

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

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3	Nahe basin, southwest Germany
4	
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12	
13	ABSTRACT
14	The new oedischiine Palatinoedischia elongata nov. gen., nov. sp. is described from the Early
15	Permian of Germany. It is characterized by a very particular broad area between R+M+CuA
16	and CuP of the tegmen. The possible closest relative is the genus Plesioidischia, also from the
17	Early Permian of Germany. They possibly constitute their own clade, but a phylogenetic
18	analysis is needed to clarify the whole superfamily Oedischioidea.
19	
20	Keywords: Insecta; Oedischiidae; Palatinoedischia elongata gen. et sp. nov.; Lower
21	Rotliegend; Saar-Nahe basin.
22	
23	1. Introduction
24	The Oedischioidea Handlirsch 1906 is a rather diverse group of Orthoptera, currently known
25	from the Late Carboniferous to the Early Jurassic. Its monophyly and limits, and the

A new stem Orthoptera (Archaeorthoptera: Oedischioidea) from the Early Permian of the Saar-

composition of the different included families are questionable (Béthoux and Nel, 2002b: 224). 26 27 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 28 29 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 30 Handlirsch, 1906, Elcanoedischiinae Gorochov, 1987a, Mezenoedischiinae Gorochov, 1987a, 31 Mesoedischiidae Gorochov, 1987b, Bintoniellidae Handlirsch, 1939, Proparagryllacrididae 32 Riek, 1956, Pruvostitidae Zalessky, 1928 (= Pruvostitinae Zalessky, 1928, Sylvoedischiinae 33 Gorochov, 1987a, Kamiinae Sharov, 1968, Kargalariinae Gorochov, 1995, Maculoedischiinae 34 Gorochov, 1987a, Tettavinae Sharov, 1968), and the Tcholmanvissiidae Zalessky, 1934 (= 35 Tcholmanvissiinae Zalessky, 1934, Tettoedischiinae Gorochov 1987a). 36

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.

46

47 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 55 (1997) characterized it in a stratigraphical context and Poschmann and Schindler (1997) 56 described this unit in terms of lithology and palaeoecology. The type locality yielded plant 57 remains (Uhl, 2008), a variety of vertebrates (e.g., Hampe, 1996, Poschmann and Schindler, 58 1997) such as fishes and rare branchiosaurs. It is extraordinary for the rich occurrence of 59 arthropods such as ostracods, spinicaudatans, syncarid crustaceans (Uhl, 1999), xiphosurids 60 (Malz and Poschmann, 1993), and insects (Hörnschemeyer, 1999). The terrestrial insect 61 remains were introduced into a lacustrine environment influenced by deltaic input and comprise 62 63 a large number of lemmatophorids, Blattinopsidae (Hörnschemeyer and Stapf, 2001), and Miomoptera (Hörnschemeyer, 1999; Brauckmann, 2007). Most of the insect fossils are wings 64 less than two centimeters long. An exceptionally preserved stem orthopteran, Nosipteron 65 niedermoschelensis Béthoux and Poschmann, 2009, has also been described from there. The 66 new locality near Sitters, which yielded the stem orthopteran described herein, shows 67 essentially the same suite of fossils encompassing plant remains, fishes, conchostracans, 68 xiphosurids, and insects. No detailed scientific exploration is available as yet. The sediments at 69 both localities show contact-metamorphism, which greatly enhanced the recognizability of the 70 insect remains as they appear as shiny, silvery fossils on the dark, gray-bluish matrix 71 (Montenary and Uhl, 2005 concerning preservation). 72

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.

