

New dragonflies and damselflies (Odonata) from the late Oligocene of Enspel (Rhineland-Palatinate, SW Germany)

André Nel, Markus J. Poschmann, and Sonja Wedmann

ABSTRACT

We describe 10 fossils of dragonfly wings and one damselfly from bituminous pelites of the late Oligocene crater lake of Enspel/Westerwald. These represent two species of Aeshnidae, one species of Gomphidae, one possible stem Libellulidae, and one species of stem Sieblosiidae. The presence of one further undetermined species of crown Libellulidae can be inferred from a well-preserved naiad. Together with an earlier described wing of Macromiidae and a naiad figured herein and possibly attributable to the family Lestidae, the Enspel biota at least comprised eight different morphotypes of Odonata. We propose three new species, *Epiaeschna wisseri* sp. nov. (Aeshnidae), *Ictinogomphus engelorum* sp. nov. (Gomphidae), and *Oligolestes stoeffelensis* sp. nov. (Sieblosiidae), based on wing venation. The lateral position of the body and the rotated head of the holotype of *Oligolestes stoeffelensis* sp. nov. confirm that the Sieblosiidae had zygopteran hammer-shaped heads. This quite diverse odonate fauna is typical of Oligocene European paleolakes and suggests a water oxygenation suitable for the development of the aquatic naiads that lasted for longer periods and niche partitioning among the adult animals in a well-structured palaeo-ecosystem.

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INTRODUCTION

The black pelitic sediments or ‘oilshales’ of Fossilagerstätte Enspel were deposited in a crater lake (e.g., Schindler and Wuttke, 2010, 2015) with a late Oligocene age of 24.79–24.56 Ma (Mertz et al., 2007). Scientific excavations by the former Landesamt für Denkmalpflege/Referat Erdgeschichte (now part of the Generaldirektion Kulturelles Erbe Rheinland-Pfalz) from 1990 until 2015 yielded rich fossil associations including plants, invertebrates, and both aquatic and terrestrial vertebrates (for an overview see Poschmann et al., 2010). More than 12,000 specimens of fossil arthropods were recovered, mostly insects (see Wedmann, 2000; Wedmann et al., 2010 for overviews).

The Odonata are relatively rare, represented by a total of about 70 fossils, roughly 0.6 per cent of all insect finds. Of those, 12 fossils of Anisoptera are wings derived from adult animals, one specimen is the adult Zygoptera: Sieblosiidae described herein, and the rest represent nymphal stages or exuviae thereof attributable to various odonate families (Wedmann, 2000; Wedmann et al., 2010; Brockhaus et al., 2020). One of these wings is attributable to the family Macromiidae (Brockhaus et al., 2020), and another one is too incomplete to allow further conclusions. Here, we describe the remaining 10 wings belonging to the families Aeshnidae, Gomphidae, and Libellulidae, along with the Sieblosiidae fossil.

MATERIAL AND METHODS

The fossils from Enspel were excavated during digging campaigns conducted by the Generaldirektion Kulturelles Erbe Rheinland-Pfalz, Direktion Landesarchäologie/Erdgeschichte and are part of the State Collection of Natural History of Rheinland-Palatinate at the Natural History Museum Mainz. The specimens are stored in plastic boxes filled with glycerin and were photographed immersed in water using a Canon EOS 600D SLR camera equipped with a Canon EFS 60 mm macro lens. Stacking software CombineZP (by Alan Hadley) served to combine photographs with differing focal planes in order to enhance depth of field. Drawings were made from enlarged photographs or directly from the specimens using a camera lucida attachment on a Leica MZ125 microscope.

We follow the higher classification of fossil and extant Odonoptera based on the phylogenetic system of Bechly (1996, 2016), and employ the dragonfly wing venation nomenclature of Riek

and Kukalová-Peck (1984), as modified by Nel et al. (1993), Bechly (1996), and Jacquelin et al. (2018).

