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A new stem Orthoptera (Archaeorthoptera: Oedischioidea) from the Early Permian of the Saar-Nahe basin, southwest Germany

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ABSTRACT

The new oedischiine *Palatinoedischia elongata* nov. gen., nov. sp. is described from the Early Permian of Germany. It is characterized by a very particular broad area between R+M+CuA and CuP of the tegmen. The possible closest relative is the genus *Plesioidischia*, also from the Early Permian of Germany. They possibly constitute their own clade, but a phylogenetic analysis is needed to clarify the whole superfamily Oedischioidea.

Keywords: Insecta; Oedischiidae; *Palatinoedischia elongata* gen. et sp. nov.; Lower Rotliegend; Saar-Nahe basin.

1. Introduction

The Oedischioidea Handlirsch 1906 is a rather diverse group of Orthoptera, currently known from the Late Carboniferous to the Early Jurassic. Its monophyly and limits, and the composition of the different included families are questionable (Béthoux and Nel, 2002b: 224). A new phylogenetic analysis is needed to solve these important questions, crucial to clarify the phylogeny of the Orthoptera, because, depending on the authors, this superfamily is considered as belonging to the stem group of the Orthoptera or of the Ensifera. Also, depending on the authors (see fossilworks database), the Oedischioidea would comprise the Oedischiinae Handlirsch, 1906, Elcanoedischiinae Gorochov, 1987a, Mezenoedischiinae Gorochov, 1987a, Mesoedischiidae Gorochov, 1987b, Bintoniellidae Handlirsch, 1939, Proparagryllacrididae Riek, 1956, Pruvostitidae Zalessky, 1928 (= Pruvostitinae Zalessky, 1928, Sylvoedischiinae Gorochov, 1987a, Kamiinae Sharov, 1968, Kargalariinae Gorochov, 1995, Maculoedischiinae Gorochov, 1987a, Tettavinae Sharov, 1968), and the Tcholmanvissiidae Zalessky, 1934 (= Tcholmanvissiinae Zalessky, 1934, Tettoedischiinae Gorochov 1987a).

The Late Carboniferous oldest fossil Orthoptera are attributed to this superfamily. It greatly diversified during the Permian. Depending of the confirmation of its monophyly, this superfamily survived the Permian-Triassic mass extinction.

It is also important to better define the limits and Permian diversity of this group through a phylogenetic analysis, in order to estimate the evolutionary changes that could have occurred during the Carboniferous, Permian, and Triassic.

Here we describe a new Early Permian fossil from the Saar-Nahe basin in southwest Germany that belongs to this group but shows some very particular forewing venational structures.

2. Material and methods

The specimen has been found by one of us (MJP) at a locality situated between the villages of Sitters and Schiersfeld in the Moschelbach valley/Rhineland-Palatinate (Fig. 1). Poschmann and Schindler (2004) described a nearby situated locality “Sitters”, which is slightly older than the one that yielded the present specimen. The fossil described here originates from the younger "Niedermoschel black shale" sensu Schindler (1997), stratigraphically belonging to the informal unit M5 of the Jeckenbach Subformation, Meisenheim Formation, Glan Subgroup of the Lower Rotliegend (Boy et al., 2012, Fig. 1).

