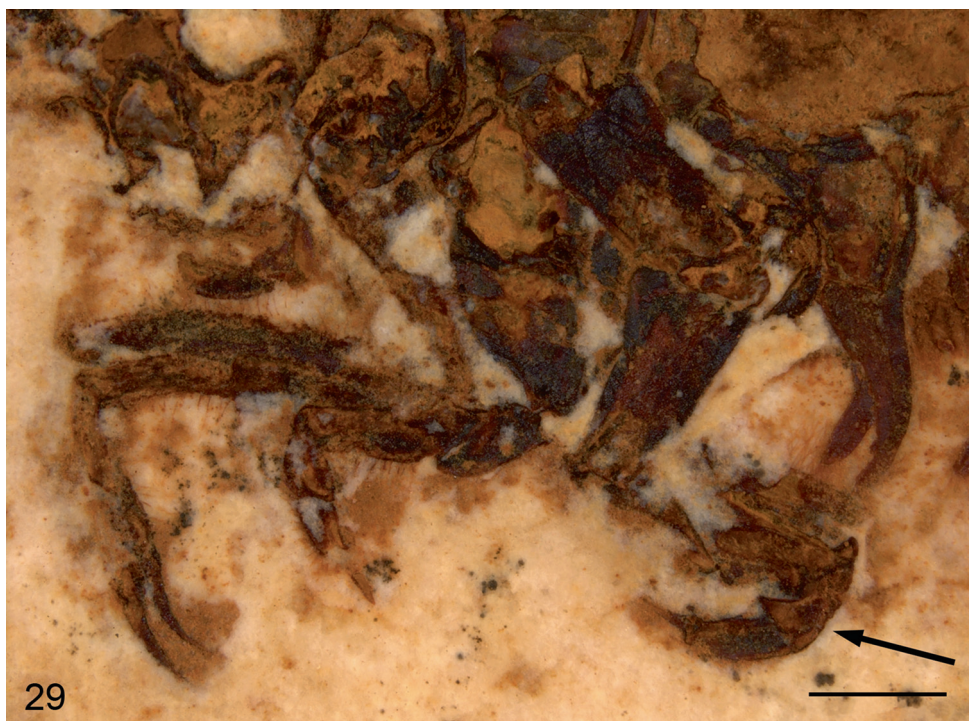
Figs 21–23. *Mickoleitia* sp., larva. (21) Specimen SMNS 66603, scale bar=5 mm; (22) specimen MB.I.2028 at MNB, scale bar=5 mm; (23) specimen without number in coll. Murata, scale bar=5 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise
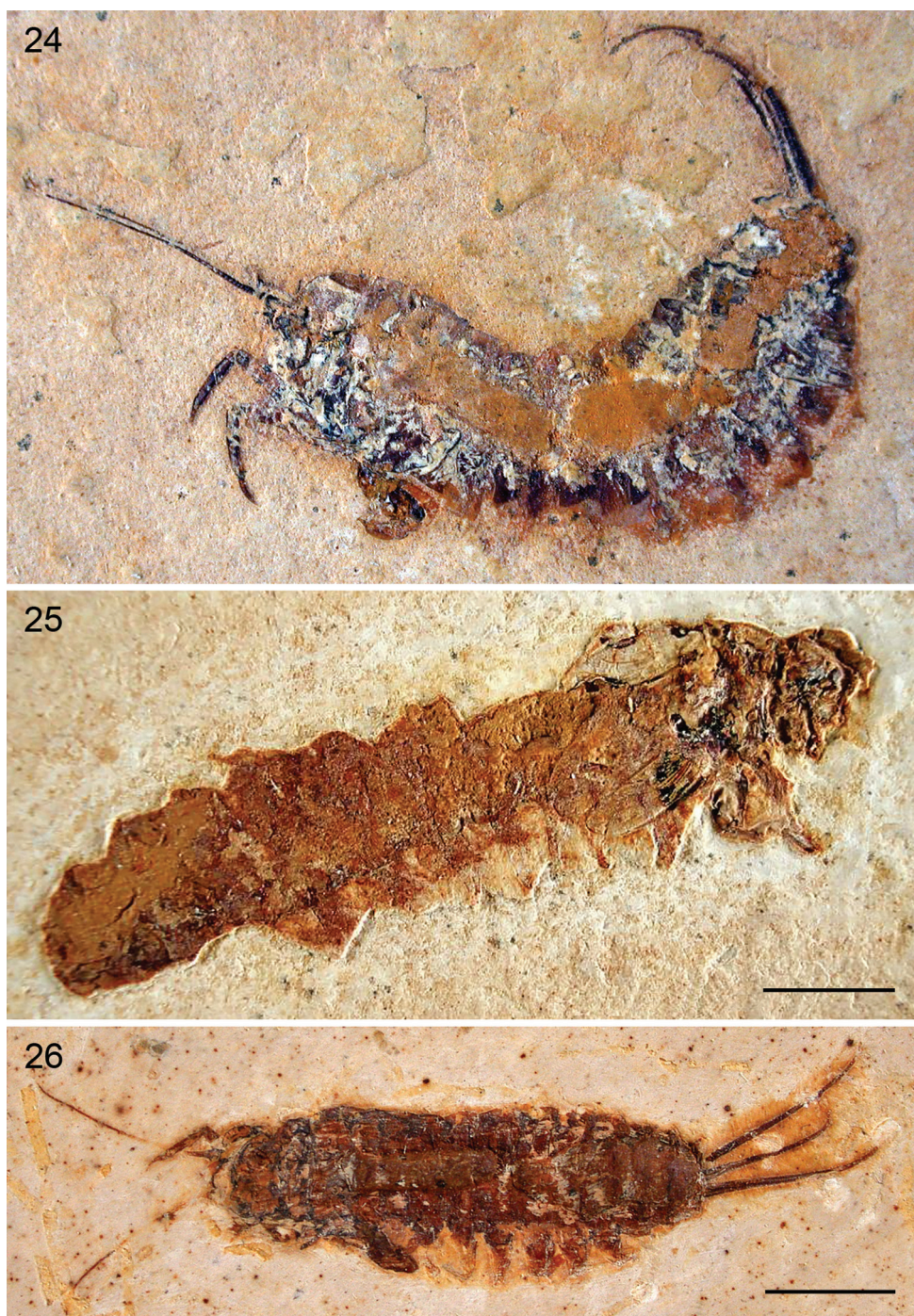
Figs 24–26. *Mickoleitia* sp., larva. (24) Specimen no. Q23 at SMF, without scale; (25) specimen no. 47 coll. Pohl WDC, large specimen with large wing pads with venation, scale bar=5 mm; (26) specimen no. Z78 coll. Pohl WDC, specimen in dorsal view, scale bar=5 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

Figs 27–28. *Mickoleitia* sp., larva, specimen SMNS 66604. (27) "Cross-section" through head with eye bulge, frontal and clypeal beak, mandibular tusks and labium; vx=vertex, fr=frons, clp=clypeus, lbr?=labrum or mandibular mola, md=mandibular tusks, lb=labium, scale bar=1 mm; (28) mouthparts with crossed mandibular tusks and dredger-bucket-like labium (photographed with alcohol cover), scale bar=0.5 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