Venation abbreviations are as follows: AA anterior anal; Arc arculus; Ax primary antenodal crossvein; Bqs crossveins in space between base of IR2, RP1/2; C costa; CuA anterior cubitus; CuP posterior cubitus; IR intercalary radial vein; MAa anterior branch of anterior media; MAb posterior branch of anterior media; MP posterior media; Mspl supplementary median vein; ‘O’ oblique vein between IR2 and RP2 distal of subnodus; Pt pterostigma; RA anterior radius; RP posterior radius; Rspl supplementary radial vein; Sn subnodal crossvein; ScP posterior subcostal; tspl trigonal planate.

SYSTEMATIC PALAEOLOGY

Class INSECTA Linné, 1758

Order ODONATA Fabricius, 1793

Family AESHNIDAE Leach, 1815

Genus *OLIGAESCHNA* Piton and Théobald, 1939

Type species. *Oligaeschna jungi* Piton and Théobald, 1939 (late Oligocene-Early Miocene, Puy-du-Mur, Center of France, Gaudant, 1993).

Other species. *Oligaeschna wedmanni* Nel and Fleck, 2014 (latest Eocene, Isle of Wight, UK), *Oligaeschna separata* (Scudder, 1890) (latest Eocene, Florissant, Colorado, USA), *Oligaeschna lapidaria* (Cockerell and Counts, 1913 in Cockerell, 1913) (latest Eocene, Florissant, Colorado, USA), *Oligaeschna cf. jungi* (Rupelian, Enspel, Germany), *Oligaeschna cf. jungi* (Rupelian, Céreste, Southern France), *Oligaeschna palaeocoerulea* (Timon-David, 1946) (Rupelian, Gypsum Mine, Camoins-les-Bains, Southern France; Rousset et al., 1996), *Oligaeschna kvaceki* Prokop et al., 2007 (Rupelian-Chattian, Moravia, Czech Republic), *Oligaeschna ashutasica* (Martynov, 1929) (Chattian, Mount Ashutas, river Irtysh, Kazakhstan), *Oligaeschna saurai* Peñalver et al., 1996 (early Miocene, Ribesalbes, Spain), *Oligaeschna bulgariensis* Nel et al., 2016 (middle Miocene, Satovcha Graben, SW Bulgaria).

Oligaeschna cf. jungi Piton and Théobald, 1939

Figures 1–4

Material. PE 2005/5032-LS a, b (part and counterpart of two forewings attached to fragments of thorax), specimen PE 2000/5005-LS a, b (part and counterpart of a nearly complete forewing), specimen Enspel PE 1995/7217-LS (a complete forewing), specimen PE 1995/9174-LS (basal two-third