The Niedermoschel black shale is known since the early 20th century (Reis, 1913). Schindler (1997) characterized it in a stratigraphical context and Poschmann and Schindler (1997) described this unit in terms of lithology and palaeoecology. The type locality yielded plant remains (Uhl, 2008), a variety of vertebrates (e.g., Hampe, 1996, Poschmann and Schindler, 1997) such as fishes and rare branchiosaurs. It is extraordinary for the rich occurrence of arthropods such as ostracods, spinicaudatans, syncarid crustaceans (Uhl, 1999), xiphosurids (Malz and Poschmann, 1993), and insects (Hörnschemeyer, 1999). The terrestrial insect remains were introduced into a lacustrine environment influenced by deltaic input and comprise a large number of lemmatophorids, Blattinopsidae (Hörnschemeyer and Stapf, 2001), and Miomoptera (Hörnschemeyer, 1999; Brauckmann, 2007). Most of the insect fossils are wings less than two centimeters long. An exceptionally preserved stem orthopteran, *Nosipteron niedermoschelensis* Béthoux and Poschmann, 2009, has also been described from there. The new locality near Sitters, which yielded the stem orthopteran described herein, shows essentially the same suite of fossils encompassing plant remains, fishes, conchostracans, xiphosurids, and insects. No detailed scientific exploration is available as yet. The sediments at both localities show contact-metamorphism, which greatly enhanced the recognizability of the insect remains as they appear as shiny, silvery fossils on the dark, gray-bluish matrix (Montenary and Uhl, 2005 concerning preservation).

In fact, the Early Permian insects from "Odernheim town site" described by Prokop et al. (2012) originate from various localities in the Rotliegend of the Saar-Nahe basin (K.-D. Weiß, pers. comm.). Some of these may originate from the Niedermoschel black shale as well.

The specimen was prepared using pneumatic chisels and studied under a Leica MZ 7.5 binocular microscope. It was coated with MgO, photographed using a Canon 600D digital camera equipped with a canon EFS 60mm macro lens and drawn using a Leica drawing tube attached to the microscope. Photographs with differing planes of focus were stacked into a composite with enhanced depth of field using the free software CombineZP by Alan Hadley.

We follow the classification and wing venation terminology of Béthoux and Nel (2002a) and Schubnel et al. (2020) for the Archaeorthoptera. Abbreviations: C costa; ScA subcosta anterior; ScP subcosta posterior; RA radius anterior; RP radius posterior; MA median anterior; MP median posterior; CuA cubitus anterior; CuP cubitus posterior; PCu postcubital vein; AA anal veins.

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3. Systematic palaeontology

Clade Archaeorthoptera Béthoux and Nel, 2002

Order Orthoptera Olivier, 1789

Superfamily Oedischioidea Handlirsch, 1906

Family Oedischiidae Handlirsch, 1906

Subfamily Oedischiinae Handlirsch, 1906

Genus ***Palatinoedischia*** nov.

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Derivation of the name: Named after the Palatinate, the region where the type locality is, and *Oedischia*. Gender feminine.

Type species: *Palatinoedischia elongata* nov. gen., nov. sp.

Diagnosis: Tegmen characters only. Tegmen narrow elongate; a well-defined vein ScA; veins in area between ScA and ScP all simple and straight; ScP with short branches; distal anterior branches of RA short; two to four rows of irregular cells in very broad area between R+M+CuA and CuP, much broader than that between M and CuA+CuPaα; anterior branch MA1 of MA shortly connected to RP; two branches of MA basal of MA1; basal part of CuA elongate; CuPaβ 'rudimentary' near its base, partly 'lost' in a net of irregular cells; no supplementary independent branch basal to fusion of CuPaα with CuA.

Palatinoedischia elongata nov. gen., nov. sp.

Figs 2, 3

urn:lsid:zoobank.org:act:A73201ED-ADFC-418D-A64E-DE1ACD0E2C7F

Derivation of the name: Named '*elongata*' after the narrow elongate tegmen.

Holotype: PE 2018/5000-LS, State Collection of Natural History of Rhineland-Palatinate, Mainz (original collector's number 751-P; see Brauckmann, 2007). Part and counterpart of a nearly complete forewing, very well-preserved with only extreme base and parts of costal and posterior margins missing.

Type horizon and locality: Early Permian, Lower Rotliegend, Meisenheim Formation, Jeckenbach Subformation, Niedermoschel black shale (sensu Schindler, 1997), probably Asselian–?Sakmarian (Schneider and Werneburg, 2012, Schneider et al., 2020); Saar-Nahe Basin south of Sitters, Germany.