Figs 29–30. *Mickoleitia* sp., larva. (29) Specimen SMNS 66599, fore-, middle and hind legs with strong tibial spur (photographed with alcohol cover), scale bar=1 mm; (30) specimen SMNS 66673, middle and hind legs, wing pad and first abdominal gill, scale bar=1 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise
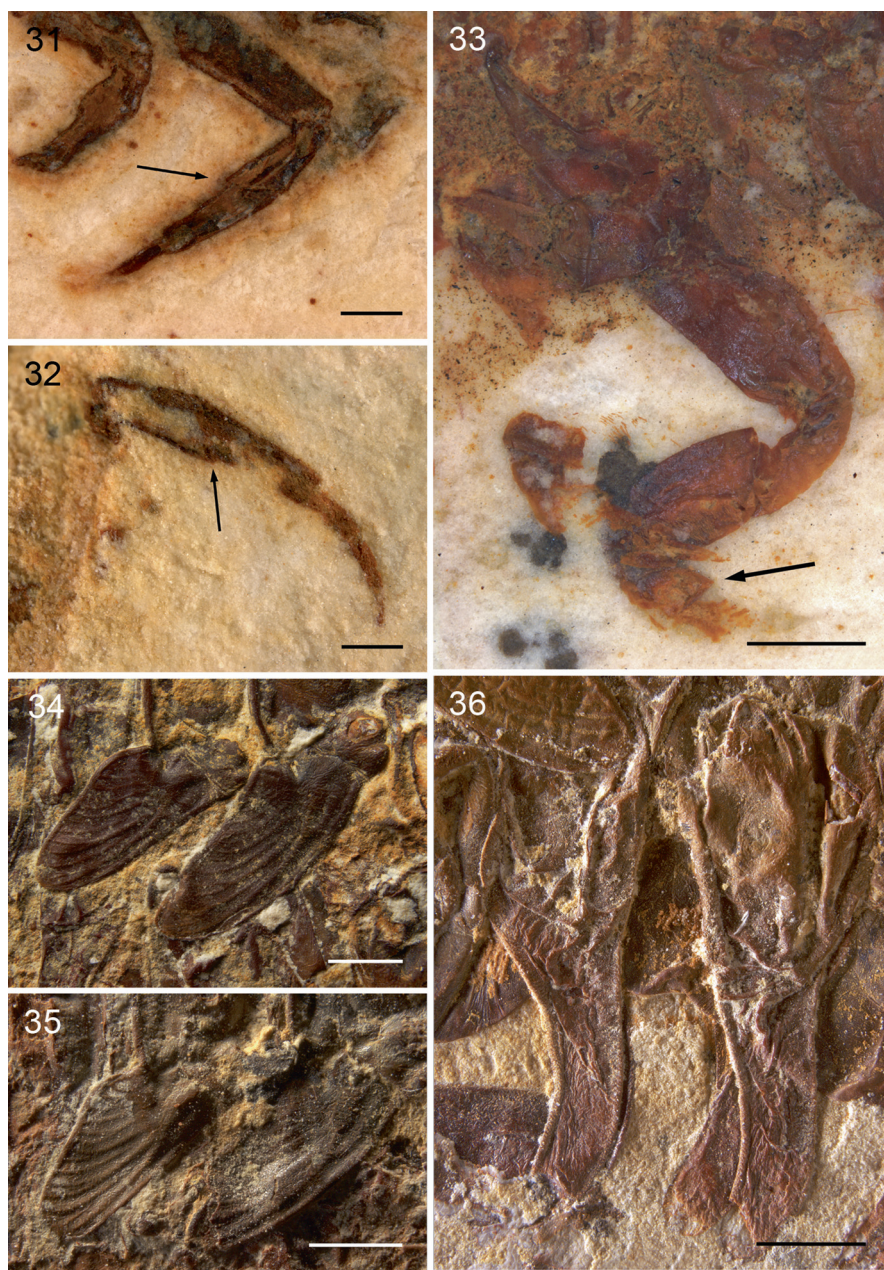
Figs 31–36. *Mickoleitia* sp., larva. (31) Specimen SMNS 66602, foreleg with suture between tibia and tarsus, pretarsus single-clawed (photographed with alcohol cover). Scale bar=0.5 mm; (32) specimen SMNS 66602, foreleg with tibiotarsal suture between tibia and tarsus, pretarsus single-clawed, scale bar=0.5 mm; (33) specimen SMNS 66605, hind leg with strong tibial spur (photographed with alcohol cover), scale bar=0.5 mm; (34) specimen SMNS 66547, wing pads with venation, scale bar=1 mm; (35) specimen SMNS 66603, wing pads with venation, scale bar=1 mm; (36) specimen SMNS 66603, abdominal gills, scale bar=1 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

Burkhard Pohl at the Wyoming Dinosaur Center (WDC, Thermopolis, WY, USA); specimen no. 512 and a specimen without number in coll. Masayuki Murata (Kyoto, Japan).

Discussion

Ecology and function of forelegs

Many of the fossil larvae are embedded with a characteristic dorsally bent body (Figs 19, 20 and 24), which seems to correspond to the posture of the living animal. The massive, strongly sclerotized body with vertexal crests, larger frontal and smaller clypeal beak, mandibular tusks, and strong mid and hind legs may suggest a burrowing or at least semi-burrowing lifestyle of the larvae of *Mickoleitia*. However, the long antennae and long terminal appendages as well as ventrally exposed gills could represent conflicting evidence for a burrowing way of life. A predatorial alimentation could be suggested by the "raptorial" position of the forelegs in the larvae, and the likewise subchelate forelegs with elongate coxae in imagines, which are combined with a skewed pterothorax (like in dragonflies) and an elongate prothorax (like in mantids and mantispids). The mandibular tusks present in *Mickoleitia* might even not have been used as burrowing device, but may have assisted in a carnivorous feeding habit. The preserved imaginal palps may also suggest that the imago was a feeding stage, contrary to modern mayflies, even though a few Recent mayfly species have the palps retained as well. The circumstance that the forelegs lack spines in larval and adult stages of *Mickoleitia* does not exclude a raptorial function, because raptorial forelegs without spines are also present in aquatic bugs like Nepidae and Belostomatidae. However, the forelegs of larvae and adult animals, which probably did not have a burrowing function (McCafferty, 1990: 38–39), might also have been used for climbing and/or grasping. Such a grasping function was already postulated for *Mesogenesia* by Kluge (2004), while McCafferty (1990) rather supposed a raptorial function. The peculiar posture of mid and hind legs that are opposed to each other may also facilitate clinging and grasping. On the other hand the circumstance that the cerci are supplied with inner and outer rows of setae rather suggests that the terminal appendages were not primarily used for swimming, because in mayflies that do show this kind of swimming behaviour only the paracercus is supplied with two rows of setae, while the cerci have only setae along their medial side. However, it cannot be entirely ruled out that the larvae were even able to swim in free water like the superficially similar gammarids. In the latter case, the "feather-like" anal appendages (Fig. 39) could have served as a swimming device analogous to the uropod tailfan of gammarids (as is suggested by the asymmetrical setation of the cerci in *Mesogenesia*), while its legs could have been used to grasp water plants as attachment for resting behaviour in turbulent water.

