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A new lobeatid insect from the Permo-Carboniferous of Niedermoschel, southwestern Germany (Archaeorthoptera)

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Abstract

The species *niedermoschelensis* sp. nov. (*Nosiapteron niedermoschelensis* gen. and sp. nov. under Linnaean nomenclature) is described on the basis of a single fossil specimen from the the Permo-Carboniferous deposits of Niedermoschel, Saar-Nahe Basin, Germany. The species is assigned to the higher taxon *Archaeorthoptera* (including among others, orthopterans and some stem orthopterans). The forewing morphology of the species suggests close relationships with lobeatid insects, a group widely represented during the Late Carboniferous, and one for which the monophyly is uncertain. The occurrence of *niedermoschelensis* sp. nov. near the Gzhelian/Asselian boundary constitutes the latest record of this group (assuming that it is monophyletic). In addition the new species exhibits a new combination of character states, including a comparatively long free part of CuA.

Key words

fossil insect, Gzhelian/Asselian boundary, *niedermoschelensis* sp. nov., *Nosiapteron* gen. nov.

Introduction

More than 15 y ago, earthworks east of Niedermoschel, a village located about 45 km southwest of Mainz (Rhineland-Palatinate, Germany), prompted collecting at a site which has been known to yield fossils since the beginning of the last century (Reis 1913). The exposed sediments belong to the Niedermoschel bed (Meisenheim Formation, 'Lower Rotliegend'; Schindler 1997) and are thus latest Late Carboniferous to earliest Early Permian (Gzhelian/Asselian boundary) in age (Königer *et al.* 2002). They represent the profundal facies of a large lake and yield an aquatic fauna consisting of vertebrates and crustaceans, such as ostracodes, conchostracans, and syncarids. The abundance of terrestrial plants and insects has been attributed to a strong deltaic input (Poschmann & Schindler 1997).

The Niedermoschel insects are preserved with remains of organic material still present, but this has probably been altered by contact metamorphism (Montenari & Uhl 2005). The insects are usually preserved as paired or isolated wings, or fragments thereof. Completely preserved large wings (> 2 cm) are rare. Animals with body and wings preserved are rare exceptions, and the number of such fossils decreases with increasing size (Hörschemeyer 1998). Hörschemeyer (1998) briefly outlined the taxonomic composition of the insect fauna, which is dominated by lemmatophoridaeans, miomopterans, and blattinopsidaeans. The latter group has been revised by Hörschemeyer & Stapf (2001).

Herein we provide the description of a large-sized archaeorthop-

teran from this Lagerstätte. *Archaeorthoptera* is a taxon including orthopterans, stem orthopterans, and a number of extinct groups, such as caloneurodeans and cnemidolestodeans (Béthoux 2007d: Appendix 2). Such insects form only a minor part of the Niedermoschel assemblage.

Methods

The fossil was photographed under alcohol immersion in both normal and polarized light using a digital camera, and a unique composite photograph was produced. Drawings were made with both the help of enlarged photographs and a SteREO Discovery V8 stereomicroscope equipped with a pair of W-PL 10x/23 eye pieces, a Plan Apo S 1.0x FWD objective, and a camera lucida. Figures were processed and arranged with image-editing software (Adobe Photoshop).

We use the cladotypic nomenclatural procedure elaborated by Béthoux (2007b, 2007c, in press) for taxa other than species, and follow suggestions of Dayrat *et al.* (2004; and references therein) for species names [see introduction and application of this approach in JOR by Béthoux & Herd (2009)]. All formal species and taxon names are written in italics. Capitals indicate a taxon name. In other words, a capitalized name written in italics does not refer to a genus but to a taxon at any level of the phylogeny. The choice of the taxonomic procedure is based on the decision of one of us (OB) and does not imply the support of the other author (MP) for all aspects of this procedure. An appendix compliant with the ICZN is provided, so as to allow the mention of the new species under a Linnaean framework. Although the paper does not consistently apply rules of the ICZN, therefore jeopardizing the availability of newly erected names, the need for experimentation with alternative nomenclatural approaches (Béthoux 2009) requires some flexibility.

