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Fossil dragonflies (Odonata: Anisoptera) from the late Oligocene Fossil-Lagerstätte Enspel (Rhineland-Palatinate, SW Germany)

THOMAS BROCKHAUS[1], OLE MÜLLER[2], ANDRÉ NEL[3], MARKUS J. POSCHMANN[4] * & TORSTEN WAPPLER[5]
[1]*An der Morgensonne 5, D-09387 Jahnsdorf/Erzgebirge, Germany*
[2]*Birkenweg 6d, D-15306 Libbenichen, Germany*
[3]*Institut de Systématique, Evolution, Biodiversité, ISYEB, UMR 7205, CNRS, MNHN, UPMC, EPHE, Muséum national d'Histoire naturelle, Sorbonne Universités, 57 rue Cuvier, CP 50, Entomologie, F-75005, Paris, France*
[4]*Generaldirektion Kulturelles Erbe Rheinland-Pfalz, Direktion Landesarchäologie/Erdgeschichte, Niederberger Höhe 1, D-56077 Koblenz, Germany*
[5]*Natural History Department, Hessisches Landesmuseum Darmstadt, Friedensplatz 1, D-64283 Darmstadt, Germany*
t.brockhaus@t-online.de; https://orcid.org/0000-0003-1553-3259
mueller.ole@gmail.com; https://orcid.org/0000-0002-1669-3804
andre.nel@mnhn.fr; https://orcid.org/0000-0002-4241-7651
markus.poschmann@gdke.rlp.de; https://orcid.org/0000-0001-9710-1673
torsten.wappler@hlmd.de; https://orcid.org/0000-0003-1592-0988
**Corresponding author.*

Abstract

Fossils of dragonflies (Odonata: Anisoptera), three larvae and one isolated hind wing, are described from the late Oligocene crater lake of Enspel (Westerwald, Germany). The larvae are interpreted to belong to one species, although representing three different ontogenetic stages. Comparison to extant taxa shows that the larvae are to be assigned to the clubtails (Gomphidae), namely to the genera *Gomphidia* or *Ictinogomphus,* or, more unlikely, *Diastatomma* in the subfamily Lindeniinae, and thus constitute the first record of larvae of this subfamily in the Oligocene. The venation pattern of the hind wing clearly shows that it belongs to a species in the family Macromiidae and thus constitutes the oldest record of this family.

Keywords: Late Oligocene, Enspel, Odonata, larvae, Gomphidae, Lindeniinae, Macromiidae

Introduction

The Fossil-Lagerstätte Enspel represents a Late Oligocene crater-lake deposit (*e.g.*, Felder *et al.*, 1998; Pirrung *et al.*, 2001; Schindler & Wuttke, 2010, 2015), which was excavated by the former Landesamt für Denkmalpflege/Referat Erdgeschichte (now part of the Generaldirektion Kulturelles Erbe Rheinland-Pfalz) from 1990 until 2015, and yielded a variety of plants, invertebrates, fish, amphibians, and mammals (for an overview see Poschmann *et al.*, 2010). The locality (Fig. 1) has an excellent age constraint and can be assigned to mammal zone MP28 based on the occurrence of eomyid rodents (Storch *et al.*, 1996; Engesser & Storch 1999), whereas radioisotopic dating of basalts on the base and top of the Enspel sequence yielded an age of 24.79−24.56 Ma for the intercalated lake sediments (Mertz *et al.*, 2007). For further details about the geological setting of the Enspel site see Schindler & Wuttke (2010, 2015) and Schäfer *et al.* (2011).

Aspects of taphonomy, palaeoecology, and taxonomic composition of the Enspel insect taphocoenosis have been approached by Wedmann (1998a, 2000) and Wedmann *et al.* (2010). Comparatively few taxa were hitherto described in more detail and received taxonomic treatment. The latter include various Hymenoptera (Wedmann, 1997, 1998b), bibionid Diptera (Wedmann, 1998a), aradid Heteroptera (Wappler & Heiss, 2006), hydrophilid (Fikáček *et al.*, 2008) and cantharidid Coleoptera (Fanti & Poschmann, 2019), in addition to larval cases of Trichoptera (Poschmann, 2006), and leaf damage attributable to insect activity (Gunkel & Wappler, 2015). Some of the insect fossils, especially among the Coleoptera, show excellent preservation of structural colors (McNamara *et al.*, 2012) or color patterns (Fanti & Poschmann, 2019). With respect to Odonata, one fossil of adult Zygoptera and both larvae and wings of Aeshnidae have been identified so far, some of the latter being assigned to *Oligaeschna jungi* Piton & Théobald, 1939 (Wedmann, 2000; Wedmann *et*

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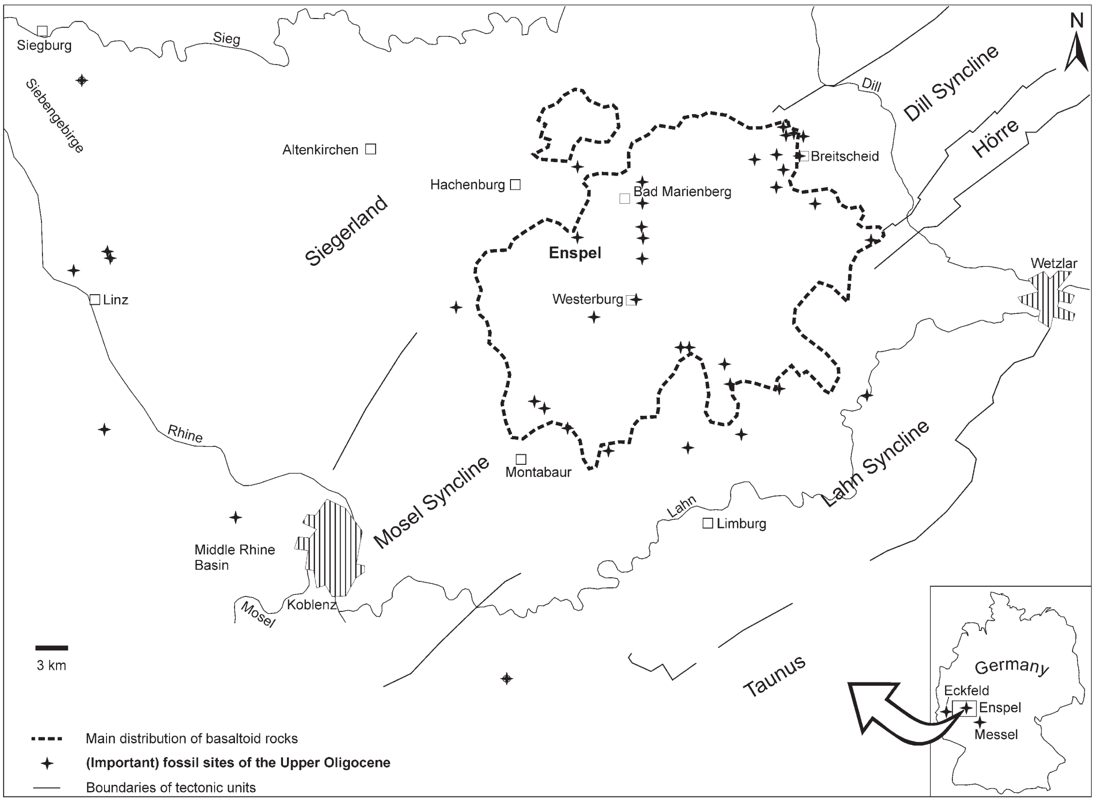

FIGURE 1. Geographical position of Enspel and further Oligocene fossil sites in the Westerwald volcanic field (modified from Schindler & Wuttke, 2010).

al., 2010). Furthermore, a single zygopteran egg-set of the coenagrionid-type has been figured by Poschmann & Wedmann (2005). In the course of these ongoing studies, we here describe further remarkable dragonfly fossils, comprising three larvae and one hindwing. The larvae can be attributed to the gomphid genera *Gomphidia* or *Ictinogomphus*, or, more unlikely, *Diastatomma,* and the hind wing belongs to the family Macromiidae and thus is the hitherto oldest record of this family.