The morphology of the larvae does not allow definite conclusions of their lifestyle, but with the limited information available we suggest that the larvae may have lived in subaquatic leaf litter, or on or in the ground of calm water habitats, or these larvae may have even been benthic organisms that were hiding with their thorax and abdomen in burrows, with antennae and forelegs stretched out into the water to catch small prey.
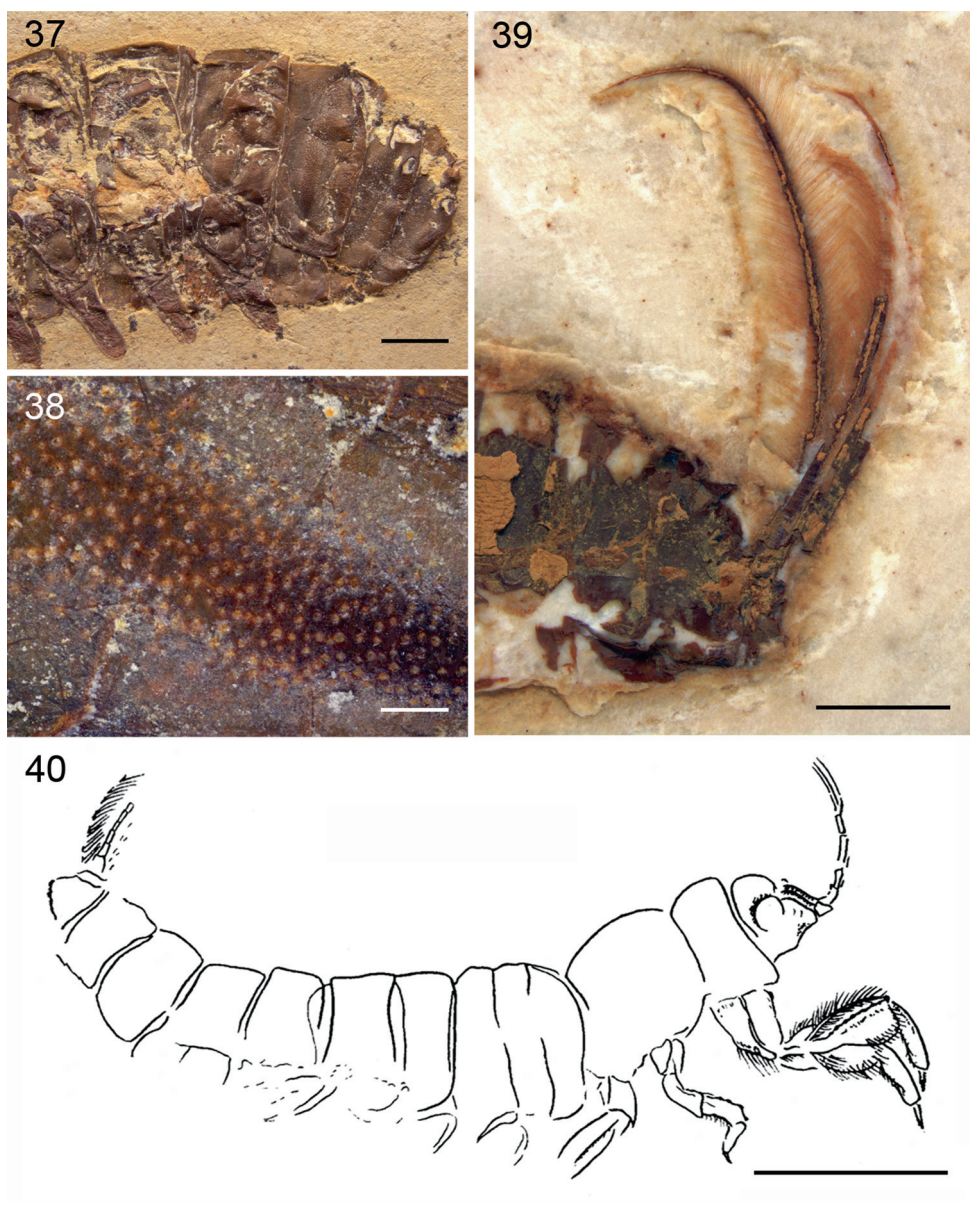
Figs 37–40. (37–39) *Mickoleitia* sp., larva. (37) Specimen SMNS 66603, abdomen, scale bar=2 mm; (38) specimen SMNS 66603, tergum VIII with setal sockets, scale bar=0.2 mm; (39) specimen SMNS 66604, terminal appendages, longer paracercus and cerci each with two rows of setae (photographed with alcohol cover), scale bar=2 mm; (40) *Mesogenesia petersae*, holotype no. 3053/333 at PIN, redrawn after Tshernova (1977: fig. 1a); scale bar=2 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise
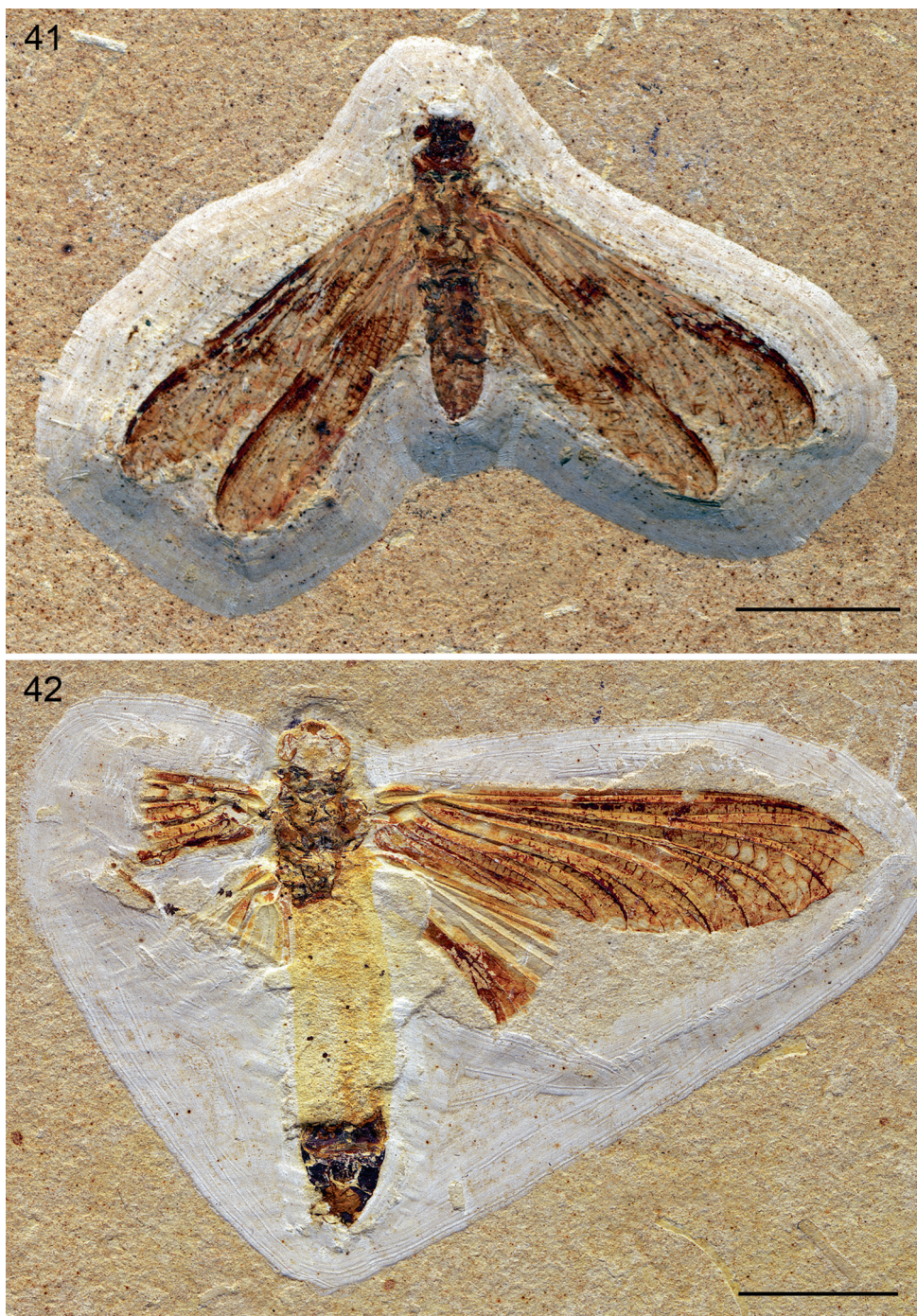
Figs 41–42. (41) *Cretereisma antiqua*, holotype SMNS 66546, scale bar=10 mm; (42) *Cretereisma schwickertorum*, holotype SMNS 66598, scale bar=10 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise
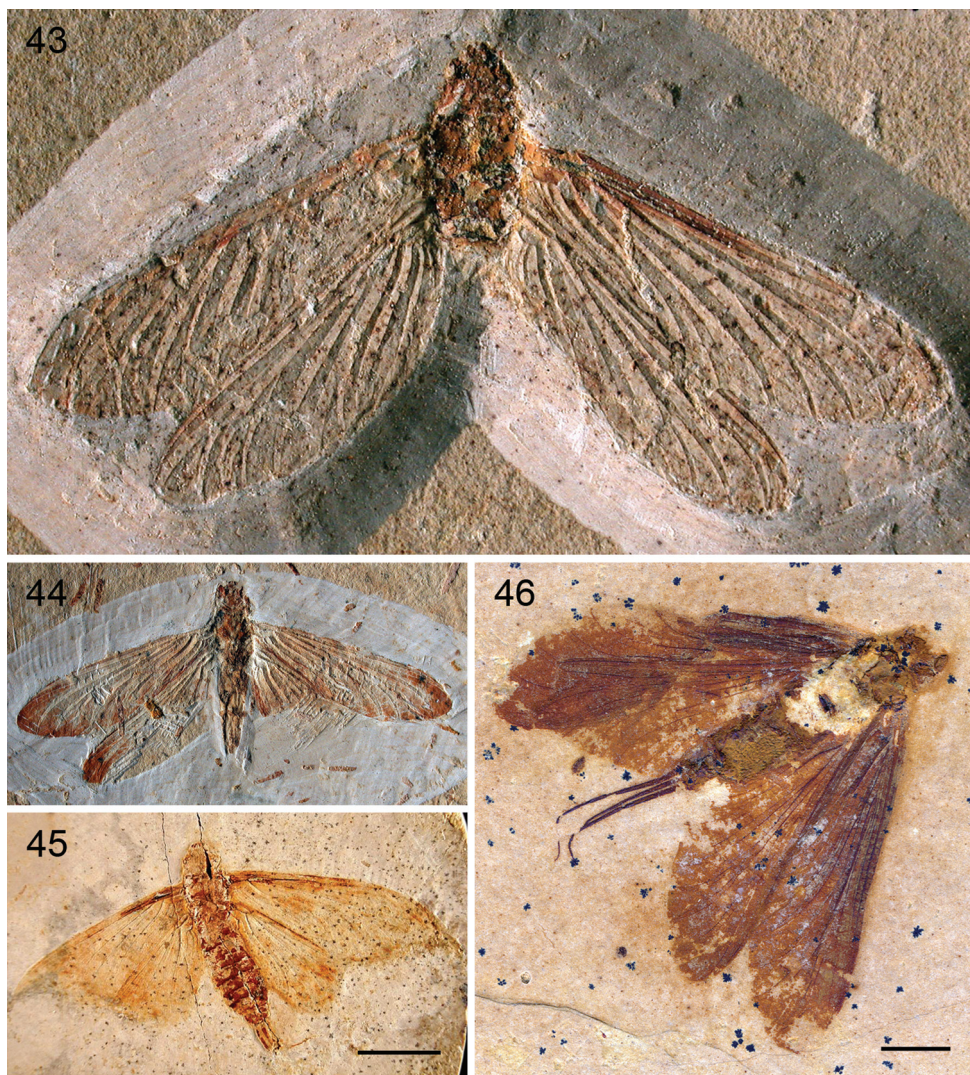
Figs 43–46. *Cretereisma* sp., adults, (43) specimen no. Q24 at SMF, without scale; (44) specimen no. Q25 at SMF, without scale; (45) specimen no. 48 coll. Pohl WDC, scale bar=10 mm; (46) specimen without number in coll. Pohl WDC, scale bar=5 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