76	The specimen was prepared using pneumatic chisels and studied under a Leica MZ 7.5
77	binocular microscope. It was coated with MgO, photographed using a Canon 600D digital
78	camera equipped with a canon EFS 60mm macro lens and drawn using a Leica drawing tube
79	attached to the microscope. Photographs with differing planes of focus were stacked into a
80	composite with enhanced depth of field using the free software CombineZP by Alan Hadley.
81	We follow the classification and wing venation terminology of Béthoux and Nel (2002a) and
82	Schubnel et al. (2020) for the Archaeorthoptera. Abbreviations: C costa; ScA subcosta anterior;
83	ScP subcosta posterior; RA radius anterior; RP radius posterior; MA median anterior; MP
84	median posterior; CuA cubitus anterior; CuP cubitus posterior; PCu postcubital vein; AA anal
85	veins.
86	urn:lsid:zoobank.org:pub:F2195993-BA7A-4BC3-8342-EF6E6AEEB13E
87	
88	3. Systematic palaeontology
89	Clade Archaeorthoptera Béthoux and Nel, 2002
90	Order Orthoptera Olivier, 1789
91	Superfamily Oedischioidea Handlirsch, 1906
92	Family Oedischiidae Handlirsch, 1906
93	Subfamily Oedischiinae Handlirsch, 1906
94	Genus <i>Palatinoedischia</i> nov.
95	urn:lsid:zoobank.org:act:066637A2-A1FE-43E0-9D3B-6E969F85CE7C
96	Derivation of the name: Named after the Palatinate, the region where the type locality is, and
97	Oedischia. Gender feminine.
98	Type species: Palatinoedischia elongata nov. gen., nov. sp.
99	Diagnosis: Tegmen characters only. Tegmen narrow elongate; a well-defined vein ScA; veins
100	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.

107 Palatinoedischia elongata nov. gen., nov. sp.

108 Figs 2, 3

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

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

111 Holotype: PE 2018/5000-LS, State Collection of Natural History of Rhineland-Palatinate,

112 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 andposterior 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

¹⁰⁶

probably ending in C; presence of a basal common stem R+M+CuA but R and M+CuA 126 127 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; 128 broad area between RA and RP with strongly curved crossveins, 2.6 mm wide; RP rather 129 concave; distance between its base and point of fusion with MA1 7.3 mm; RP+MA1 0.8 mm 130 long; MA1 long and straight, with an apical fork; RP with five branches; CuA separated from 131 132 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 133 ending into RP and separating again distally; concave MP simple; CuA fused with CuPaa 2.5 134 135 mm of its base; CuA+CuPaa posteriorly pectinate, with three visible branches; CuPa long basal of its fusion with CuA, 4.7 mm long; CuPaß simple, well discernible as a vein distinctly wider 136 than crossveins at its base, but poorly defined distally and partly lost in an irregular net of cells 137 in a broad area between CuA+CuPaa and CuPb; division of CuP into CuPa and CuPb 10.6 mm 138 from wing base; CuPb simple; PCu and two anal veins, all simple; area between R+M+CuA 139 140 and CuP very broad, 2.9 mm wide, with a net of 3-4 rows of irregular cells in-between.

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142 **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 CuPaß is 'rudimentary' near its base, partly 'lost' in a net of 150 irregular cells. Similar 'aberrant' situations can occur for some other Permian Orthoptera, e.g., 151 'Tettoedischia minuta Sharov, 1968, undoubtedly closely related to Macroedischia within 152 Tettoedischiinae, has a free and simple CuPaa, without any clear anterior branch reaching 153 CuA'; Béthoux and Nel, 2002b: 224). A similar situation occurs in the panorthopteran family 154 Geraridae Scudder, 1885 (Béthoux and Nel, 2003). The pattern of venation fits quite well with 155 those of the Oedischiinae, in the presence of a well-defined vein ScA, a series of regular 156 crossveins in subcostal area and area between ScP and R/RA, ScP and RA well separated, broad 157 areas between RA and RP and between R/RP and MA, and basal fork of M very close to point 158 159 of separation between M and CuA. We consider that the venation of *Palatinoedischia* nov. gen. is compatible with an attribution to the Orthoptera. 160