Diagnosis: As for the genus by monotypy.

Description: Tegmen 62.3 mm long, 10.7 mm wide, rather narrow elongate and slightly falcate; a well-defined ScA, 10.6 mm long; area between C and ScA poorly preserved, ca. 1.4 mm wide; crossveins between ScA and ScP simple, straight and short, perpendicular to ScP and ScA, those between ScP and C poorly preserved, but apparently also short; area between costal margin and ScP ca. 1.7 mm wide; base of RP 27.0 mm distal of wing base; ScP and R+(M+CuA) well separated, 1.2 mm apart with numerous straight crossveins in between; ScP probably ending in C; presence of a basal common stem R+M+CuA but R and M+CuA separating close to wing base, with a 0.7 mm wide area in-between at level of separation of M with CuA; RA convex, simple, with a narrow distal area with short veinlets between it and C; broad area between RA and RP with strongly curved crossveins, 2.6 mm wide; RP rather concave; distance between its base and point of fusion with MA1 7.3 mm; RP+MA1 0.8 mm long; MA1 long and straight, with an apical fork; RP with five branches; CuA separated from M in basal third of wing, at 13.8 mm from wing base; basal stem of M very short, 0.6 mm long; neutral MA with three distal branches, most basal one simple, second forked; and third (MA1 ending into RP and separating again distally; concave MP simple; CuA fused with CuPaα 2.5 mm of its base; CuA+CuPaα posteriorly pectinate, with three visible branches; CuPa long basal of its fusion with CuA, 4.7 mm long; CuPaβ simple, well discernible as a vein distinctly wider than crossveins at its base, but poorly defined distally and partly lost in an irregular net of cells in a broad area between CuA+CuPaα and CuPb; division of CuP into CuPa and CuPb 10.6 mm from wing base; CuPb simple; PCu and two anal veins, all simple; area between R+M+CuA and CuP very broad, 2.9 mm wide, with a net of 3-4 rows of irregular cells in-between.

4. Discussion

This forewing corresponds to that of a clade Panorthoptera Crampton, 1928 sensu Béthoux and Nel (2002a: 27) because of the following synapomorphies: CuPa differentiated into two branches (CuPaα and CuPaβ) just basal of the fusion of the anterior one (CuPaα) with CuA (synapomorphy of Panorthoptera); ScP probably reaching anterior wing margin and not RA; MA1 and MA2 can be differentiated; CuA+CuPaα with at least two posterior branches; CuPb simple. *Palatinoedischia* nov. gen. shares with the Orthoptera (sensu Béthoux and Nel, 2002a: 38-39) the MA forked; MP, CuPaβ, CuPb, and PCu simple.

Nevertheless, the vein CuPaβ is 'rudimentary' near its base, partly 'lost' in a net of irregular cells. Similar 'aberrant' situations can occur for some other Permian Orthoptera, e.g., '*Tettoedischia minuta* Sharov, 1968, undoubtedly closely related to *Macroedischia* within Tettoedischiinae, has a free and simple CuPaα, without any clear anterior branch reaching CuA'; Béthoux and Nel, 2002b: 224). A similar situation occurs in the panorthopteran family Geraridae Scudder, 1885 (Béthoux and Nel, 2003). The pattern of venation fits quite well with those of the Oedischiinae, in the presence of a well-defined vein ScA, a series of regular crossveins in subcostal area and area between ScP and R/RA, ScP and RA well separated, broad areas between RA and RP and between R/RP and MA, and basal fork of M very close to point of separation between M and CuA. We consider that the venation of *Palatinoedischia* nov. gen. is compatible with an attribution to the Orthoptera.