Mesogenesia

Mesogenesia petersae (Fig. 40) is a fossil nymph that was described by Tshernova (1977) from the Jurassic of Transbaikals in the mayfly family Palingeniidae. This attribution was already disputed by McCafferty (1990, 1991, 2004) and Kluge (2004), as it is only based on superficial similarities with the Recent genus *Heterogenesia*. The holotype, which is the single known specimen of the genus, shares several derived similarities with the putative larvae of *Mickoleitia*, such as its peculiar body shape, head with a

triangular frontal process, saddle-like pronotum, forelegs with elongated free coxae and subchelate telopodite, opposite orientation of middle and hind legs, and possibly ventrally directed abdominal gills. Furthermore, the fossil shows exactly the same peculiar posture as many of the Crato larvae, viz., a "subchelate" position of the forelegs, a dorsally bent body, and upward directed antennae and terminal filaments. The only differences to the Crato larvae are the toothed claws, and especially the broadened femora of the forelegs. According to Kluge (pers. commun. 2011) the abdominal gills pictured as ovoid and plate-like in the original description are insufficiently preserved to draw definite conclusions on their morphology. Taking all characters into account, there is convincing evidence that *Mesogenesia* is a distinct genus that belongs to the new family Mickoleitiidae. We tentatively agree with the synonymy of *Archaeobehningia* Tshernova, 1977 with *Mesogenesia* proposed by Kluge (2004: 356), because of the free coxae and broadened femora of the forelegs, orientation of mid and hind legs, and the apparently primitive lateral position of the wing pads.

Cretereisma

The two species of *Cretereisma* that were described from adults by Willmann (2007a) are easily distinguished from *Mickoleitia* by their different wing venation. *Mickoleitia* lacks the characteristic pairwise orientation of the longitudinal wing veins that is one of the main autapomorphies of *Cretereisma* (Willmann 2007a).

The previous attribution of the "abacaxi" larvae to *Cretereisma* is contradicted by the shared similarities of these larvae with the adult holotype of *Mickoleitia longimanus*, such as the elongate free coxae of the forelegs, the subchelate posture of the forelegs, and the widened anal area of the hind wing. Finally, the size of the largest larvae (which still have rather small wing pads and, thus, probably do not represent the ultimate instar) rather corresponds to the bigger size of *Mickoleitia* than to the smaller size of the two *Cretereisma* species.

Phylogenetic Systematics of the stem group of mayflies

Willmann (2007a,b) proposed a new phylogenetic reclassification of the stem group of Ephemeroptera. As in the meantime several publications made new evidence available, a revision of this reclassification is necessary (Fig. 56).

Palaeoptera and Hydropalaeoptera. The basal splitting events of Pterygota represent a longstanding problem of insect phylogeny that is also known as the "Palaeoptera problem". There is considerable amount of conflicting evidence from the fossil record, comparative morphology, and genomic data for each of the three possible alternatives (Palaeoptera vs Metapterygota vs Chiastomyaria). The following three characters of wing venation could be interpreted as putative synapomorphies of Panephemeroptera and Odonatoptera (=Hydropalaeoptera): long intercalary veins (incl. IR1 and IR2); "rope-ladder"-like pattern of strictly straight perpendicular cross-veins between the longitudinal veins instead of an archaeodictyon (which is also absent in basal Odonatoptera like Erasipteridae, contrary to some original descriptions, as is clearly visible in photos of the type material, e.g., Brauckmann 1991: Tafel 19), or irregular and often oblique
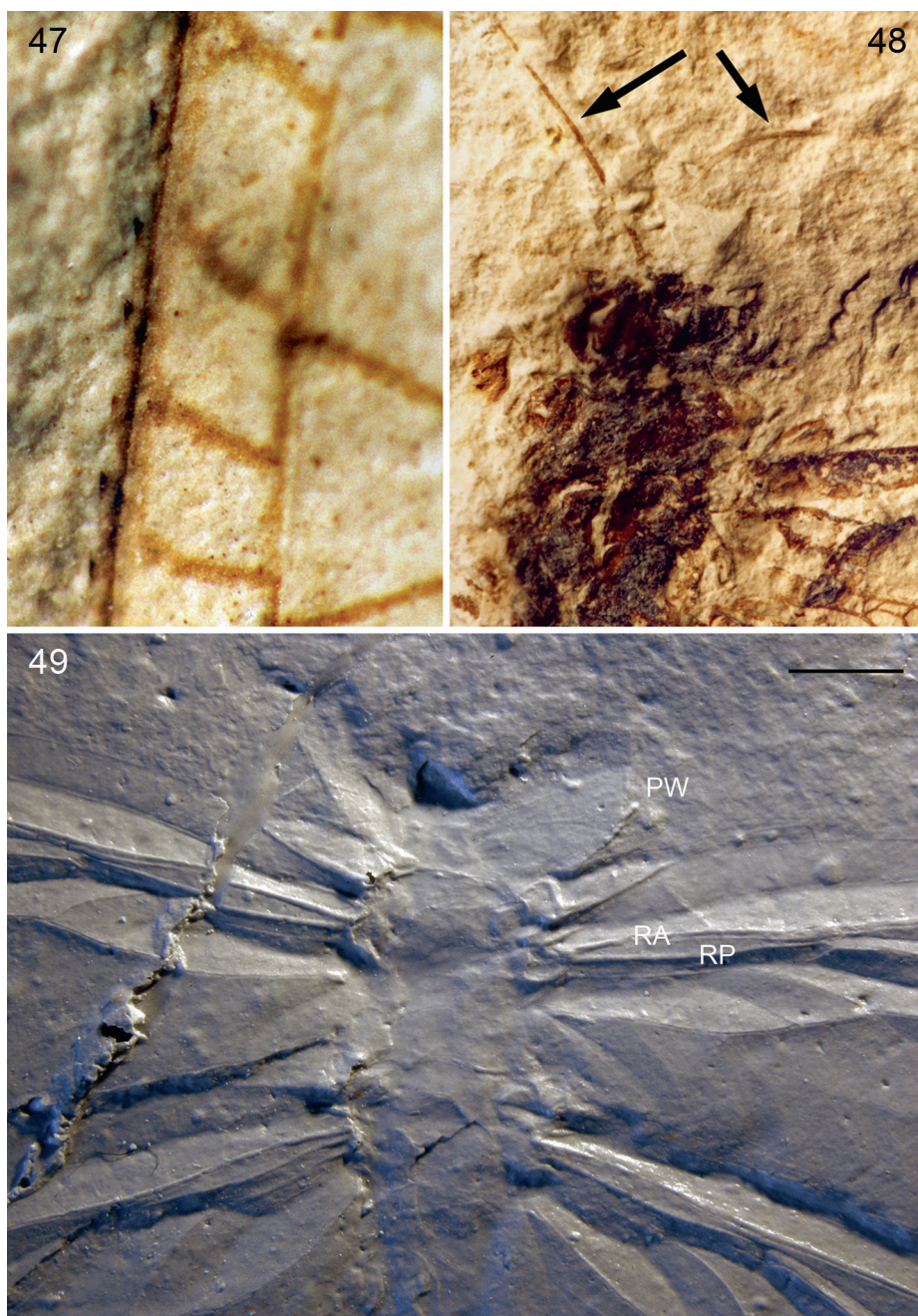
Figs 47–49. (47–48) *Protereisma permianum*, neotype MCZ 3405b. (47) Serrated costal margin, without scale; (48) head with long antennae (marked by arrows), without scale; (49) Eugeropteridae gen. et sp.n., cast of undescribed fossil specimen from the Upper Carboniferous of La Rioja (Argentina) in coll. Javier Muzón (ILPLA), note the widely separated bases of RA and RP and the prothoracic winglets (PW), scale bar=2.5 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

or sigmoidal cross-veins; costal margin serrated in the ground plan (Fig. 47). A further putative synapomorphy is the fused larval galeolacinia of Ephemeroptera and Odonata (Staniczek 2001). Willkommen & Hörnschemeyer (2007) and Willkommen (2008, 2009) described in detail striking similarities and fusions in the wing bases of Ephemeroptera and Odonata that could also be interpreted as shared derived characters. Additional support for the monophyly of Hydropalaeoptera has been proposed by Kukalová-Peck et al. (2009), based on a hypothetical ground plan reconstruction of ancestral wing articulation, but these interpretations partly rest on much disputed fossil evidence. We could only study a very good plaster cast (in coll. Bechly, SMNS) of the paratype of the palaeodictyopteran *Mazonopteron wolfforum* with well-preserved wing articulation, and could not find any hint for a serial arrangement of basal wing articulation sclerites in this specimen as originally proposed by Kukalová-Peck (1983), but rather identified two or three large articulatory plates similar to Odonatoptera.