Material and methods

The number of fossil specimens from Enspel kept in the Natural History Collection of Rhineland-Palatinate totals more than 23,000 fossils, with the largest share of about 12,300 specimens accounting for insects (MJP, unpublished data). Odonata are generally rare, in addition to very few fossils of odonatan wings, 67 fossils attributable to larval stages of Odonata were identified, with the highest share of 41 specimens (about 60%) originating from layer S14 (Fig. 2). However, this is probably due to favourable preservational factors present in the basal layer of S14 (Poschmann & Wedmann, 2005; Uhl & Poschmann, 2018), which yielded at least 28 specimens (for some, the exact position within S14 has not been recorded).

The studied specimens were found during excavations conducted by the Generaldirektion Kulturelles Erbe Rheinland-Pfalz, Direktion Landesarchäologie/Erdgeschichte, and are part of the Natural History Collection of Rhineland-Palatinate, Mainz, Germany. Photographs were taken (by MJP) with the specimens immersed in water using a Canon EOS 600D SLR camera equipped with a Canon EFS 60 mm or a Canon MP-E 65 mm macro lens, respectively. Depth of field was enhanced by stacking photographs of differing focal planes into a composite using the software CombineZP (by Alan Hadley). Drawings were made (by OM) from photographs using graphic tablets Wacom Intuos and Surface Book.

Systematic palaeontology

Oder Odonata Fabricius, 1793
Suborder Epiprocta Lohmann, 1996
Infraorder Anisoptera Sélys Longchamps in Sélys Longchamps & Hagen, 1854
Clade Gomphida Bechly, 1996
Family Gomphidae Rambur, 1842
Subfamily Lindeniinae Jacobson & Bianchi, 1905

Genus and species unidentified
(Figs 3–7)

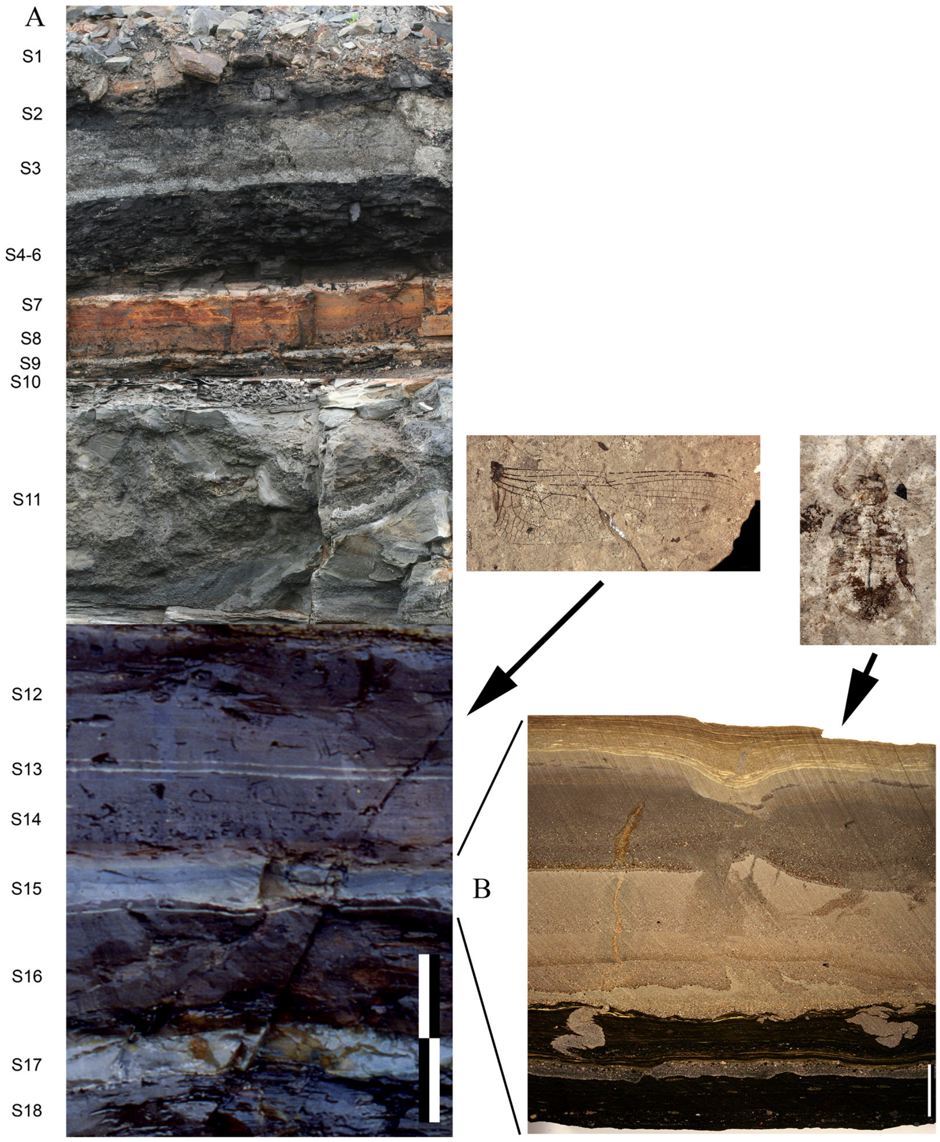

FIGURE 2. Partial stratigraphy of Enspel fossil site. **A**, Profile of excavated Enspel sequence, compiled from photographs of various digging sites. Scale bar = 20 cm. **B**, Event layer S15 and base of oil-shale layer S14 enlarged. Scale bar = 10 mm. Black arrows: origins of odonate fossils described herein indicated (modified from Uhl & Poschmann, 2018).

Diagnosis. All tarsi two-segmented; abdomen broad, rounded, almost as wide as long (according to Theischinger & Endersby, 2009).

Locality and horizon. Enspel/Westerwald, southwest Germany. Late Oligocene: 24.9–24.5 Ma. Mammal Zone MP 28.