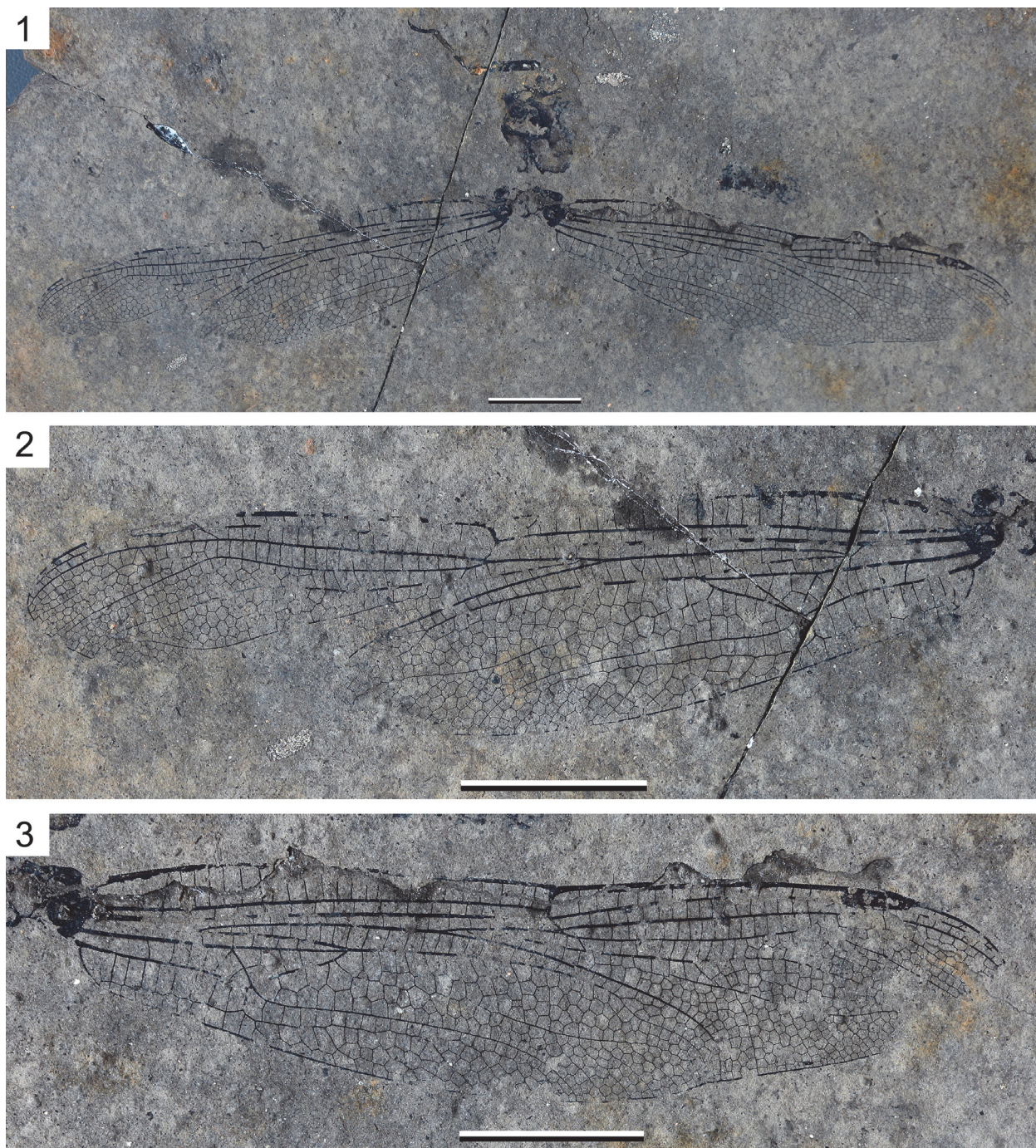


FIGURE 1. *Oligaeschna cf. jungi*, specimen PE 2005/5032-LS a. **1**, Overall view of fossil with two forewings, remains of the thorax, and one leg; **2**, Left forewing enlarged; **3**, Right forewing enlarged. Scale bars are 10 mm.

of a hind wing), all stored at the State Collection of Natural History of Rhineland-Palatinate.

Description. PE 2005/5032-LS a (Figures 1.1–3, 3.1–2): Forewing, hyaline, 50.0 mm long, 11.3 mm wide; distance from base to arculus 5.2 mm; from arculus to nodus 19.3 mm; from nodus to pterostigma 15.3 mm, from nodus to wing apex

25.2 mm; pterostigma 4.3 mm long, 0.8 mm wide, covering five cells; pterostigmal brace elongate, distinctly oblique and sigmoidal; 16 secondary antenodal crossveins distal of Ax2 and four between Ax2 and Ax1; Ax2 at level of mid part of discoidal triangle; Ax1 well basal to arculus; arculus strongly angled; 14 antesubnodal crossveins; at