Under this assumption, the morphological evidence in favour of Metapterygota would be considered as convergently developed in Odonata and Neoptera. In any case, the loss of moulting in winged stages seems to have evolved independently in Odonata and Neoptera, as is suggested by fossil larval stages of Palaeozoic Palaeodictopterida, Ephemerida (e.g., Protereismatidae), Odonatoptera and Neoptera (Kukalová-Peck 1978, 2009), with gradual increase in wing length of the laterally spread wing pads that are more curved in earlier larval stages. The same accounts for the convergent loss of the paracercus, which is suggested by its presence in the stem group odonate *Namurotypus sippeli* (Bechly et al. 2001) and its absence in Palaeodictyopterida. The typical dicondylic mandibular articulation of Odonata and Neoptera (Staniczek 2000, 2003a) is related to the highly adaptive mode of feeding and may also be prone to convergence. The separate stems of RA and RP may represent a symplesiomorphy of mayflies and basal stem group odonates like Eugeropteridae (Fig. 49), so that the fusion of basal stems of RA and RP could be interpreted as a convergence of "higher" Odonatoptera (in which the radial stem is always still developed as "double-barreled" structure) and Neoptera.

On the other hand, some characters that have previously been suggested as synapomorphies of Palaeoptera or Hydropalaeoptera are only of doubtful value: The palaeopterous condition of the wings is of unclear polarity (Willmann 1998; Willkommen 2008), with wing folding present in Neoptera and the extinct palaeodictyopteroid group Diaphanopterodea. Bristle-like antennae have been suggested as synapomorphy of Recent Ephemeroptera and Odonata, but later have been disputed because of reconstructions of putative basal stem group mayflies (*Triplosoba*, *Lithoneura*) and stem group dragonflies (*Namurotypus*). However, none of the actual fossil material of these taxa has the antennae preserved (Brauckmann 1991; Willmann 1999; Prokop & Nel 2009). Nevertheless, the preservation of longer antennae in a few other crucial fossils (the meganeurid "*Titanophasma*" *fayoli*, Protereismatidae and Misthodotidae; Fig. 48) clearly shows that the bristle-like antennae of Recent Ephemeroptera and Odonata must indeed be due to convergent evolution. The aquatic larvae of Ephemeroptera and Odonata do not show any shared adaptations to an aquatic lifestyle, so that a convergence seems to be rather likely.

Many fossil Ephemeroptera and Odonata, including stem group representatives like Protereismatidae or "Protozygoptera", are preserved in lateral view with the wings held vertically over the body, as in alive resting position of Ephemeroptera and many Odonata. However, no fossils of Palaeodictyopterida are known with this kind of preservation at all, which may suggest that they did not have truly palaeopterous wings at all, and a different resting position (either spread, or even folded flat over the abdomen like Neoptera). Since no unambiguous synapomorphies for an inclusion of Palaeodictyopterida into Palaeoptera have been proposed yet, it cannot be excluded that Palaeodictyopterida are stem group representatives of all pterygotes.

Thesoneuridae. Willmann (2007b) rejected Carpenter's (1944) attribution of *Thesoneura* to Homoiopteridae within Palaeodictyoptera and considered this genus as possibly the most basal stem group representative of mayflies. However, the attribution of this genus to Homoiopteridae was also supported by Kukalová (1969), Brauckmann & Herd (2002), and more recently by Prokop et al. (2006), who all considered Thesoneuridae as a synonym of Homoiopteridae because of the nearly identical wing venation (e.g., curved origin of CuP on CuA and sigmoidal course of CuP, apically converging CuA). Based on a comparison of the wing venation of *Thesoneura americana* with typical homoiopterids like *Homoioptera gigantea* and *Lycocercus pictus*, we consider the attribution of *Thesoneura* to Homoiopteridae as well supported. The alleged basal separation of veins R and Rs, which is emphasized by Willmann (2007b), could either be a reversal, or rather be based on a misinterpretation of the fossil by Carpenter (1944). Only a redescription of the type could finally solve this question.

Triplosobida. Triplosoba pulchella was often considered to be the most basal stem group mayfly. Willmann (2007a) still tentatively included *Triplosoba* at the very base of Panephemeroptera, while Willmann (2007b) found no support for such a relationship and excluded this genus from the stem group of mayflies. Prokop & Nel (2009) rediscovered and revised the holotype and attributed this fossil to Palaeodictyopterida, probably more closely related to Diaphanopterodea. Prokop & Nel (2009) dismissed the similarities in wing venation (presence of intercalary veins IR1 and IR2, and straight cross-veins between longitudinal veins) with Ephemerida and Odonatoptera, and maintained that similar states occur in Palaeodictyopterida, such as Calvertiellidae and Namuronigxiidae (sic, should be Namuroningxiidae). However, these palaeodictyopterid taxa neither have clearly developed veins IR1 and IR2, nor straight cross-veins. Furthermore, *Triplosoba* clearly has three terminal appendages, while the median appendage is always suppressed in all Palaeodictyopterida with preserved terminalia. The speculation by Prokop & Nel (2009) that this could be an artefact of preservation is not reasonable, considering the fact that the median appendage is well preserved in *Triplosoba*, as well as in most fossil mayflies and in all fossil thysanurans. Even though the presence of a median appendage is a plesiomorphy that would not preclude a sister group relationship of *Triplosoba* with Palaeodictyopterida, such a relationship is not suggested by any potential synapomorphies. Based on these arguments we doubt the placement of *Triplosoba* in Palaeodictyopterida and consider this fossil to be more

closely related to Panephemeroptera and/or Odonatoptera. We, therefore, restore the separate higher taxon Triplosobida for Triplosobidae within Palaeoptera.

Syntonopterida–Bojophlebiidae. *Bojophlebia prokopi* was described by Kukalová-Peck (1985) as most basal mayfly from the Upper Carboniferous of the Czech Republic. Based on this description and the provided drawings, Willmann (2007a,b) supported this phylogenetic position. Our own examination of the holotype of *Bojophlebia prokopi* confirms the conclusions of Prokop et al. (2010): The description of Kukalová-Peck includes several errors. In fact, major parts of the basal right fore and hind wings are clearly not preserved in the fossil specimen (compare Figs 51 and 52), such as wing bases, costal brace, and anal brace. Thus, we could not verify any of the crucial characters that would allow placing *Bojophebia* within Panephemeroptera (compare Figs 51 and 52). Prokop et al. (2010) excluded Bojophlebiidae also from Syntonopteroidea, because their main apomorphies (characteristic constriction of the area between AA1+2 and AA3+4, presence of a concave longitudinal vein IN- between them, and a constriction of the area between AA3+4 and the first branch of the concave AP at the same point) are not visible in the holotype of *Bojophlebia*, which has a broader anal area. Therefore, Prokop et al. (2010) considered *Bojophlebia* as a Pterygota incertae sedis. The same authors mentioned one character (distinct anterior curve or 'zigzag' of AA1+2) as a possible synapomorphy of Bojophlebiidae, Syntonopteroidea and Ephemeroptera. However, this character is hardly visible in the holotype of *Bojophlebia*. Therefore, we suggest classifying *Bojophlebia* as Hydropalaeoptera incertae sedis and, consequently, also not support the taxon Ephemerontoida.