Palatinoedischia nov. gen. has two to four rows of irregular cells in the area between R+M+CuA and CuP, while nearly all the described Oedischioidea have a distinctly narrower area with one row of cells. A similar situation occurs in *Gerarus* Scudder, 1885. *Palatinoedischia* nov. gen. strongly differs from the Geraridae in the simple MP and CuPb, narrow elongate tegmen, and very short stem of M (Béthoux and Nel, 2003).

Also, affinities with the Tcholmanvissiidae sensu Béthoux and Nel (2002b) are excluded because *Palatinoedischia* nov. gen. has an anterior branch of MA ending into RP, and no supplementary independent branch basal to fusion of CuPaα with CuA. The Bintoniellidae and the Proparagryllacrididae also have no anterior branch of MA ending into RP (Riek, 1955, 1956, 1976; Sharov, 1968; Gorochov, 1987b, 1989, 2013; Béthoux and Beckemeyer, 2007).

The Mezenoedischiinae have a narrow area between MP and the anterior stem of CuA + CuPaα, and the presence of only one branch of MA posterior to base of MA1, unlike two in *Palatinoedischia* nov. gen. (Carpenter, 1966; Sharov, 1968; Gorochov, 1987a; Béthoux et al., 2002; Béthoux and Beckemeyer, 2007). The Elcanoedischiinae (*Kansasoedischia* Gorochov

1987a, *Elcanoedischia* Gorochov 1987a, *Metoedischia* Martynov 1928); and the Sylvoedischiinae (*Stenoedischia* Gorochov 1987a, *Sylvoedischia* Sharov 1968) differ from *Palatinoedischia* nov. gen. in the presence of only one branch of MA posterior to base of MA1 (Martynov, 1928; Sharov, 1968; Gorochov, 1987a). The Sylvoedischiinae also have broader tegmina compared to their length. The Pruvostitidae have ScP with longer branches than in *Palatinoedischia* nov. gen., and either only one branch of MA posterior to base of MA1 and/or a long basal stem of M before its separation into MA and MP, and/or no fusion between anterior branch of MA and RP, unlike *Palatinoedischia* nov. gen. (Zalessky, 1929; Gorochov, 1987a,c, 2013). The Mesoedischiidae also have a long stem of M (Sharov, 1968; Gorochov, 2005).

The Oedischiinae Handlirsch, 1906 have a short stem of M as in *Palatinoedischia* nov. gen. *Oedischia* Handlirsch, 1906 has only one branch of MA posterior to base of MA1 (Sharov, 1968). *Sinoedischia* Hong, 1985 has such two branches, but the basal half of the tegmen is not preserved, so that the length of basal part of M and the pattern of the cubital veins are unknown, rendering the position of this taxon uncertain (Hong, 1985: figs 29-30). *Anhomalophlebia* Handlirsch, 1919 has a basal stem of M longer than in *Palatinoedischia* nov. gen. and no fusion of a branch of MA with RP (see figure in the internet site http://mediaphoto.mnhn.fr/media/14986360852690vFhvxWDuH8srHmM).

Afroedischia Geertsema and van Dijk, 1999 has a very long stem of M, and no fusion of a branch of MA with RP (Geertsema and van Dijk, 1999: figs 1-2). *Anelcana* Carpenter, 1986 (replacement name for *Parelcana* Carpenter, 1966) differs from *Palatinoedischia* nov. gen. in the area between ScA and ScP quite narrow, a very short basal part of CuA and a short CuPaβ (Carpenter, 1966: fig. 19). *Kamaites* Zalessky, 1929 is based on a very incomplete wing not showing the essential structures to be compared to the other Orthoptera (Zallesky, 1929: fig. 9). *Nobloedischia* Beckemeyer, 2011a differs from *Palatinoedischia* nov. gen. in the presence of only one branch of MA posterior of MA1, presence of long anterior branches of RA, narrower