Description. Three fossils of dragonfly larvae constitute the base of the following description. The smaller larvae PE 2012/5282-LS (Figs 3, 6A) and PE 2007/5005-LS (Figs 5, 6C) are dorso-ventrally flattened, whereas the larger fossil PE 2010/5654-LS (Figs 4, 6B) is seen in dorso-lateral view. The overall length of the fossils is 7.9 mm, 10.2 mm, and 23.7 mm, respectively. The larvae apparently have a broad, strongly dorso-ventrally flattened body. Table 1 shows the morphometrics of the relevant structures.

The head appears to be wider than long, with the lateral margins of the eyes and the anterior structures of the head capsule forming an anteriorly tapering triangle. In all cases, the labia are in an extended position and the inner margins of the praementum are clearly discernable, as well as the labial palps with their terminal hooks. Although their bases are concealed by the head capsules, a rectangular form of the prementa is indicated. The palpi are invariably closed. The palpi and the distal margin of the praementum are well exposed (Figs 3E, 4D, 5C). The palpi have a blunt termination and the proximal inner margin shows a delicate dentation. The movable terminal hooks are strong and short (0.2 mm). The ligula is slightly curved with a weak dentation indicated.

External wing buds or wing sheets are most clearly exposed in PE 2010/5654-LS and are oriented parallel to

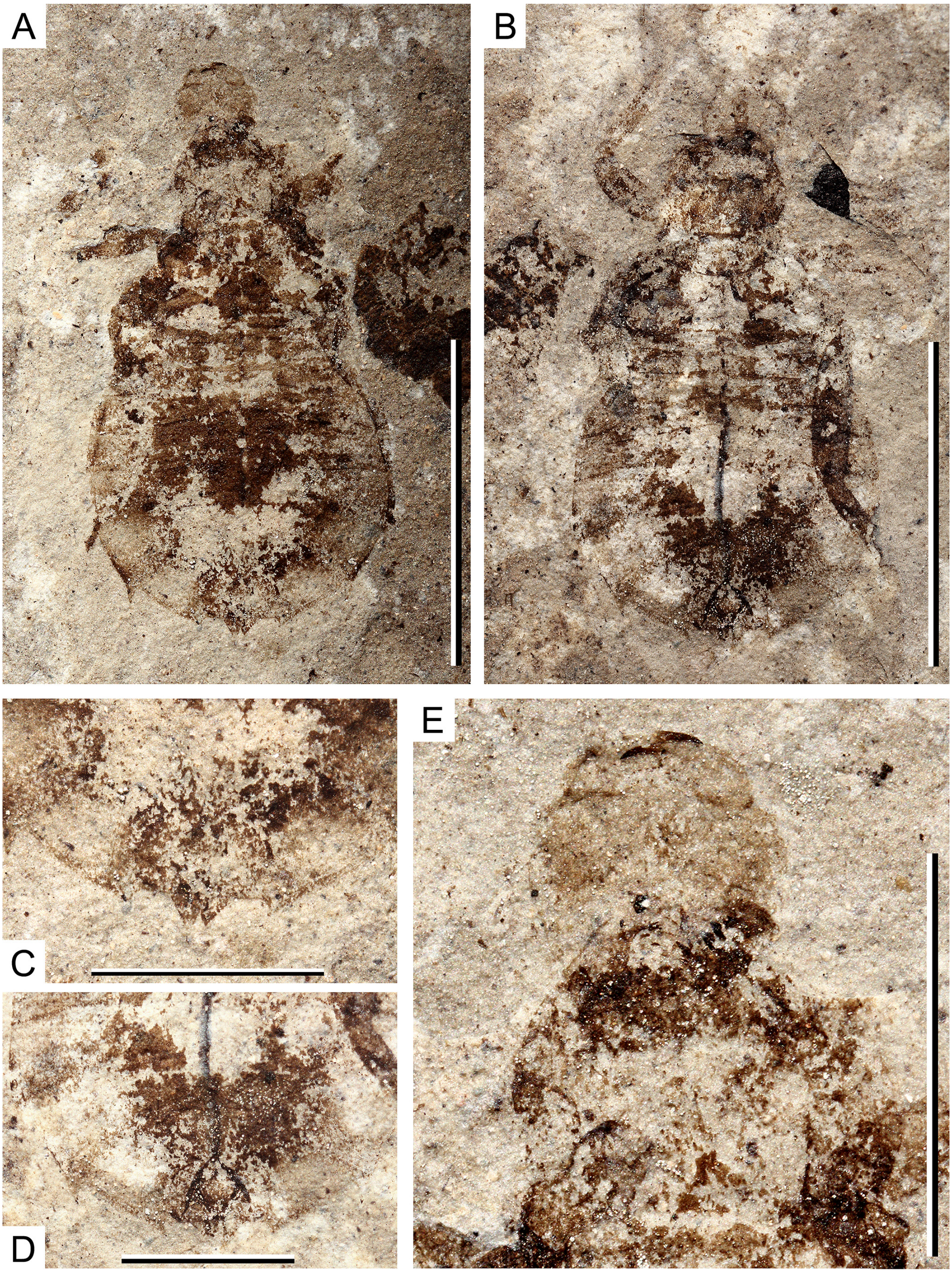

FIGURE 3. Specimen PE 2012/5282-LS. **A**, Habitus of part PE 2012/5282-LSa. **B**, Habitus of counterpart PE 2012/5282-LSb. **C**, Posterior end of abdomen in PE 2012/5282-LSa. **D**, Posterior end of abdomen in PE 2012/5282-LSb. **E**, Head with extended labium in PE 2012/5282-LSa. Scale bars = 5 mm in **A** and **B**, and 2 mm in **C**–**E**.

each other with their tips reaching the posterior margin of the third abdominal segment (Fig. 4A, B). The legs are strong, and the hind legs are much longer than the relatively short fore and mid legs (Table 1). The posterior femora reach the sixth abdominal segment if outstretched. The articulation of the relatively long tarsi is not preserved in any of the fossils.

The abdomen is round to slightly egg-shaped with the widest point at the sixth and seventh segment. Lateral spines are present at the seventh to ninth abdominal