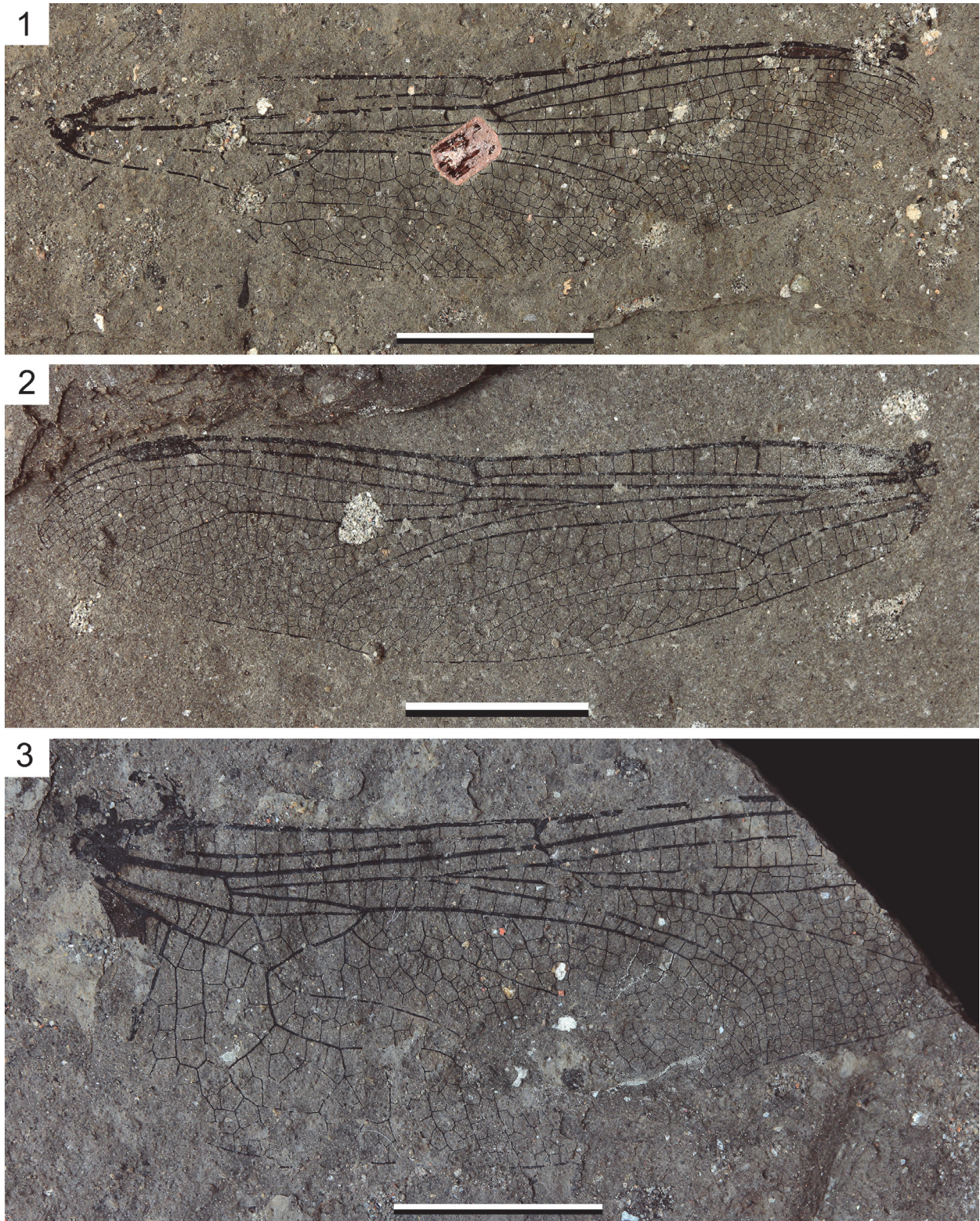


FIGURE 2. *Oligaeschna cf. jungi*. **1**, PE 2000/5000-LS a, forewing; **2**, PE 1995/7217-LS, forewing; **3**, PE 1995/9174-LS, hindwing. Scale bars are 10 mm.