areas between R+M+CuA and CuP and between CuPa and CuPb (Beckemeyer, 2011a: figs 1-3). *Scalaeoptera* Bolton, 1922 is based on a very fragmentary tegmen, impossible to compare to the other Paleozoic Orthoptera (Bolton, 1922: fig. 27). *Xeroptera* Bolton, 1922 is also based on an incomplete tegmen; it possibly does not belong to the Archaeorthoptera but to a very different group, the Paoliida (sensu Prokop et al., 2014), because it has a series of anterior branches of CuA, a rather broad area between CuA and CuP, and apparently no branches of CuP ending into CuA (Bolton, 1922: fig. 26). This taxon needs to be revised.
Loxoedischia Beckemeyer, 2011b shares many characters with *Palatinoedischia* nov. gen. in the pattern of the veins Cu and M, ScP and ScA. Nevertheless, it has anterior branches of RP, no branch of MA ending into RP (Beckemeyer, 2011b: fig. 1).

The tegmen of *Plesioidischia baentschi* Schlechtendal, 1906 (in Handlirsch, 1906) from the upper Meisenheim or Disibodenberg Formation of Nonnweiler near Birkenfeld/Nahe, revised by Guthörl (1934: fig. 58), greatly resembles that of *Palatinoedischia* nov. gen., with only the following differences: the area between R+M+CuA and CuP is only slightly wider than that between M and CuA+CuPaα, the veins in area between ScA and ScP are clearly irregular while they are all simple and straight in *Palatinoedischia* nov. gen. Bolton (1922: 92-93, text-fig. 29, pl. 6, fig. 3) described and figured a *Plesioidischia* sp. from the 'Middle Coal Measures (binds between 'Brooch' and 'Thick' coals); Tipton, Staffs' in UK. This fossil is the basal third of a tegmen, but it does not show the broadened area between R+M+CuA and CuP of *Plesioidischia baentschi*. It probably corresponds to a different genus; we consider it as an Oedischioidea *incertae sedis*.

5. Conclusion

Palatinoedischia nov. gen. does not fit with any of the described Oedischioidea. It seems to be close to *Plesioidischia baentschi* because of the great similarities in the wing venations.

Plesioidischia is also known from the early Permian of Germany, but the new fossil clearly corresponds to a different genus and species. Both could belong to the same clade, characterized by the broadened area between R+M+CuA and CuP. We provisionally attribute it to the Oedischiinae, but a phylogenetic analysis of the whole Oedischioidea is necessary to clarify the relationships and definitions of its different components. The monophyly of the whole group and its components are questionable. Thus the comparison of any new taxon to the different families and genera can only be based on similarities and not on well-defined synapomorphies.