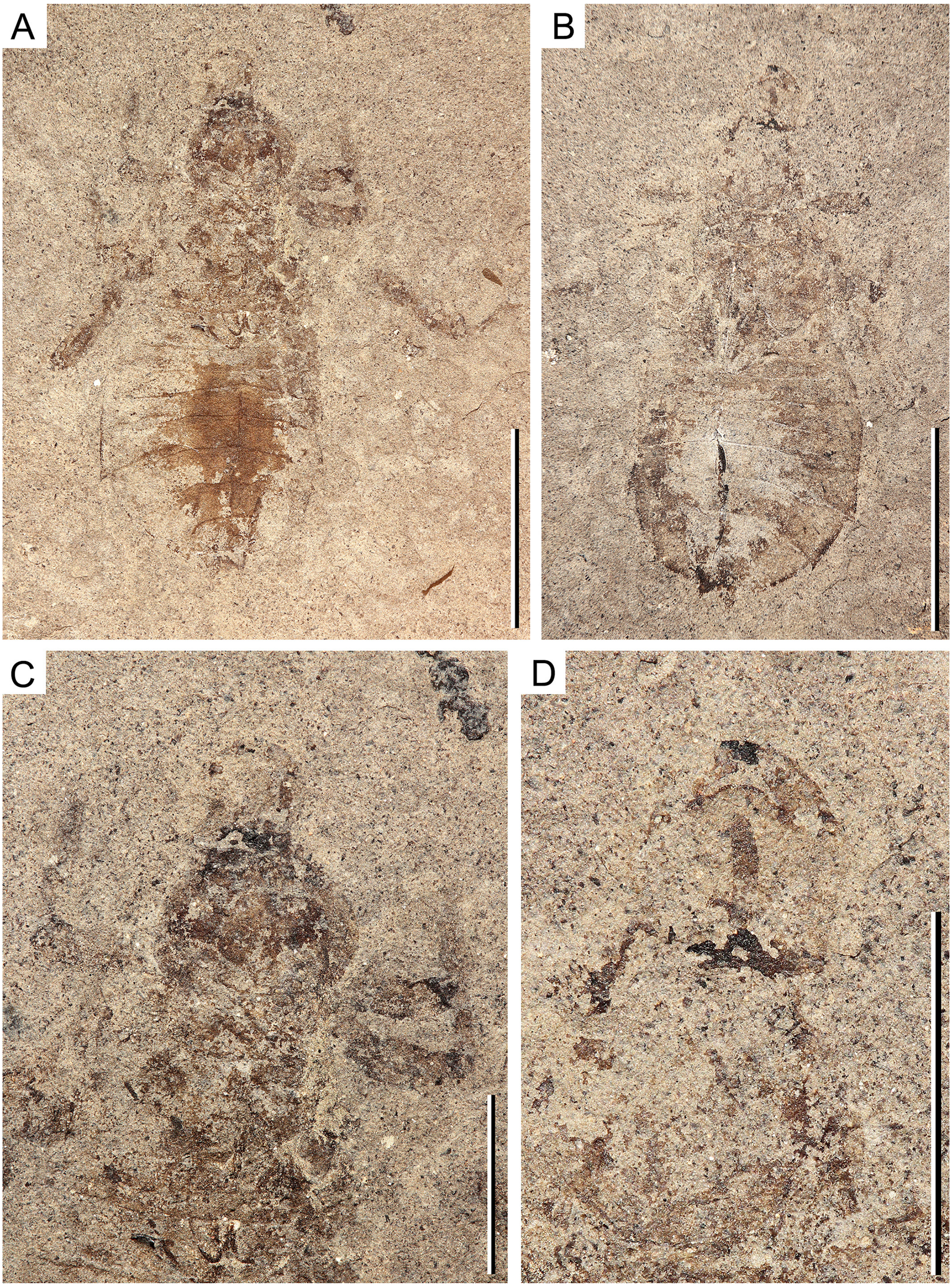

FIGURE 4. Specimen PE 2010/5654-LS. **A**, Habitus of part PE 2010/5654-LSa. **B**, Habitus of counterpart PE 2010/5654-LSb. **C**, Anterior body with extended labium in PE 2010/5654-LSa. **D**, Head with extended labium in PE 2010/5654-LSb. Scale bars = 10 mm in **A** and **B**, and 5 mm in **C** and **D**.

segments. Dorsal spines with acute tips can clearly be recognized at the sixth to seventh segment, and less prominent dorsal spines were also present at the eighth and perhaps at the ninth segment. On segments three to seven, the spines stretch over the entire respective tergites and apparently together they form some kind of dorsal keel. The lateral margins of the ninth segment extend beyond the short tenth segment. A short, conical anal pyramid is indicated by the preserved epi- and paraprocts (Figs 3C, D, 5D). Cerci are not clearly preserved. Especially

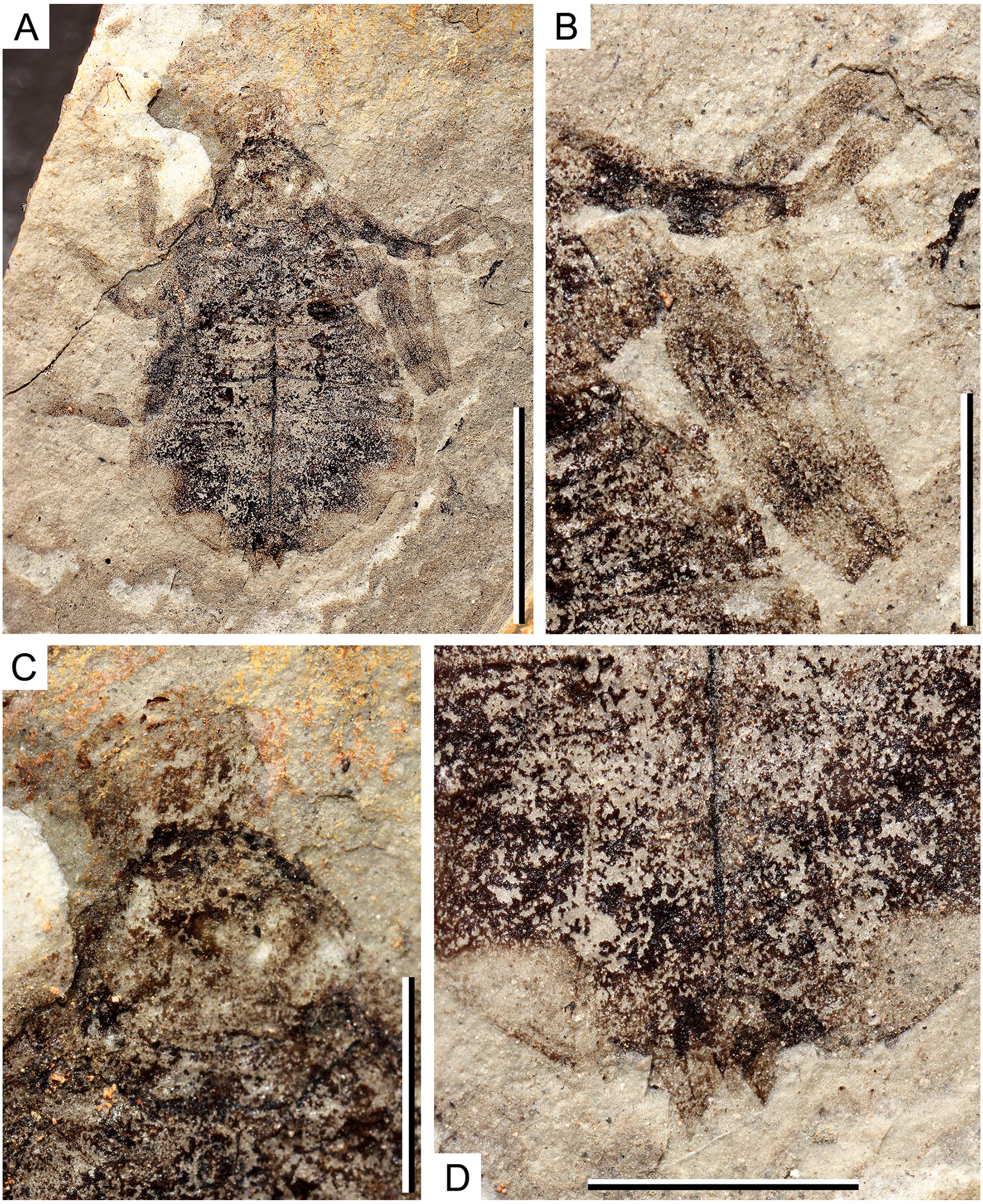

FIGURE 5. Specimen PE 2007/5005-LS. **A**, Habitus. **B**, Detail of legs, note preservation of color patterns. **C**, Head with extended labium. **D**, Posterior end of abdomen. Scale bars = 5 mm in **A**, and 2 mm in **B**–**D**.

specimen PE 2007/5005-LS shows transverse color bands on the legs and a color pattern of contrasting dark and pale patches on its body (Fig. 5A, B).