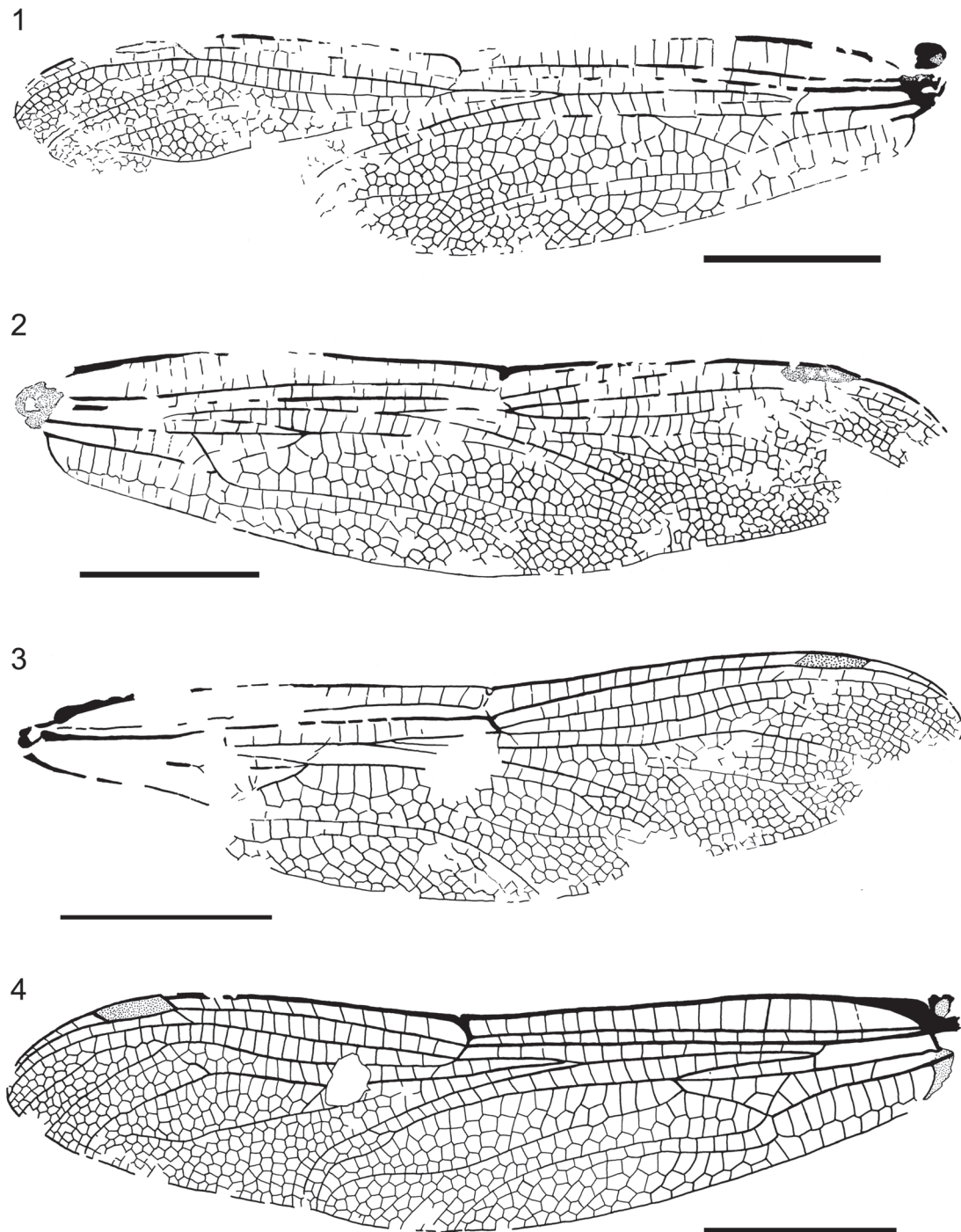


FIGURE 3. *Oligaeschna* cf. *jungi*, interpretative drawings of wings. **1**, PE 2005/5032-LS a, left forewing; **2**, PE 2005/5032-LS a, right forewing; **3**, PE 2000/5000-LS a, forewing; **4**, PE 1995/7217-LS, forewing. Scale bars are 10 mm.

most 14 postnodal crossveins and 17 postsubnodals; hypertriangle elongate, with four crossveins; discoidal triangle elongate, divided into five cells; three rows of cells in basal part of postdiscoidal area; median space free; submedian space with

five crossveins plus CuP stronger than other crossveins; Mspl strongly curved, four rows of cells between Mspl and MA; four Bq crossveins; oblique vein 'O' one cell distal of base of RP2; MA with a smooth curve opposite base of Rspl; beyond this