It must be emphasized that uninominal species names are applicable under a nomenclatural approach using ranks and onomatophore-based taxon conceptualization (*i.e.*, as under the Linnaean approach). In addition, regarding taxon names used in this paper, *Archaeorthoptera/Archaeorthoptera* refers to a taxon which is above the family-group names under a Linnaean hierarchy, and therefore is not regulated by the ICZN. Owing to its definition and delimitation, the taxon name *Miamia* is valid both as a cladotypic taxon name and as an ICZN-compliant generic name (Béthoux 2008a). In summary, concerns regarding the recourse to an alternative nomenclatural approach are, in this case, not fully justified. On the other hand, the comments subsection benefits from the avoidance of numerous monotypic generic names, which are by

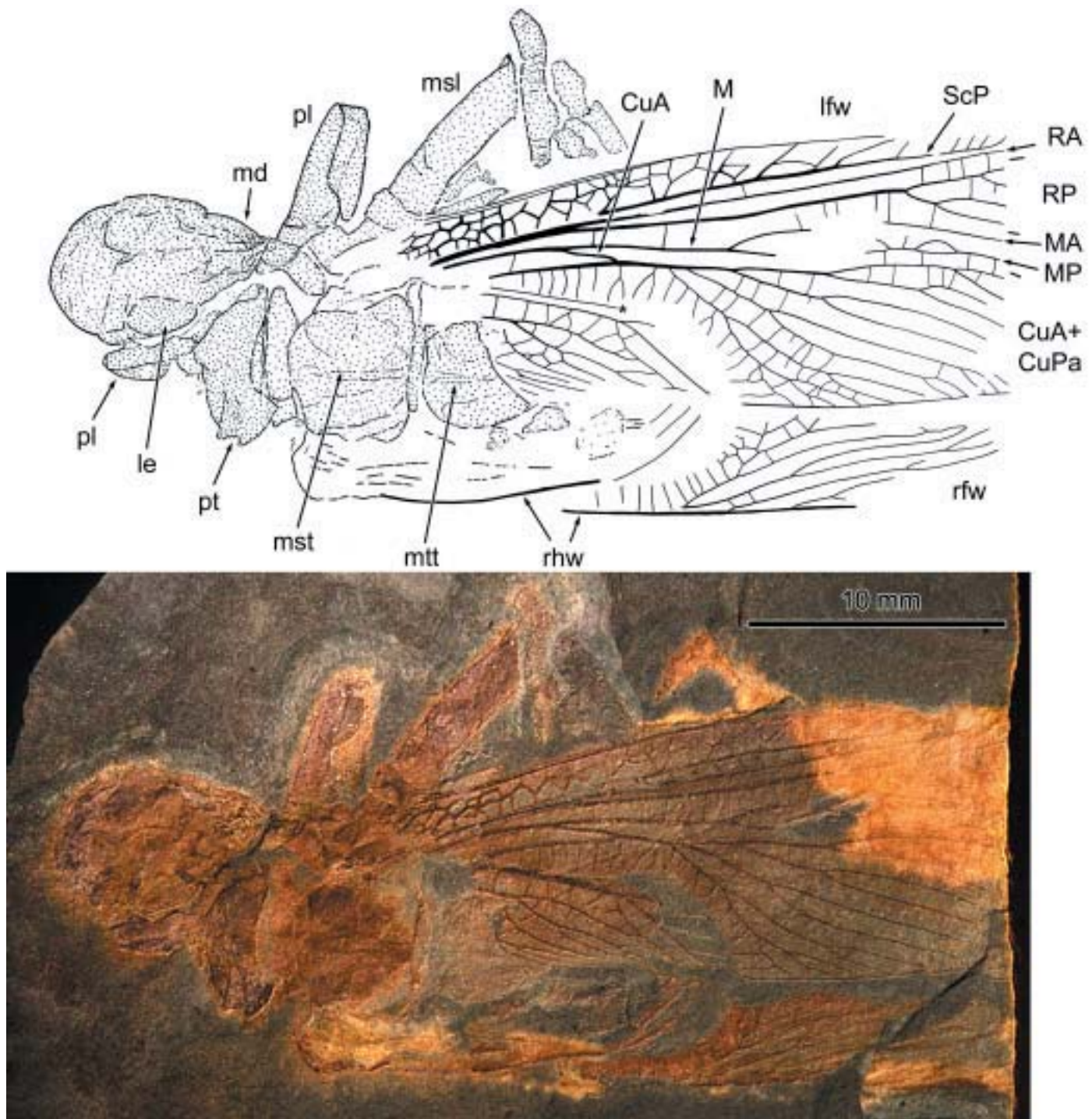


Fig. 1. Species *niedermoschelensis* sp. nov., holotype (PE2008/5007-LS), drawing (remains of the left hind wing omitted; with tentative interpretation) and photograph (negative imprint, composite); see text for wing venation abbreviations; other abbreviations: le, lateral eye; md, mandible; msl, mesothoracic leg; mst, mesothorax; mtt, metathorax; pl, prothoracic leg; pt, prothorax; lfw, left forewing; rfw, right forewing; rhw, right hind wing; * indicates CuPb. See Plates.

definition synonyms of specific epithets, therefore supernumerary (Béthoux in press). In addition, assignment of the new species to the taxon *Archaeorthoptera* is objectively ascertained, owing to the occurrence of the defining character state of this taxon in the new species (Béthoux in press).