Remarks. All three fossil Anisoptera larvae described above show the same morphological characteristics and are therefore considered to belong to one species. This is furthermore corroborated by the fact that they all originate from oil-shale layer S14, and thus are of approximately the same age and may well originate from the same microhabitat. The two specimens PE 2012/5282-LS and PE 2007/5005-LS probably represent earlier ontogenetic stages than PE 2010/5654-LS, which most likely represents the penultimate larval stage indicated by its larger size and well developed wing sheets.

With respect to taxonomy, a morphological comparison shows that larvae of the broadly similar, co-occurring Macromiidae (see below) have decidedly longer 'spider-like' legs, as exemplified by *Macromia* Rambur, 1842 and closely related taxa (*e.g.*, Nesemann, 2011: fig. 13; Orr, 2005; Orr & Kalkman, 2015: pl. 3; Brochard *et*

TABLE 1. Morphometrics of the fossil larvae from the Late Oligocene of Enspel (in mm, * approximate value, ? unknown or unsure).

Repository number	PE 2012/5282-LS	PE 2007/5005-LS	PE 2010/5654-LS
Total length	7.9	10.2	23.7
Head width	2.0*	2.6*	5.5*
Praementum distal width	1.3	1.8	2.9
Labial palp length incl. terminal hook	0.7	1.0	1.9
Tibia 1	?	2.1	?
Tibia 2	?	2.6	?
Tibia 3	?	2.9	?
Femur 1	1.5	1.9	3.7
Femur 2	2.1	2.9	4.3*
Femur 3	?	3.1	5.5*
Tarsus	?	0.9	?
Fore wing bud	?	?	1.4
Hind wing bud	?	?	2.2
Abdomen length	4.4	6.4	13.2
Abdomen max. width	4.7	6.7	11.4
Anal pyramid	0.8	1.0	1.3
Abdominal segments with lateral spines	7–9	7–9	7–9
Lateral spine on 8th segment	0.3	0.4	0.4
Abdominal segments with dorsal spines	?	2–9 ?	6–9 ?
Dorsal spine on 8th segment	?	0.3*	?

TABLE 2. Compilation of references used with respect to the larval morphology of extant lindeniine species.

Genus	Species	Reference
Gomphidia	*G. madi*	Suhling & Müller, 1996: Fig. 35
	G. quarrei	Suhling *et al*., 2014: Pl. 19, Fig. 1
	G. t-nigrum	Butler, 2007: Figs. 1, 3
Diastatomma	*bicolor*	Karsch, 1893: Pl. 4, Fig. 9
Ictinogomphus	*I. acutus*	Butler, 2011: Fig. 1; Adu, 2018
	I. decoratus	Orr, 2005: 53
	I. ferox	Suhling & Müller, 1996: Fig. 41
	I. ferox	Suhling *et al*., 2014: Pl. 19, Fig. 4
	I. ferox	Adu, 2018: Figs. 1–4
	I. lieftincki	Orr & Kalkman, 2015: Pl. 3
	I. pertinax	Dudgeon, 1999
	I. rapax	Butler, 2007: Fig. 2
Lindenia	"Lindeniinae"	Nesemann *et al*., 2011: Image 10
	L. tetraphylla	Brochard & van der Ploeg, 2013: Fig. 16
	L. tetraphylla	Brochard *et al*., 2018: 187
Gomphidictinus	*G. perakensis*	Ferro & Sites, 2006: Figs 1–4
Sinictinogomphus	*S. clavatus*	Reels, 2009: Pl. 3; Tsurusaki *et al*., 2016: Fig. 1C

FIGURE 6. Interpretative drawings. **A**, PE 2012/5282-LSa. **B**, PE 2010/5654-LSa. **C**, PE 2007/5005-LS.

al., 2018: 211; *Phyllomacromia* Suhling *et al*., 2014: pl. 26, fig. 1), and *Macromia* larvae are also more slender. In fact, the 'masks' of these larvae (Figs 3E, 4D, 5C) do not correspond to those of the libelluloid dragonflies, spoon-shaped with broad palpi (Novelo-Gutiérrez & Che Salmah, 2006). Further comparison to extant species revealed that morphological correspondence is greatest with larvae of Gomphidae, namely those in the subfamily Lindeniinae, which currently comprises eight genera: †*Cratolindenia* Bechly, 2000, †*Burmalindenia* Schädel & Bechly, 2016*, Diastatomma* Burmeister, 1839*, Gomphidia* Sélys, 1854*, Gomphidictinus* Fraser, 1942*, Ictinogomphus* Cowley, 1934*, Lindenia* de Haan, 1826*,* and *Sinictinogomphus* Fraser, 1939. Larvae are known from only about one-fourth of the species in these genera. Morphological and morphometric data of these taxa were—as far as known—compared to the fossil larvae, and the references used are compiled in Table 2. The Cretaceous *Cratolindenia* and *Burmalindenia* are known from adult animals only, *i.e.* fore and hind wings in limestone of the Crato Formation in Brazil and from wing fragments in Burmese amber, respectively. The reconstructed habitus of the Enspel fossils (Fig. 7) is closely comparable to the habitus of some larvae of species in the extant genera *Gomphidia*, *Diastatomma, Ictinogomphus*, and *Lindenia*. Larvae of *Lindenia* are again slightly more slender than the fossils

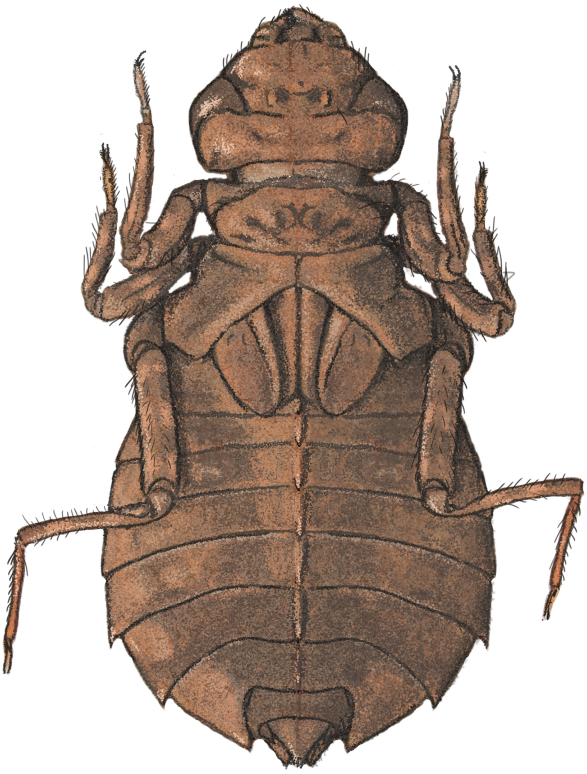

FIGURE 7. Attempted reconstruction of the Enspel lindeniine gomphid larva, mainly based on specimen PE 2007/5005-LS.