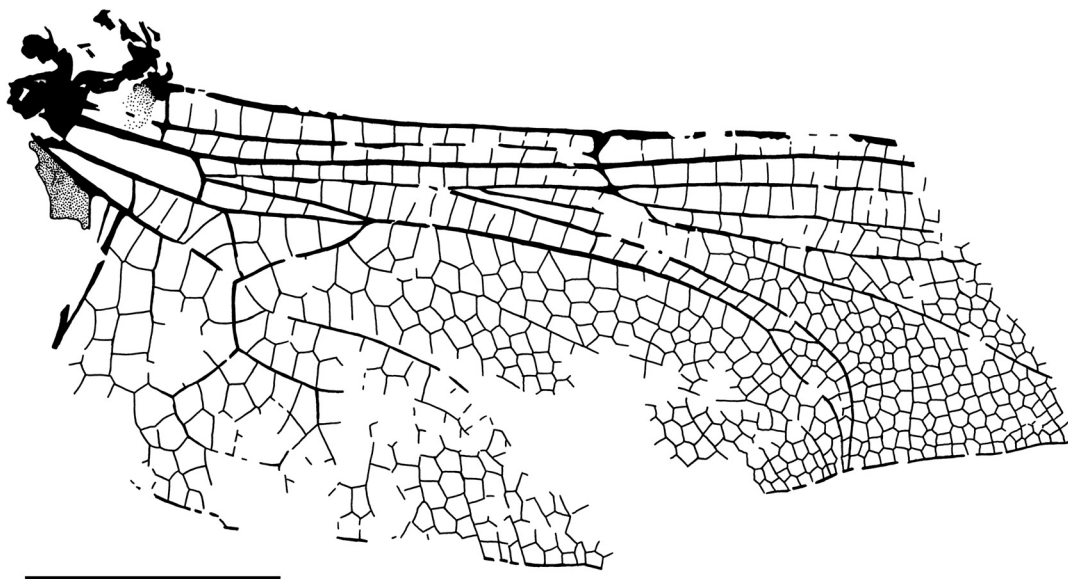


FIGURE 4. *Oligaeschna cf. jungi*, interpretative drawing of hind wing PE 1995/9174-LS. Scale bar is 10 mm.

level, two rows of cells between MA and RP3/4; Rspl strongly curved, with four rows of cells between it and IR2; IR2 unforked, with a posterior curve; four rows of cells between IR2 and RP2 in broadest part; RP2 distinctly but smoothly curved at level of pterostigma.

Specimen PE 2000/5005-LS a (Figures 2.1, 3.3): Forewing, hyaline, 45.1 mm long, 10.3 mm wide; distance from base to arculus 7.2 mm; from arculus to nodus 14.0 mm; from nodus to pterostigma 14.8 mm, from nodus to wing apex 22.7 mm; pterostigma 3.9 mm long, 0.8 mm wide, covering four cells; pterostigmal brace elongate, distinctly oblique and sigmoidal; exact number of secondary antenodal crossveins unknown Ax2 at level of mid part of discoidal triangle; Ax1 well basal to arculus; arculus strongly angled; 12–13 antesubnodal crossveins; 13 postnodal crossveins and 12 postsubnodals; hypertriangle elongate; discoidal triangle elongate, divided into five cells; three rows of cells in basal part of postdiscoidal area; median space free; Mspl strongly curved, four rows of cells between Mspl and MA; three Bq crossveins; oblique vein 'O' one cell distal of base of RP2; MA with a smooth curve opposite base of Rspl; beyond this level, two rows of cells between MA and RP3/4; Rspl strongly curved, with four rows of cells between it and IR2; IR2 unforked and with a posterior curve; four rows of cells between IR2 and RP2 in broadest part; RP2 distinctly but smoothly curved at level of pterostigma.