Contrary to the redescription provided by Willmann (1999) and contrary to Prokop et al. (2010), the holotype of *Lithoneura lameerei* clearly has a small costal brace (Figs 53 and 54; also visible in fig. 10b in Willmann 1999), so that a closer relationship of Syntonopteroidea with Ephemerida could also be supported by this putative synapomorphy, as already suggested by Rasnitsyn (2002). Prokop et al. (2010) maintained that *Anglolithoneura* lacks a costal brace, but according to the available figures, the crucial region of the wing base (distinctly basal of the curved origin of CuA on CuP) is not preserved in the holotype. Since the costal brace in *Lithoneura* is small, inconspicuous and very close to the wing base, it was previously overlooked. Likewise, it is well possible that a costal brace was overlooked in other Syntonopteridae.

Willmann (2007b) suggested that the triadic branching of veins RS, MA, MP and CuA represents a synapomorphy for Bojophlebiidae, Syntonopteridae and mayflies. However, this character state is possibly also present in *Thesoneura*. It is clearly present in some other basal Palaeodictyopterida (e.g., Spilapteridae), as well as in basal Odonatoptera (e.g., Meganisoptera). Therefore, this character state might even be a putative synapomorphy of all Palaeoptera, but is too weak to allow any definite conclusions.

Syntonopteroidea. Willmann (2007a,b) considered Syntonopteroidea as a paraphyletic grade and placed *Lithoneura* closer to Ephemerida than *Syntonoptera*. More recently Prokop et al. (2010) have revised all known fossils and redefined a monophyletic Syntonopteroidea that includes the families Syntonopteridae (genera *Syntonoptera*,
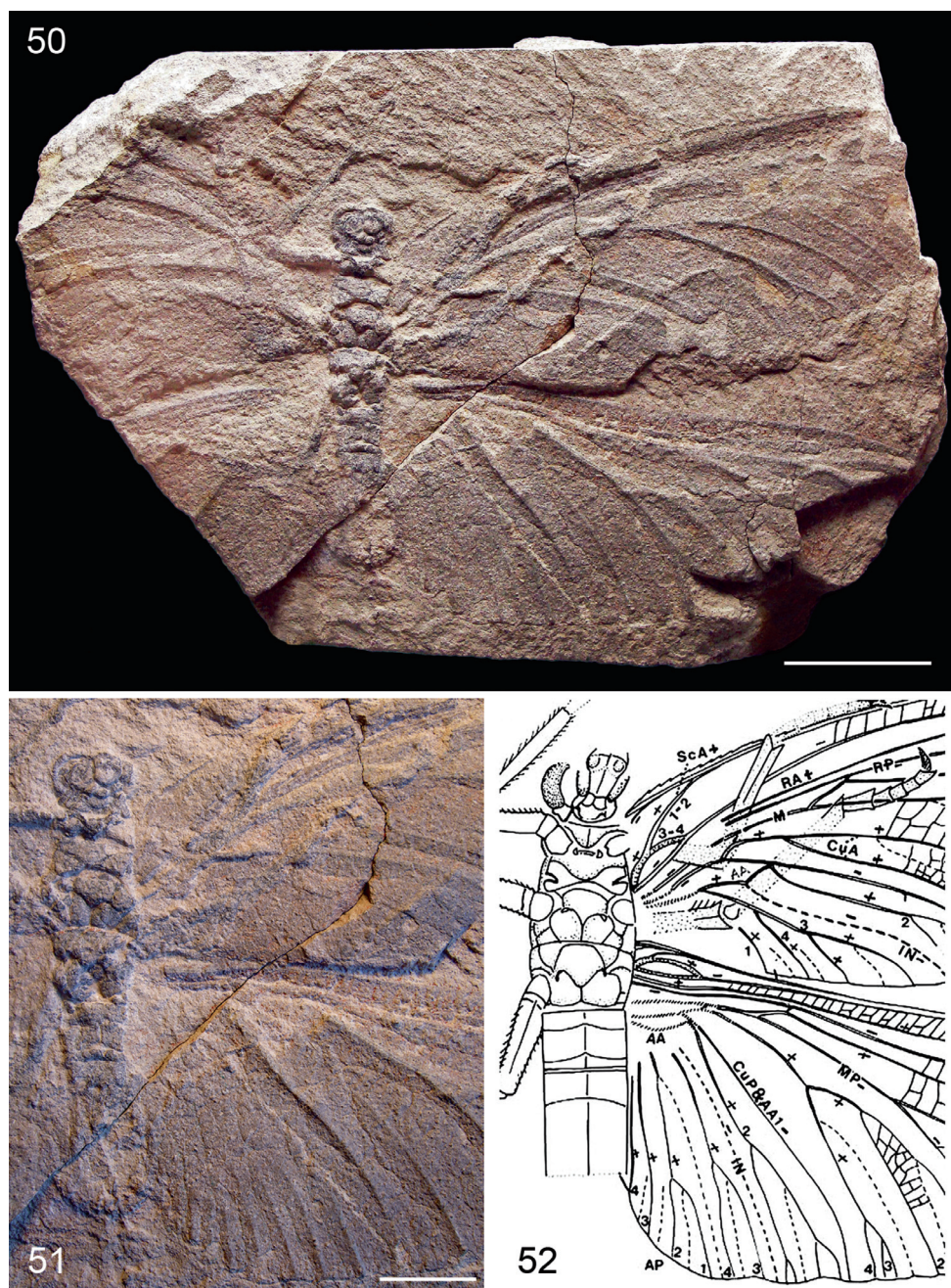
Figs 50–52. *Bojophlebia prokopi*, holotype no. 1/1985, Národní Museum, Prague. (50) Total ventral view, scale bar=50 mm; (51) body and basal half of left wing pair in ventral view, scale bar 25 mm; (52) corresponding part of original drawing after Kukalová-Peck (1985: fig.2). This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise
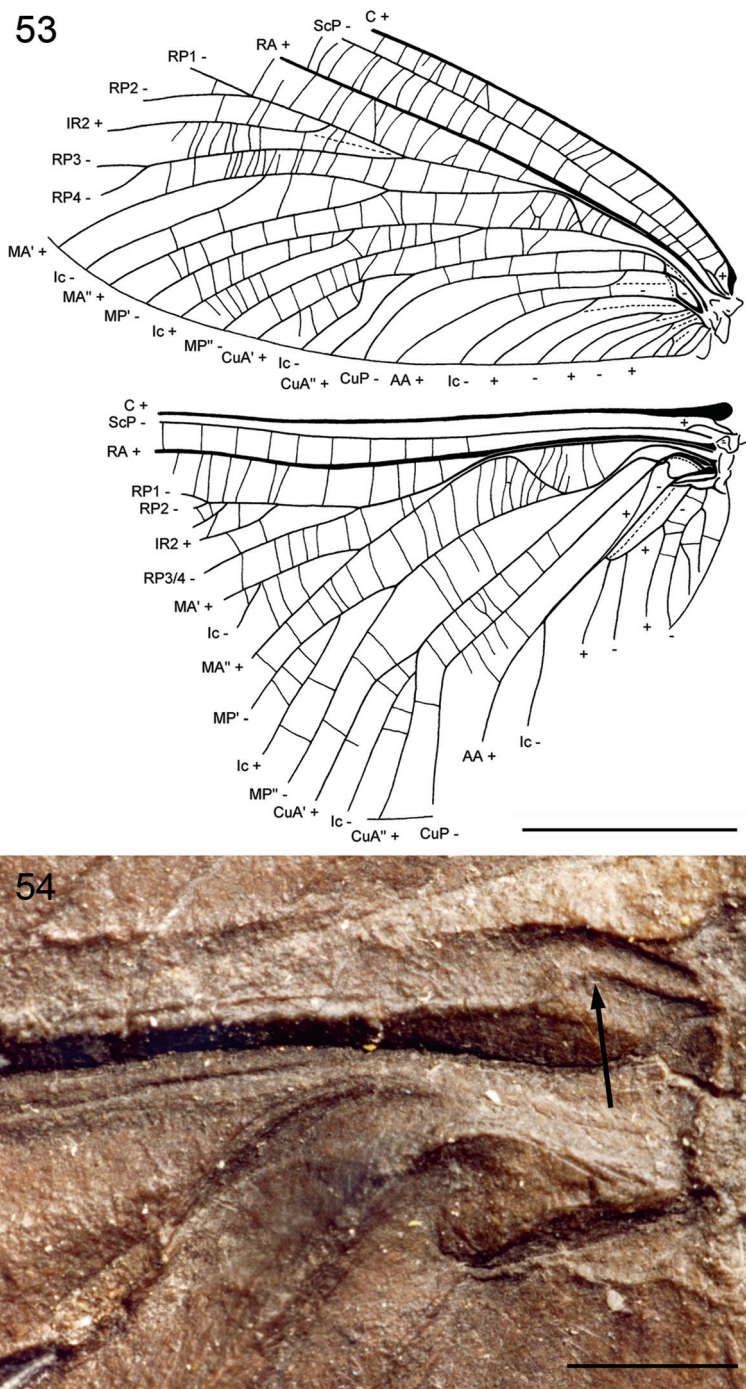
Figs 53–54. *Lithoneura lameerei*, holotype MCZ 4537. (53) Drawing of left wing pair, scale bar=10 mm; (54) left hind wing base with small costal brace, scale bar=2 mm. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