We use the wing venation nomenclature elaborated by Béthoux & Nel (2002) for *Archaeorthoptera*, itself based on that of orthopter-

ans (Béthoux & Nel 2001) and on the serial insect wing venation pattern (Lameere 1922, 1923). Corresponding abbreviations are repeated herein for convenience: ScP, posterior subcosta; R, radius; RA, anterior radius; RP, posterior radius; M, media; MA, anterior media; MP, posterior media; CuA, anterior cubitus; CuP, posterior cubitus; CuPa, anterior branch of CuP; CuPb, posterior branch of CuP; AA, anterior analis; AA1, first anterior Analis; AA2, second

anterior Analis. A vein (or vein sector) is said to be convex if located on an elevation, and concave if located in a depression. Criticisms expressed by Gorokhov (2005) regarding this homologization hypothesis are addressed in Béthoux (2007a). Subsequent comments by Rasnitsyn (2007) are addressed in Béthoux (2008b).

Systematic Palaeontology

Taxon *Archaeorthoptera* nom. Béthoux & Nel, 2002, dis.-typ.

Béthoux, 2007d

Species *niedermoschelensis* sp. nov.

Fig. 1

Etymology.—After the village of Niedermoschel (Rhineland-Palatinate, Germany), located near to the collecting site.

Diagnosis.—Forewings: basal to the fusion of CuA with CuPa, area between ScA and ScP with a dense network of strong crossveins; R branched basally; RP simple for a long distance; RP and M branched; CuA (diverging from M + CuA) long; CuA + CuPa with numerous branches, without weak posterior veinlets vanishing in the area between CuA + CuPa and CuPb; crossvein network loose.

Material.—PE2008/5007-LS, positive and negative imprints, part of the Landessammlung für Naturkunde Rheinland-Pfalz (Mainz, Germany), currently housed at the Generaldirektion Kulturelles Erbe, Referat Erdgeschichte (Mainz, Germany).

Description.—Holotype (Fig. 1): more or less completely preserved animal, showing head, thorax with legs attached, incomplete forewings, and incomplete and poorly visible hind wings; total preserved length 37.6 mm; head 8.5 mm long, with large oval lateral eyes and strong, chewing mouthparts; prothorax with lateral extensions, but veins not preserved; prothoracic legs less strong than mesothoracic legs, metathoracic legs not visible; left forewing, preserved length about 24 mm, width 10.4 mm; estimated length about 36 mm; basal to the fork of M, ScA distinct from, and parallel to, anterior wing margin; area between ScA and ScP with a dense network of strong crossveins (*i.e.*, without evident branches of ScP); distal to the fusion of CuA with CuPa, ScP with weakly individualized anterior branches, with crossveins between them; R branched about 7 mm distal to wing base; as preserved, RA simple; RP branched 13.1 mm distal to its origin, with four preserved branches; M and CuA diverge about 6.5 mm distal to wing base; M branched 6.4 mm distal to its origin; MA diverging obliquely; as preserved, MA and MP simple; MP with an eye; free part of CuA 2.1 mm long; CuA + CuPa with a main anterior stem emitting posterior branches, themselves branched, totalling 13 main branches (as preserved), some of these with apical forks; area between CuA + CuPa and CuPb broadly filled with crossveins; as preserved, CuPb simple and weak; AA1 branched and reticulated with the anterior branch of AA2; AA2 branched; crossvenation loose; right forewing: CuA + CuPa with at least 12 main branches; area between CuA + CuPa and CuPb filled with crossveins.

Geological settings.—Niedermoschel bed (Gzhelian/Asselian boundary; Meisenheim Formation, 'Lower Rotliegend'); Niedermoschel (Rhineland-Palatinate, Germany).

Comments.—The relief of main veins is weakly marked, preventing an identification of the veins of the mediocubital area based on convexity

and concavity. However, the new species can be considered as a close relative of lobeattid insects, based on the branching pattern of CuA + CuPa (numerous branches with no consistent organization, but with a stronger anterior stem) and the location of the bifurcation of R [*viz.* in a proximal position; see Béthoux (2005), Béthoux & Nel (2004, 2005), Liu *et al.* (2009), Prokop & Ren (2007)]. Based on fossils in which forewing three-dimensional morphology is known, Béthoux (2005) and Prokop & Ren (2007) assessed that lobeattid insects exhibit the mediocubital organization defining *Archaeorthoptera*, *viz.* a fusion of CuA (diverging from M + CuA) with (a branch of) CuP (Béthoux 2007d). The species *niedermoschelensis* sp. nov. then can be assigned to this taxon.