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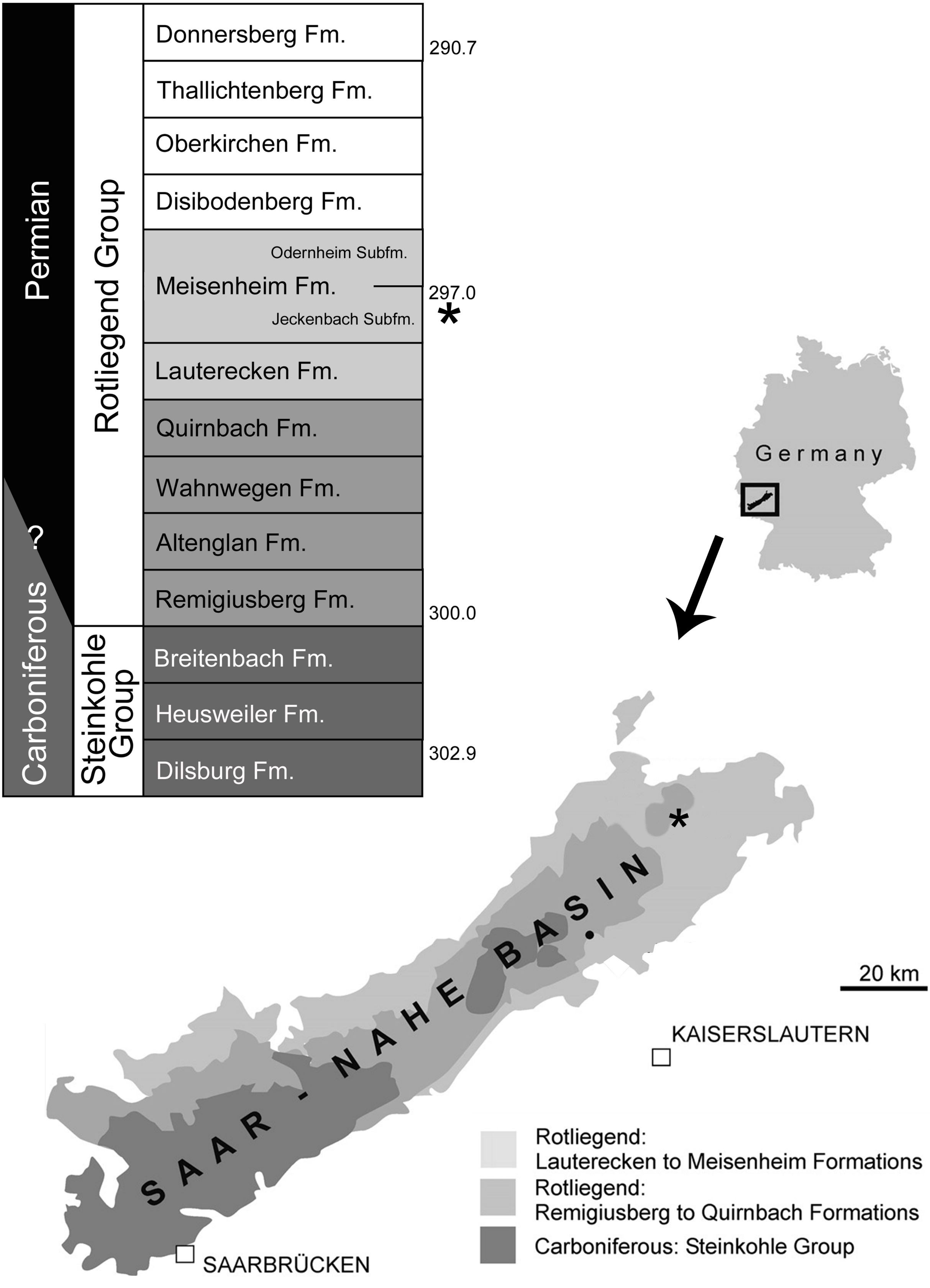
Figure captions:

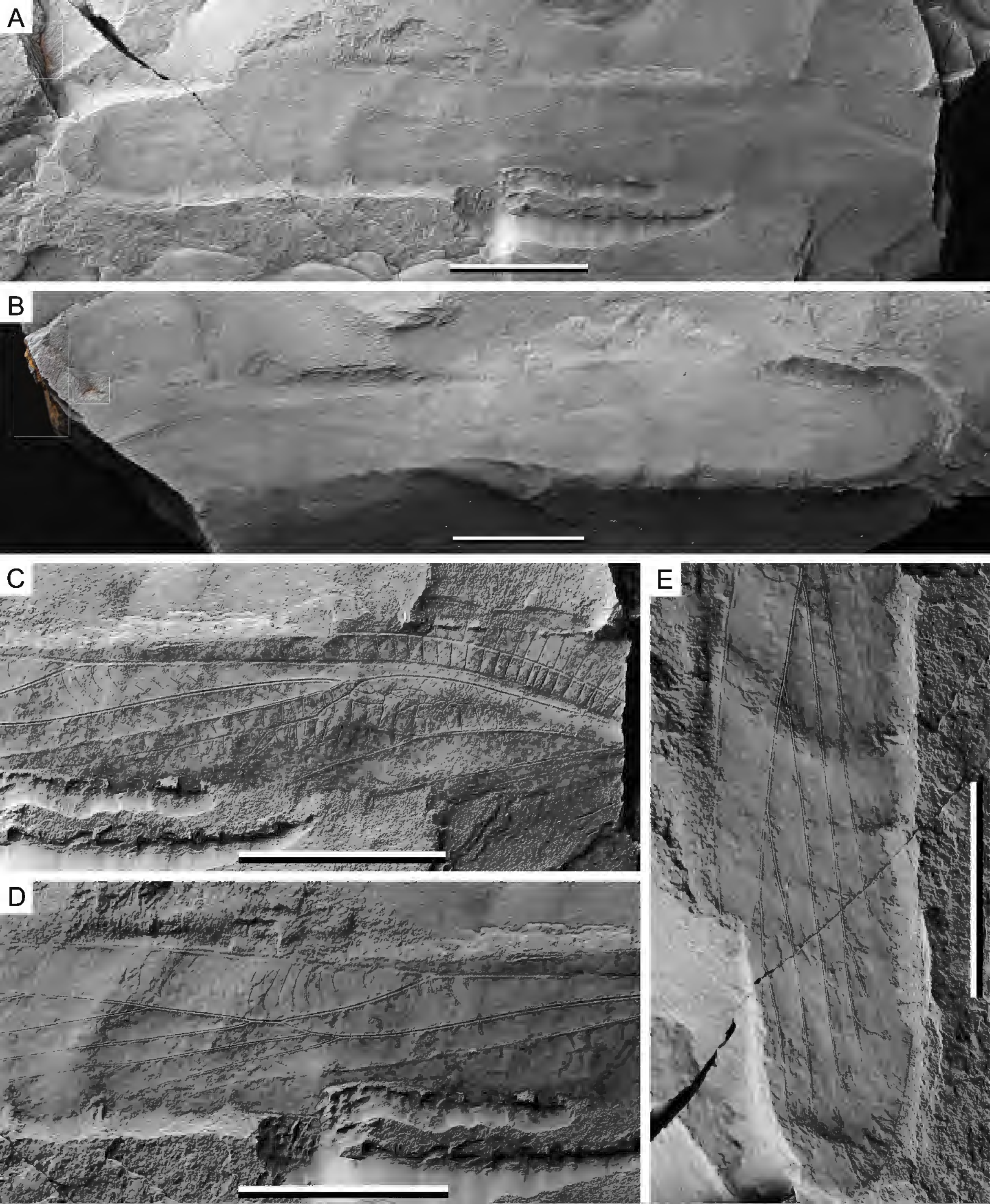
Fig. 1. Simplified geographical position and geology (with approximate ages, mya) of the Saar-Nahe Basin, with both the ‘Niedermoschel black pelite’ and the Sitters locality indicated by black asterisks (modified after Sanchez et al., 2010).