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 175 Sylvoedischiinae (Stenoedischia Gorochov 1987a, Sylvoedischia Sharov 1968) differ from 176 Palatinoedischia nov. gen. in the presence of only one branch of MA posterior to base of MA1 177 (Martynov, 1928; Sharov, 1968; Gorochov, 1987a). The Sylvoedischiinae also have broader 178 tegmina compared to their length. The Pruvostitidae have ScP with longer branches than in 179 Palatinoedischia nov. gen., and either only one branch of MA posterior to base of MA1 and/or 180 181 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, 182 2013). The Mesoedischiidae also have a long stem of M (Sharov, 1968; Gorochov, 2005). 183

184 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, 185 1968). Sinoedischia Hong, 1985 has such two branches, but the basal half of the tegmen is not 186 preserved, so that the length of basal part of M and the pattern of the cubital veins are unknown, 187 rendering the position of this taxon uncertain (Hong, 1985: figs 29-30). Anhomalophlebia 188 Handlirsch, 1919 has a basal stem of M longer than in Palatinoedischia nov. gen. and no fusion 189 of branch of MA with RP (see figure in the internet 190 а site 191 http://mediaphoto.mnhn.fr/media/14986360852690vFhvxWDuH8srHmM).

Afroedischia Geertsema and van Dijk, 1999 has a very long stem of M, and no fusion of a 192 branch of MA with RP (Geertsema and van Dijk, 1999: figs 1-2). Anelcana Carpenter, 1986 193 (replacement name for Parelcana Carpenter, 1966) differs from Palatinoedischia nov. gen. in 194 the area between ScA and ScP quite narrow, a very short basal part of CuA and a short CuPaß 195 (Carpenter, 1966: fig. 19). Kamaites Zalessky, 1929 is based on a very incomplete wing not 196 showing the essential structures to be compared to the other Orthoptera (Zallesky, 1929: fig. 9). 197 Nobloedischia Beckemeyer, 2011a differs from Palatinoedischia nov. gen. in the presence of 198 only one branch of MA posterior of MA1, presence of long anterior branches of RA, narrower 199

areas between R+M+CuA and CuP and between CuPa and CuPb (Beckemeyer, 2011a: figs 13). *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 210 the upper Meisenheim or Disibodenberg Formation of Nonnweiler near Birkenfeld/Nahe, 211 212 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 213 214 than that between M and CuA+CuPaa, the veins in area between ScA and ScP are clearly irregular while they are all simple and straight in Palatinoedischia nov. gen. Bolton (1922: 92-215 93, text-fig. 29, pl. 6, fig. 3) described and figured a Plesioidischia sp. from the 'Middle Coal 216 Measures (binds between 'Brooch' and 'Thick' coals); Tipton, Staffs' in UK. This fossil is the 217 basal third of a tegmen, but it does not show the broadened area between R+M+CuA and CuP 218 of Plesioidischia baentschi. It probably corresponds to a different genus; we consider it as an 219 Oedischioidea incertae sedis. 220

221

222 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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- 390 Figure captions:
- 391
- Fig. 1. Simplified geographical position and geology (with approximate ages, mya) of the SaarNahe Basin, with both the 'Niedermoschel black pelite' and the Sitters locality indicated by
 black asterisks (modified after Sanchez et al., 2010).
- 395

396	Fig. 2. Palatinoedischia elongata nov. gen., nov. sp., holotype PE 2018/5000-LS. Photographs
397	of forewing, whitened with MgO. A. Part PE 2018/5000-LSa. B. Counterpart PE 2018/5000-
398	LSb. C. Basal portion of part. D. Middle portion. E. Apical portion, rotated 90° counter-
399	clockwise. Scale bars: 10 mm.
400	
401	Fig. 3. Palatinoedischia elongata nov. gen., nov. sp., holotype PE 2018/5000-LS. Drawings.
402	A. Part PE 2018/5000-LSa. B. Counterpart PE 2018/5000-LSb. C. Interpretative drawing of

403 wing venation combined from part and counterpart. Scale bar: 10 mm.

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