Lithoneura, *Gallolithoneura* and *Anglolithoneura*) and Miracopteridae (genus *Miracopteron*). Prokop et al. (2010) discussed and refuted the paraphyly hypothesis of Willman (2007b), and confirmed *Lithoneura* has member of a monophyletic Syntonopteridae. We concur with Prokop et al. (2010) and thus reject the taxon Ephemeronta. We agree with Willmann (2007a,b) to use Panephemeroptera as taxon, which includes all fossil taxa that are closer related to modern Ephemeroptera than to Palaeodictyopterida, Odonatoptera and Neoptera and, thus, in the original meaning of a pan-monophylum (sensu Lauterbach 1989). We also concur with Willmann (2007a,b) that the remaining taxa (e.g., Protereismatidae, Mesephemeridae, Cretereismatidae and Recent Ephemeroptera) constitute a monophyletic group, but we prefer the older and more widely known name Ephemerida (=Euephemeroptera *sensu* Kluge 2004) over the new name Reticulata. We restrict the well-known taxon Ephemeroptera to the mayfly crown group.

Permoplectoptera and Cretereismatidae (Cretoplectoptera). Willmann (2007a,b) considered *Cretereisma* to belong to his group Heptabranchia, based on the attribution of the strange "abacaxi" larvae to the genus *Cretereisma*. This attribution was reasonable based on the evidence available to Willmann, but cannot longer be maintained according to the new evidence described in the present publication, which does not support a position of *Cretereisma* closer to crown group Ephemeroptera than to Permoplectoptera. Willmann (2007a,b) suggested the branching of CuA as synapomorphy for a taxon Mesephemeriformia, excluding *Litophlebia*, *Cretereisma*, Misthodotidae and Protereismatidae. However, Prokop & Nel (2010) showed in their revision of Syntopteridae that these putative basal stem group mayflies had a broadly branched CuA. The same holds for *Bojophlebia*, but not for *Triplosoba* (Prokop & Nel 2009). Consequently, this character is at least of unclear polarity, but rather represents a symplesiomorphy. Willmann listed a reduced anal area in the hind wing as synapomorphy of *Cretereisma*, *Litophlebia* and Mesephemeriformia, even though *Cretereisma* and *Mesephemera* do have a hind wing anal area that is equally distinct to that of Protereismatidae and Misthodotidae, while the hind wing of *Litophlebia* is not known at all. The common elongate ovoid shape of the wings was already discussed by Willmann (2007b: 115) as a potential synapomorphy of Protereismatidae, *Litophlebia* and *Cretereisma*. We would add the reduced branching of CuA as a further putative synapomorphy of these three taxa. Indeed, *Cretereisma* might even represent a late offshot of Protereismatidae with a highly derived wing venation. Consequently, we restore the taxon Permoplectoptera *sensu* Kluge (2004) for the taxa Protereismatoidea (Protereismatidae, Jarmilidae, Misthodotidae, Oboriphlebiidae), Mesoplectopteridae, Mesephemeroidea (Mesephemeridae, Palingeniopsidae and Sharephemeridae), Litophlebiidae and Cretereismatidae, but not including the new family Mickoleitiidae. We elevate the rank of Permoplectoptera to preserve the well-established ordinal rank for crown group Ephemeroptera.

Willmann (2007b) established the two new genera *Arnulfias* and *Eurekter* for two species that were previously classified in the genus *Misthodotes*, excluded them from the family Misthodotidae, but considered them to be most closely related to the Misthodotidae s.str. (*Misthodotes*+*Thuringopteryx*) within a new taxon Misthodotida.

However, both new genera have to be considered as nomina nuda because no differential diagnoses were provided. Therefore, we refrain from endorsing the taxon Misthodotida.

Tintorinidae, described from the Middle Triassic of Monte San Giorgio by Krzeminski & Lombardo (2001), plesiomorphically lack a costal brace typical for Panephemeroptera, and autapomorphically differ from all Panephemeroptera by a short vein ScP. We therefore concur with Kluge (2004) to exclude this enigmatic taxon from Panephemeroptera and Permoplectoptera, and tentatively consider it as Hydropalaeoptera incertae sedis.

Mesoplectopteron longipes was described by Handlirsch (1918) as a fossil mayfly larva from the Triassic of Vosges with 8(!) pairs of abdominal gills, which would suggest a position between Permoplectoptera (9 pairs) and Coxoplectoptera+Ephemeroptera (7 pairs). However, the original description and drawing by Handlirsch suggests that the gills are poorly preserved and the interpretation therefore rather dubious. Furthermore, the larvae of the Recent mayfly species *Acentrella joosti* (Baetidae) have been described by Zimmermann & Braasch (1979) as *Baetis joosti* with 8 pairs of gills, but according to Kluge (pers. commun. 2011) this is only an atavism in a single specimen, while three of the paratypes (in coll. Kluge) only have 7 pairs of gills.

Coxoplectoptera. The curved costal brace that crosses ScP (Fig. 12) is an imaginal character that represents a synapomorphy with Ephemeroptera, which uniquely possess this character state among Recent insects. Among the larval characters, the presence of just 7 pairs of abdominal gills, compared to 9 pairs in Palaeozoic stem group mayflies (e.g., Protereismatidae), the presence of a single tarsal segment, compared to 5 tarsal segments in the larvae of Protereismatidae, and the single pretarsal claw, compared to paired claws in Protereismatidae, demonstrate a sister group relationship of Coxoplectoptera with Ephemeroptera (together constituting the Heptabranchia sens. nov.) rather than with Permoplectoptera.

Two plesiomorphic characters exclude a position of Coxoplectoptera within crown group Ephemeroptera: lateral nymphal wing pads with pronounced articulation represent a very primitive character state that is otherwise only known from Palaeozoic pterygote larvae; unlike in larvae of Ephemeroptera, abdominal tergites and sternites are distinctly separated and do not form continuous abdominal rings.

Ephemeroptera. Willmann (2007b) considered the fossil Hexagenitidae as a paraphyletic grade and included *Cratogenitoides* (synonymized with *Protoligoneuria* by Staniczek 2007) with Recent Ephemeroptera in his taxon Alulata. However, the monophyly of Hexagenitidae is supported by a unique and highly derived wing venational character as synapomorphy (CuA in forewing divided into CuA1 and CuA2 with an intercalated vein iCu that has 3–5 triads), which cannot plausibly be considered as a symplesiomorphy. On the other hand the proposed paraphyly of Hexagenitidae would only be supported by the diminished hind wing size, which is under a reductive trend within the ephemerid lineage anyway. Furthermore, there is no evidence for a basal position of Hexagenitidae outside the crown group of Recent mayflies (Staniczek 2007).

We, therefore, reject the taxon Alulata and synonymize the taxon Triangulifera with Ephemeroptera (=Euplectoptera sensu Kluge 2004), which we restrict to the crown group of Recent mayflies.

According to Ogden et al. (2009) the most basal clade within Ephemeroptera is Siphluriscidae, based on morphological and molecular evidence. *Siphluriscus chinensis* (sole extant representative of Siphluriscidae) and *Chromarcys magnifica* (the most basal Oligoneuriidae) have a very plesiomorphic costal brace (Zhou & Peters 2003; Kluge 2004): it is elongate, straight and distinctly separate from the costal margin, so that it looks similar to the costal brace of Protereismatidae, Cretereismatidae, Mickoleitiidae, and other stem group mayflies. The only difference is a lack of basal cross-veins between costal brace and costal margin. The strongly bent arcular costal brace, which is fused to the costal margin, consequently does not seem to be an autapomorphic ground plan character of Ephemeroptera, but rather represents a convergently derived character state within crown group mayflies.