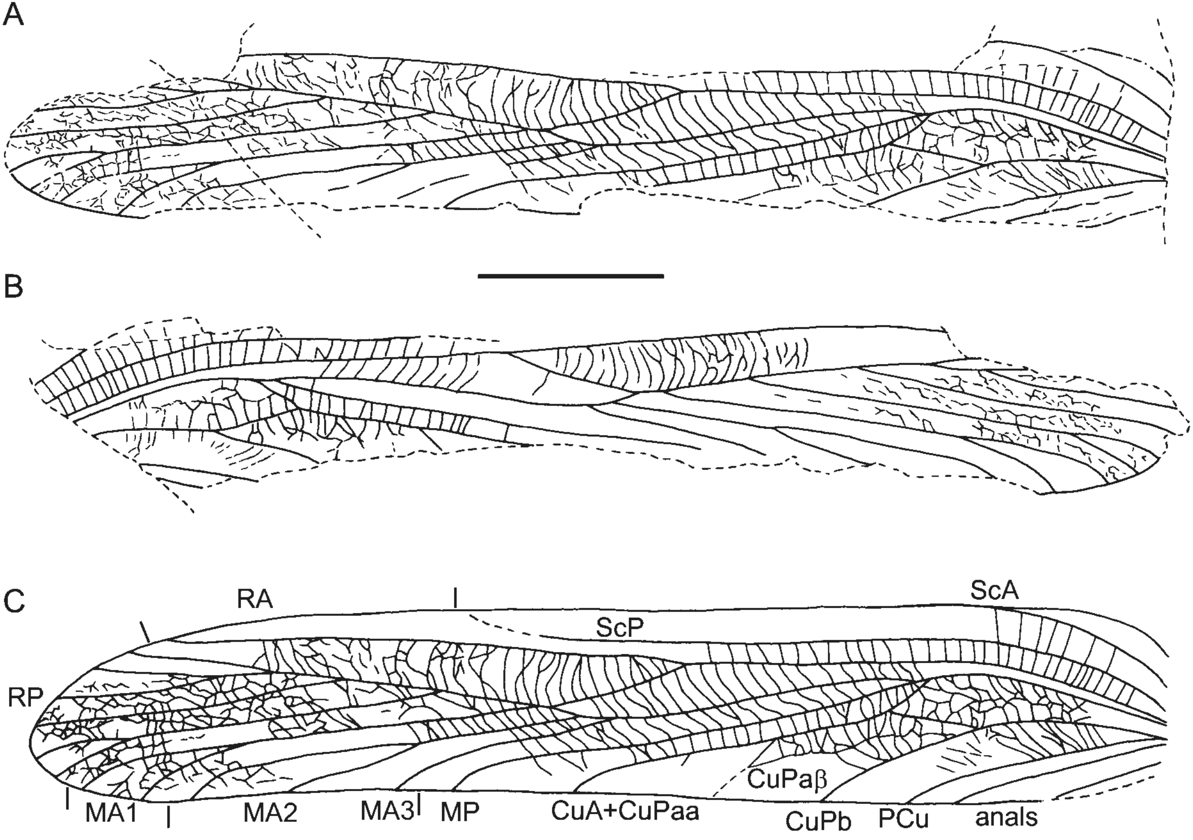
Fig. 2. *Palatinoedischia elongata* nov. gen., nov. sp., holotype PE 2018/5000-LS. Photographs of forewing, whitened with MgO. **A**. Part PE 2018/5000-LSa. **B**. Counterpart PE 2018/5000-LSb. **C**. Basal portion of part. **D**. Middle portion. **E**. Apical portion, rotated 90° counter-clockwise. Scale bars: 10 mm.

Fig. 3. *Palatinoedischia elongata* nov. gen., nov. sp., holotype PE 2018/5000-LS. Drawings. **A**. Part PE 2018/5000-LSa. **B**. Counterpart PE 2018/5000-LSb. **C**. Interpretative drawing of wing venation combined from part and counterpart. Scale bar: 10 mm.



Permian
Carboniferous
?
Rotliegend Group
Steinkohle Group
Donnersberg Fm.
Thallichtenberg Fm.
Oberkirchen Fm.
Disibodenberg Fm.
Odernheim Subfm.
Meisenheim Fm.
Jeckenbach Subfm.
Lauterecken Fm.
Quirnbach Fm.
Wahnwegen Fm.
Altenglan Fm.
Remigiusberg Fm.
Breitenbach Fm.
Heusweiler Fm.
Dilsburg Fm.
290.7
297.0
*
300.0
302.9
Germany
SAAR - NAHE BASIN
*
20 km
KAISERSLAUTERN
SAARBRÜCKEN
Rotliegend: Lauterecken to Meisenheim Formations
Rotliegend: Remigiusberg to Quirnbach Formations
Carboniferous: Steinkohle Group


A
B
C
D
E


A
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MA2
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CuA+CuPaa
CuPaβ
CuPb
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