from Enspel, and the lateral and dorsal spines are only weakly developed (Brochard & van der Ploeg, 2013: fig. 16; Popowa in Brochard *et al.*, 2018: 187). Thus, this genus can be ruled out. The larvae of the monospecific genus *Sinictinogomphus* are decidedly more slender (Reels, 2009: pl. 3; Tsurusaki *et al.*, 2016: fig. 1C) and thus can likewise be ruled out. Table 3 shows the ratio of total length to maximum width of abdomen for PE 2012/5282-LS and PE 2007/5005-LS in comparison to extant species of further genera in the subfamily Lindeniinae. PE 2010/5654-LS is dorso-laterally embedded and therefore not considered in Table 3. Morphologically closest to the Enspel fossils are species in the genera *Gomphidia*, *Ictinogomphus*, *Gomphidictinus*, and *Diastatomma*. In contrast to the fossils, *Gomphidictinus perakensis* (Laidlaw, 1902) has much more strongly developed lateral spines on abdominal segments 3–9 in addition to very prominent dorsal spines. Furthermore, the larvae of this species were collected from fast running tropical creeks and waterfalls, respectively (Ferro & Sites, 2006), employing a habitat much different from that assumed for the Enspel larvae. The larva of *Diastatomma bicolor* Sélys, 1869 shows no dorsal abdominal spines at all (see Karsch, 1893: pl. 4, fig. 9). Therefore, attribution of the Enspel larvae to this genus can be considered as unlikely, but variability in this character is rather high. As a result, we consider the three fossils from Enspel as most probably belonging to either *Gomphidia* or *Ictinogomphus* (see Fig. 8 for comparison), or, more unlikely, *Diastatomma* (see Table 2 for references), genera whose extant representatives are largely confined to Africa and Asia (Davies & Tobin, 1985; Tsuda, 1991).

The discovery of larvae of this subfamily in the Oligocene of Germany is congruent with the presence of several adult Oligocene and Miocene Lindeniinae known from Eurasia (see list in Schädel & Lechner, 2017).

Superfamily Libelluloidea Leach, 1815
Family Macromiidae Needham, 1903
(Figs 9, 10)

Diagnosis. Hindwing characters only. Hypertriangle and discoidal triangle free; 11 antenodals; two Bqs crossveins; broad anal triangle; broad membranule; anal loop divided into nine cells.

Locality and horizon. Enspel/Westerwald, southwest Germany. Late Oligocene: 24.9–24.5 Mya. Mammal Zone MP 28.

Description. Hindwing (Figs 9, 10) hyaline, except brown extreme base, 47.2 mm long, 13.8 mm wide; distance from base to arculus 6.2 mm, from arculus to nodus 15.0 mm, from nodus to pterostigma 18.2 mm, from pterostigma to wing apex 6.2 mm; pterostigma 3.0 mm long, 0.7 mm wide, covering two cells; pterostigmal brace weak, but oblique; no secondary antenodal crossvein between Ax0 and Ax1, Ax1 4.6 mm from wing base,

FIGURE 8. Extant lindeniine gomphid larva showing general habitus similar to the Enspel larvae. Final instar exuvium of *Ictinogomphus ferox* (Rambur, 1842), Lake Kivu, Kibuye, Rwanda (leg. MJP, August 2003). Scale bar = 10 mm.

TABLE 3. Ratios of total length to body width of fossil and extant larvae of Lindeniinae.

Specimen or species	Ratio total body length/body width	Reference
PE 2007/5005-LS	1,5	this paper
PE 2012/5282-LS	1,7	this paper
Gomphidia bredoi	1.9–2.0	Müller *et al*., 2005
Gomphidia gamblesi	2.1	Müller *et al*., 2005
Gomphidia madi	1,9	Suhling & Müller, 1996: Fig. 35
Gomphidia quarrei	2,1	Suhling *et al*., 2014: Pl. 19, Fig. 1
Gomphidia t-nigrum	1,9	Butler, 2007
Gomphidictinus perakensis	1,7	Ferro & Sites, 2006
Ictinogomphus acutus	2,2	Butler, 2011: Fig. 1
Ictinogomphus decoratus	2,0	Orr, 2005
Ictinogomphus ferox	2,1	Suhling *et al*., 2014: Pl. 19, Fig. 4
Ictinogomphus ferox	2,2	Suhling & Müller, 1996: Fig. 41
Ictinogomphus ferox	1.7–1.8	Adu, 2018: Fig. 1A, B
Ictinogomphus lieftincki	2,0	Orr & Kalkman, 2015
Ictinogomphus pertinax	1,9	Dudgeon, 1999
Ictinogomphus rapax	2,0	Butler, 2007: Fig. 2

well basal of arculus; Ax1 and Ax2 not distinguishable from other antenodals, 11 antenodals, all complete; five crossveins between RA and RP basal and two distal of base of RP3/4, two Bqs crossveins in area between RP and IR2 basal of oblique crossvein 'O'; base of RP3/4 9.2 mm from arculus; base of RP2 aligned with subnodus; one oblique vein 'O' two cells distal of subnodus; 12 postnodal crossveins, not aligned with 11–12 postsubnodal crossveins; median space free; submedian space only crossed by CuP, an intermediate crossvein and a rather weak PsA; hypertriangle free; arculus angulate; posterior part (crossvein) of arculus distinctly shorter than anterior part [RP & MA]; sectors of arculus distinctly stalked, 1.6 mm long; distance between arculus and discoidal triangle 1.4 mm; discoidal triangle free, broad with basal side 2.0 mm long, anterior side 3.0 mm long, distal side 2.4 mm long; five rows of cells in broad anal area; anal margin angular with a broad membranule and a broad anal triangle (male); anal loop large, transverse elongate, pentagonal, divided into nine cells, no midrib; basal CuA before its branching distinctly prolonged but straight, 3.4 mm long; CuAa not branched, distinctly curved towards hind margin; cubital area with four rows of cells between CuA and posterior wing margin; area between MP and CuA with one row of cells; MP distinctly curved, ending on posterior wing margin well basal of nodus level; postdiscoidal area with two rows of cells distal of triangle; no Mspl; MA and RP3/4 distinctly undulated distally and parallel up to hind margin; a rather well-defined Rspl; no basal furcation of IR2 basal of lestine oblique vein; area between IR2 and RP2 weakly broadened distally with two rows of cells near posterior wing margin; IR1 weak, zigzagged.