Evolutionary significance of abdominal appendages

An important clue to the problem of the sometimes proposed homology of abdominal gills and abdominal styli is provided by Protereismatidae (Kluge 1989). Larval protereismatids have abdominal gills (lateral position, winglet-like) on segments 1–9, while male adult protereismatids (just like Ephemeroptera) have strongly developed genital claspers (leglets) on segment 9. Consequently, at least the gills on abdominal segment 9 cannot be homologous to leglets (telopodites). Since all abdominal gills clearly appear to be serially homologous, a general homology of mayfly gills with abdominal telopodites can be excluded. This is also supported by the different places of origin for gills (dorsolateral) in Permoplectoptera, Coxoplectoptera and Ephemeroptera compared to abdominal styli (ventrolateral) in apterygote insects. Since gonostyli and abdominal styli are clearly serially homologous in Archaeognatha (having coxal plates, muscles, and a single segment with apical spine), these abdominal styli must be telopodites as well. Consequently, they cannot be homologized with ephemerid abdominal gills, even though such a homology seems to be suggested by the fact that basal ephemerids like Protereismatidae have larvae with abdominal gills on segments 1–9 and the distribution of abdominal styli in basal apterygote insects suggests their presence on abdominal segments 1–9 in the hexapod ground plan (retained in extinct Monura and the most basal Recent bristletail *Ditrigoniophthalmus oreophilus*; Koch 2003). A fossil apterygote insect with segmented abdominal telopodites with paired claws has been found in the Upper Carboniferous of Mazon Creek (Fig. 55). The authenticity of this fossil has recently been disputed by Béthoux & Briggs (2008), so that a final interpretation has to be based on a careful re-evaluation of the accuracy of the preparation technique applied by Kukalová-Peck. The evidence presented by Béthoux & Briggs (2008) appears to be flawed by some factually incorrect claims concerning the distributions of pyrite grains, which are according to Baird et al. (1986) "usually surrounding or occurring just above fossil nuclei", so that their presence together with needle scratches rather seems to be evidence against fudging preparation. However, we concur with
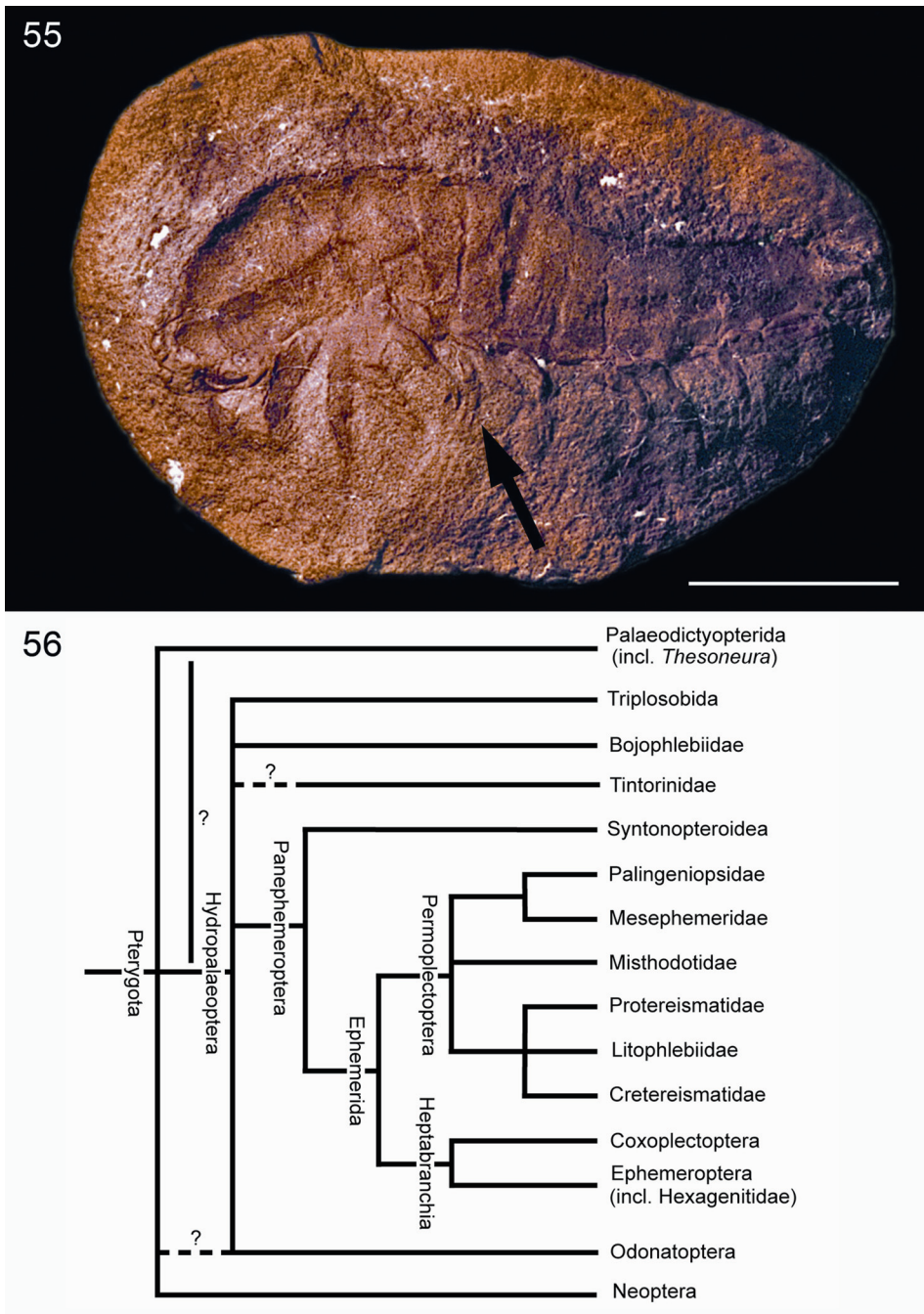
Figs 55–56. (55) Apterygote fossil stem group insect (maybe *Ramsdelepidion*, but not Monura and not Cercopodata!) from the Upper Carboniferous of Mazon Creek, with segmented abdominal leglets with paired claws, scale bar=10 mm; (56) phylogenetic tree and suggested reclassification of stem group mayflies. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/ise

Bitsch & Nel (1999) that this fossil from Mazon Creek may be identical to the alleged silverfish *Ramsdelepidion* from the same locality, and concur with Willmann (2003) that they are best considered as stem group representatives of hexapods.

Thoracic styli of Archaeognatha differ from abdominal styli in the lack of musculature and the lack of a terminal spine. They are clearly exites and not homologous to abdominal styli. However, the fact that many Recent Archaeognatha do possess styli (leg exites) on the meso- and metathoracic coxae could suggest a homology of these thoracic coxal styli with pterygote wings on the same segments. On the other hand, there is also considerable evidence for a serial homology of mayfly gills with thoracic wings (Kluge 2004; Kukalová-Peck 1978, 2008), which is also suggested by some Palaeozoic insect larvae. If wings would be homologous to thoracic exites and mayfly gills are serially homologous to wings, then mayfly gills could not be derived from terga (contra Kluge 2004), but would have to be derived from abdominal leg exites. The latter would have to be considered as secondarily reduced in Archaeognatha and Zygentoma. However, the circumstance that the gills of stem group mayflies like *Mickoleitia* articulate on the abdominal terga, similar to the wing pads on the thorax, could be seen as evidence for a tergal origin of these gills (and wings).

The similarity of wing pads to abdominal gills in some mayfly larvae, as well as in Paleozoic insect larvae, is very suggestive for a serial homology of these structures. The conflicting embryological (Bocharova-Messner 1959) and genetic (Averof & Cohen 1997) evidence for a leg origin of wings must be re-evaluated (see below). This puzzling problem notwithstanding, the fact that modern genomic and cladistic analyses have provided strong evidence for a position of insects within paraphyletic crustaceans, greatly increases the plausibility of the hypothesis of a biramous leg in the ground plan of Hexapoda. This does not necessarily imply an endorsement of the disputed multiple leg exite hypothesis of Kukalová-Peck (2008). Thoracic coxal styli of Archaeognatha may be vestiges of such a biramous leg, but could also represent an autapomorphy, because such coxal styli are not found in any other group of basal hexapods. The homology of coxal styli with wings is by the way also contradicted by the circumstance that the pleura of the insect thorax is formed by subcoxal leg elements. Consequently, wings could at best be derived from subcoxal exites, but not from a coxal exite.

Recently, Niwa et al. (2010) presented genetic and embryological evidence that may reconcile the apparently incompatible paranotal and exite hypotheses. Though their findings point to shared developmental modules for induction of styli, paranota, tracheal gills and wings, the authors maintain that this "not necessarily indicate serial homologies or stepwise modifications among these organs". Although there remain many questions concerning the evolutionary origin of insect wings, our findings in Coxoplectoptera support a tergal origin of mayfly gills, so the hypothesis of Niwa et al. (2010) has to be modified: wings and gills originated as expansions from tergal plates, while leg-genes were only recruited to control the mobility of these appendages.

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