Among lobeattids, only the taxon *Miamia* nom. Dana, 1864, dis.-typ. Béthoux, 2008a has been defined (Béthoux 2008a). The new species does not exhibit the defining character state of this taxon, *viz.* a fusion of CuPa with M + CuA (*i.e.*, prior to the divergence of CuA from M + CuA). The monophyly of the lobeattid group is not demonstrated (Béthoux 2005, 2008a), and the group is not defined. Therefore, the only possible taxonomic assignment of *niedermoschelensis* sp. nov. is to *Archaeorthoptera*.

The species *niedermoschelensis* sp. nov. differs from other lobeattids such as species assigned to *Miamia*, and the species *elongata* Brongniart, 1893: 433, *silvatica* Laurentiaux & Laurentiaux-Vieira, 1980, and *schneideri* Béthoux, 2005 by its comparatively long CuA in the forewings [see Béthoux (2005, 2008a), Béthoux & Nel (2004)]. Its comparatively small forewing size allows *niedermoschelensis* sp. nov. to be distinguished from *cubitalis* Handlirsch, 1911 and *mazonus* Béthoux, 2005 (Béthoux 2005). In addition the loose forewing crossvenation distinguishes it from *elongata*, *cubitalis*, and *mazonus*. Regarding *huangheense* Prokop & Ren, 2007 and *liuae* Liu *et al.*, 2009 (which are most likely synonyms), *niedermoschelensis* sp. nov. lacks a connection of the anterior branch of MA with RP (or of MA for *liuae*), and well-individualized branches of ScP, diagnostic of the former species [in Prokop & Ren (2007), according to the text and their fig. 4, the anterior branch of MA is fully fused with RP in *huangheense*, *contra* their fig. 5]. Although the available material is incomplete, the erection of a new species is justified.

Discussion

Lobeattid insects exhibit a homogenous morphology from which no Permian groups seem to derive. They appear as a constant component of Late Carboniferous insect faunas and have been reported from the Tupo Formation (Namurian B-C, China, Liu *et al.* 2009, Prokop & Ren 2007), Mazon Creek (Westphalian D, Béthoux 2005, Béthoux 2008a), the North Coal basin of Pas-de-Calais (Westphalian C, France, Béthoux 2008a), and Commentry (Stephanian B-C, France, Béthoux & Nel 2004). The occurrence of the species *niedermoschelensis* sp. nov. near the Gzhelian/Asselian boundary constitutes the latest record of the group (assuming that it is monophyletic).

Paradoxically, *niedermoschelensis* sp. nov. exhibits a long free part of CuA, which is most probably a plesiomorphy within *Archaeorthoptera*: most lobeattid species have a short CuA (*e.g.*, *schneideri*, *elongata*; it is nonexistent in *Miamia*; see references above), while *huangheense*, the earliest lobeattid, and putative outgroups of lobeattids [*e.g.*, *dumasii* Brongniart, 1879, *macroptera* Van Beneden & Coemans, 1867, *palmiformis* Bolton, 1922; see Béthoux 2003; Béthoux & Nel 2004, 2005] exhibit a long one. The species *niedermoschelensis* sp. nov. may therefore occupy a very basal position with respect to other lobeattids, together with *huangheense*.

Conclusion

The importance of the various character-state combinations exhibited by lobeattid insects will have to be evaluated based on a numerical cladistic analysis involving Palaeozoic *Archaeorthoptera* as a whole, taking into account recent revisions and newly described material. The character-state combinations of *huangheense* and *niedermoschelensis* sp. nov. might be important for supporting the monophyly of lobeattids, or of a subgroup within lobeattids.

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Appendix 1.

Nosipteron gen. nov.

Type species. — *Nosipteron niedermoschelensis sp. nov.*

Etymology. — Anagram of 'Sinopteron', name of related genus.

Composition. — *Nosipteron niedermoschelensis sp. nov.*

Diagnosis. — By monotypy, that of the type species.

Discussion. — The unique character-state combination of the type species justifies the erection of a new genus.

Nosipteron niedermoschelensis sp. nov.

Fig. 1

Etymology. — After the village of Niedermoschel (Rhineland-Palatinate, Germany), located nearby the collecting site.

Diagnosis. — Forewings: basal to the fusion of CuA with CuPa, area between ScA and ScP with a dense network of strong crossveins; R branched basally; RP simple for a long distance; RP and M branched; CuA (diverging from M + CuA) long; CuA + CuPa with numerous branches, without weak posterior veinlets vanishing in the area between CuA + CuPa and CuPb; crossvein network loose.

Material. — PE2008/5007-LS, positive and negative imprints, part of the Landessammlung für Naturkunde Rheinland-Pfalz (Mainz, Germany), currently housed at the Generaldirektion Kulturelles Erbe, Referat Erdgeschichte (Mainz, Germany).

Description. — See above.