Remarks. Following Bechly (1996, 1999), the isolated hind wing PE 2006/5003-LS from the Late Oligocene of Enspel falls in the Macromiidae because of the following combination of derived characters: RP3/4 and MAa distinctly undulate; two primary antenodal brackets Ax1 and Ax2 indistinguishable from secondaries; sectors of arculus stalked; areas without crossveins basal and distal of subnodus ('cordulegastrid gap' and 'libellulid gap') shortened; cubital cell (between CuP-crossing and pseudo-anal crossvein PsA) divided by an accessory cubito-anal crossvein.

Among the extant Macromiidae, affinities with the Nearctic genus *Didymops* Rambur, 1842 (*Didymops floridensis* (Davis, 1921) and *Didymops transversa* (Say, 1839)) are excluded because the hypertriangle is free while crossed in *Didymops*; the anal loop is larger than in *Didymops*; and the part of the anal area basal and below the anal loop is again larger than in *Didymops* (Davis, 1921; Needham & Westfall, 1955). Affinities with the Asiatic genus *Epophthalmia* Burmeister, 1839 are excluded because the discoidal triangle is free and broad, nearly equilateral, while it is crossed and clearly narrower in *Epophthalmia*. Nevertheless, the membranule and the anal triangle of PE 2006/5003-LS are broad as in *Epophthalmia* (see Lieftinck, 1931).

FIGURE 9. Isolated hind wing of Macromiidae, PE 2006/5003-LS. **A**, Photograph of part PE 2006/5003-LSa. **B**, Photograph of counterpart PE 2006/5003-LSb. Scale bars = 10 mm.

The differences between the Eurasiatic genus *Macromia* and the African genus *Phyllomacromia* Sélys, 1878 are found in the body structures, especially the male terminalia (May, 1997; Dijkstra, 2005). Thus, it is not possible to discriminate between the two genera. The extant distribution of these two genera is not sufficient to attribute PE 2006/5003-LS to *Macromia* because several extant Afrotropical genera of Odonata are also known in the European late Eocene and Oligocene (Nel & Fleck, 2014).

Three fossils are currently attributed to the genus *Macromia*, viz., an adult specimen of the extant species *Macromia amphigena* Sélys, 1871 from Pleistocene lake diatomites of Shiobara (Tachigi Prefecture, Japan) (Asahina, 1959); a nymph attributed to the genus *Macromia*, and *Macromia pilifera* (Lin, 1982), both from the Early-Middle Miocene (18.5–18.0 Ma) of Shanwang (Shandong Province, China) (Lin, 1982; Zhang, 1989; Zhang *et al*., 1994; Yu *et al*., 2017). *Macromia pilifera*, based on an adult specimen, has a crossed hindwing hypertriangle, unlike PE 2006/5003-LS; and a hindwing length of 56 mm (Zhang *et al*., 1994: text-fig. 8), instead of 47.2 mm in PE 2006/5003-LS.

Two fossil species are currently attributed to *Epophthalmia*, viz. *Epophthalmia biordinata* Lewis, 1969 (Miocene, Langhian, 15.8–15.5 Ma, Latah Formation, Marshall Creek Area, Spokane, Washington, USA) and *Epophthalmia zotheca* Zhang, 1989 (adult, Early–Middle Miocene of Shanwang, Shandong Province, China).

Epophthalmia biordinata is based on a hind wing of a female specimen. Nel & Paicheler (1994) considered its generic attribution as probable. Lewis (1969) justified this attribution rather than to *Macromia* on the basis of 'possessing more antenodal crossveins'. Lewis (1969: pl. 1, fig. A) figured 12 antenodals for *Epophthalmia biordinata* (plus two basal of Ax1 that are very dubious as Ax1 is the most basal one in these dragonflies). In the extant *Epophthalmia* spp., there are 8–12 hind wing antenodals (Lieftinck, 1931; Zha & Jiang, 2010), but in the extant *Macromia chaiyaphumensis* Hämäläinen, 1985, there are 7–9 such veins, nine in *Macromia sombui* Vick, 1988, while there are 11 in *Macromia berlandi* Lieftinck, 1941

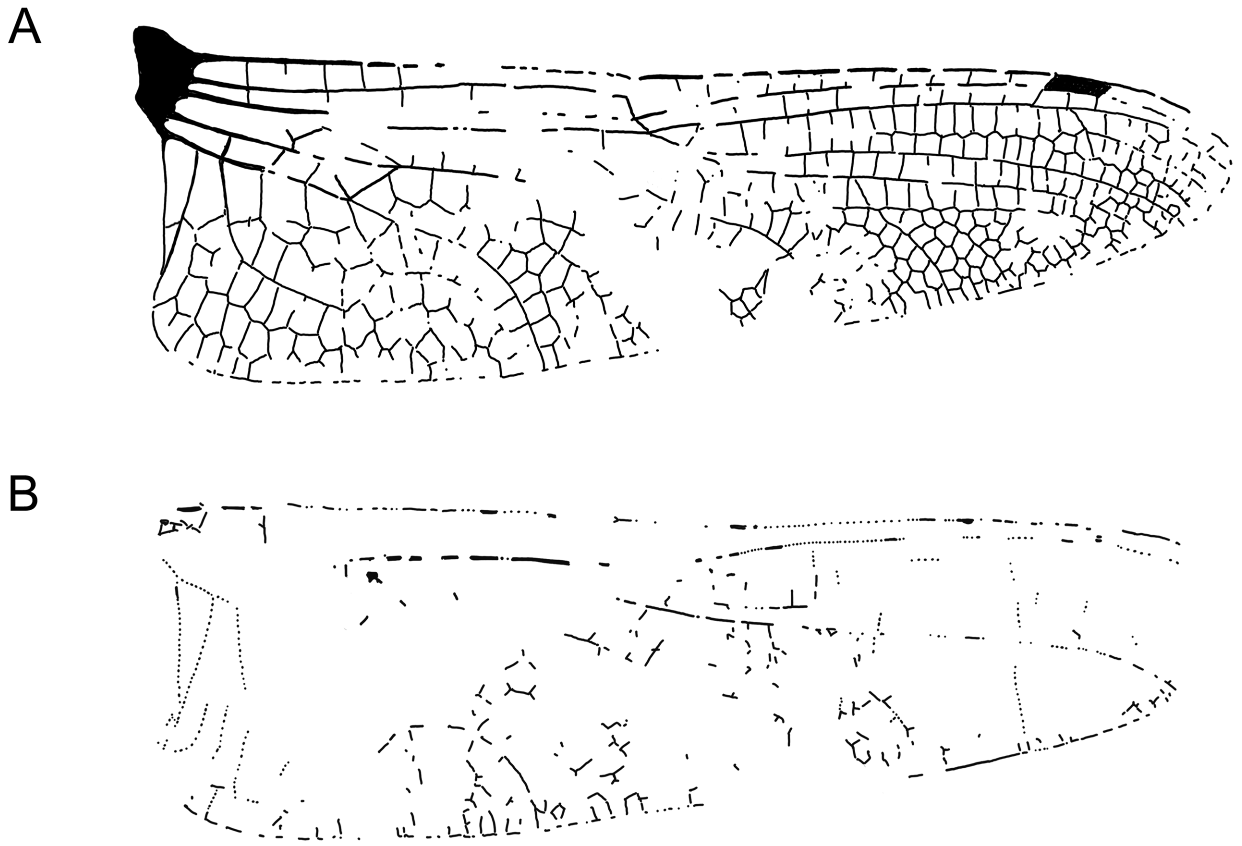

FIGURE 10. Isolated hind wing of Macromiidae, PE 2006/5003-LS. **A**, Drawing of part PE 2006/5003-LSa. **B**, Drawing of counterpart PE 2006/5003-LSb. For scales, see Fig. 9.

(Lieftinck, 1941; Hämäläinen, 1985; Vick, 1988; van Tol, 1994). Thus, the number of antenodals is not sufficient to discriminate the two genera. Lewis (1969) also indicated that 'the anal loop of M.C. 1 in *Epophthalmia* are much closer allied than in the other three genera', which is a rather imprecise character. We could not find any major differences between the anal loops of *Macromia* and *Epophthalmia*. Lewis (1969) figured five Bqs crossveins between the base of IR2 and the oblique vein 'O', unlike in the extant *Epophthalmia* and *Macromia* spp. that have two or three such veins. Lastly, he figured a free and broad discoidal triangle very similar to those of the *Macromia* spp. rather than to *Epophthalmia*. The type specimen of *Epophthalmia biordinata* should be revised before its attribution to *Epophthalmia* rather than to *Macromia*.

Epophthalmia zotheca is based on a male hindwing; it has 13 antenodals, a broad anal membranule and a broad anal triangle, supporting an attribution to *Epophthalmia* (Zhang, 1989: text-figs 21–22). Nevertheless, its discoidal triangle is rather broad as in *Macromia*. As a result, with only the hind wing characters at hand, we are confident to assign the specimen to Macromiidae incertae sedis, but refrain from a closer determination.

Discussion

The recovered fossils from Lake Enspel lived in a, at that time, meromictic and eutrophic crater lake without outlet and covering an area of about 1.7 × 1.3 kilometres (see Pirrung *et al.*, 2001; Schindler & Wuttke, 2010). The climate can be characterized as humid warm temperate with a mean annual temperature of 15–17 °C (Cfa-type sensu Köppen), based on the taphoflora (Uhl & Herrmann, 2010) and insect association (Wedmann *et al.*, 2010). The dragonfly larvae have a broad, almost round abdomen, with rather strong lateral spines, in dorsal view and are here assigned to the genus *Gomphidia* or *Ictinogomphus*. Extant larvae of these taxa are considered as hiders (*sensu* Corbet, 1999; Suhling *et al.*, 2015), *i.e.*, larvae that cover their body with detritus and act as sit-and-wait predators in their respective habitats in the low-energy environments of running waters or in standing waters. The observed color patterns resemble a patchwork of light and shade near the water surface (Suhling *et al.*, 2015) and suggest that these contribute to cryptic behavior in addition to camouflage by collecting fine detritus. We find habitats ideal for this ecological type of larvae in the vegetation-rich shallow-water zones of Lake Enspel. The existence of such zones is furthermore indicated by the occurrence of *e.g*., crocodiles (Frey & Monninger, 2010), relatively abundant caddisfly larvae (Poschmann, 2006), and the well preserved macroflora (Köhler & Uhl, 2014). For example, the aquatic plant *Groenlandia* has its richest occurrence at the base of layer S14 (Uhl & Poschmann, 2018) just as the (gomphid) dragonfly larvae. Assuming that these larvae lived in these vegetation-rich, shallow-water zones furthermore explains their rareness as fossils, because the vegetation may form a kind of taphonomic filter by preventing dead larvae or exuviae from entering the open lake and eventually from reaching the anoxic lake bottom where they could be finally buried and subsequently fossilized (*cf*., Wuttke & Poschmann, 2010). The abdominal dorsal and lateral spines of the gomphid larvae can be interpreted as a defense against predators, namely aquatic vertebrates, such as fishes and amphibians (Suhling *et al*., 2015). At Lake Enspel, fishes are represented by a single species of cyprinid, *Palaeorutilus enspelensis* (Böhme, 1996), which fed on insects, but preferably on smaller forms drifting on the lake surface, as indicated by the form of its dental bone adapted for this purpose and by fossilized content of its intestine comprising remains of weevils (Böhme, 1996; MJP, unpubl. observ.). More probably the gomphid larvae were preyed upon by pelobatid tadpoles, which were highly abundant in Lake Enspel (*e.g*., Maus & Wuttke, 2002) and in some cases reached body lengths of more than 20 cm and then became potentially carnivorous. The tadpoles lived at least in shallow-water regions close to the shore as testified by the sandy fill of their intestines (Maus & Wuttke, 2002). This, on the other hand, suggests that small tadpoles were preyed upon by the dragonfly larvae among other prey items such as a variety of aquatic insect larvae (see Wedmann *et al*., 2010).

With respect to adult dragonflies from Enspel, extant Macromiidae are extremely fast fliers, hence their common names 'cruisers' or 'river cruisers'. Given the closed nature of Lake Enspel with no connection to larger flowing waters, the macromiid, and the aeschnid dragonflies as well, presumably patrolled as 'hawker predators' the open spaces along the lake margins in search of prey.

Conclusion

Cenozoic fossils of gomphid larvae are known from the Eocene and Oligocene (Nel & Paicheler, 1994; Bechly, 2015), and Upper Pliocene (Schumann, 1974), while the fossil record of representatives of the subfamily Lindeniinae is very scarce and only consists of fragments of adult insects (Nel & Paicheler, 1994; Bechly, 2015; Schädel & Lechner, 2017). A wing fragment from the Late Oligocene locality Rott was described as *Ictinogomphus fur* (Hagen, 1863), but rather has to be considered as Anisoptera *incertae sedis* following Nel & Paicheler (1994). The fossils from Enspel described herein are thus the first record of larvae of Lindeniinae from the Oligocene.

Although the oldest record of the anisopteran 'libelluloid' clade Cavilabiata goes to the Middle Jurassic (Huang & Nel, 2007), the representatives of its extant families are scarce or even absent in the Mesozoic. The Libellulidae, one of the most derived families, is recorded in the Turonian at least by a stem representative (Fleck *et al*., 1999; Kohli *et al*., 2016). Crown Libellulidae are known in the earliest Eocene and the Oligocene (Fleck *et al*., 2000). Curiously, the 'less derived' family Macromiidae is unknown before the Miocene. In their detailed review of the known crown group fossils for the order Odonata, Kohli *et al.* (2016) proposed the Miocene *Epophthalmia biordinata* Lewis, 1969 as oldest known representative of this small family. Wighton (1988) indicated the presence of a macromiid nymph in the Aptian Crato Formation (North-East Brazil), but this fossil probably corresponds to another group among those listed by Bechly (2007) from this formation. The hind wing from Enspel described herein is the hitherto oldest record of the family Macromiidae.

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