Specimen PE 1995/7217-LS (Figures 2.2, 3.4): Forewing, hyaline, 48.8 mm long, 11.5 mm wide; distance from base to arculus 5.5 mm; from arculus to nodus 18.9 mm; from nodus to pterostigma 14.9 mm, from nodus to wing apex 24.2 mm; pterostigma 4.2 mm long, 0.8 mm wide, covering three cells; pterostigmal brace elongate, distinctly oblique and sigmoidal; 14 secondary antenodal crossveins distal of Ax2 and four between Ax2 and Ax1; Ax2 at level of mid part of discoidal triangle; Ax1 well basal to arculus; arculus strongly angled; 14 antesubnodal crossveins; 12 postnodal crossveins and 16 postsubnodals; hypertriangle elongate, with four crossveins; discoidal triangle elongate, divided into five cells; three rows of cells in basal part of postdiscoidal area; median space free; submedian space with three crossveins plus CuP stronger than other crossveins; Mspl strongly curved, four rows of cells between Mspl and MA; three Bq crossveins; oblique vein 'O' one cell distal of base of RP2; MA with a smooth curve opposite base of Rspl; beyond this level, two rows of cells between MA and RP3/4; Rspl strongly curved, with four rows of cells between it and IR2; IR2 unforked but with a rudiment of asymmetrical anterior branch, and with a posterior curve; four rows of cells between IR2 and RP2 in broadest part; RP2 distinctly but smoothly curved at level of pterostigma. Specimen PE 1995/9174-LS (Figures 2.3, 4). Basal two-third of a hind wing; hyaline; preserved part 42.2 mm long, 16.7 mm wide; distance between base and arculus 6.4 mm, between arcu-

lus and nodus 15.3 mm; two primary antenodal crossveins Ax1 and Ax2 visible, with no secondary crossvein basal of Ax1, five between Ax1 and Ax2, between C and ScP; nine antenodal crossveins distal of Ax2, distance between base and Ax1 5.0 mm, between Ax1 and Ax2 6.4 mm; median space free; four crossveins in submedian area; arculus between Ax1 and Ax2, slightly closer to Ax1; RP and MA nearly meeting at their base in arculus; posterior part of arculus not aligned with anterior part; hypertriangle crossed by four veins; discoidal triangle elongate, divided into five cells; 4–5 rows of cells in basal part of postdiscoidal area; convex trigonal planate tspl in postdiscoidal area rather well-defined but short and zigzagged; Mspl long, with a strong concave bend, and with four rows of cells between it and MA; MA and RP3/4 not parallel in their distal part, and MA with a concave bend before wing margin, two rows of cells between MA and RP3/4; base of RP2 aligned with subnodus; oblique vein 'O' one cell distal of base of RP2; RP2 more or less parallel with IR2; Rspl distinctly curved, with four rows of cells between it and IR2; anal angle strongly angular (male); membranule broad and darkened; anal loop closed, well-defined, broad and large, 3.0 mm long and 5.5 mm wide, divided into nine cells; two rows of cells between MP and CuAa between their base and nodus level; CuA with posterior branches that define groups of cells, and six rows of cells between it and posterior wing margin.

Remarks. These fossils have all the synapomorphies of the family Aeshnidae as defined by Bechly (1996), i.e., 'aeshnid bulla' in distal part of MA; Rspl distinctly curved with more than one row of cells between it and IR2, and area in between divided by oblique intercalary veins; three rows of cells in basal part of postdiscoidal area between level of distal angle of discoidal triangle and level of mid-fork; hypertriangle traversed by at least three crossveins. Following the study of von Ellenrieder (2002), these fossils would fall near the extant *Oplonaeschna* de Selys-Longchamps, 1883, from the shape of the veins Rspl, IR2, and RP2. The closest modern genera differ either in the narrower area between Rspl and IR2 with less than three rows of cells, or in the forked IR2 (see Martin, 1908-1909, 1911). The fossils differ from the extant genus *Oplonaeschna* in the longer pterostigma covering three cells or more and in the presence of three rows of cells in basal part of postdiscoidal areas instead of two. The general pattern of venation fits quite well with the Cenozoic genus *Oligaeschna* Piton and Théobald, 1939 (revised in

Nel et al., 1994). The Oligocene genus *Kvacekia* Prokop and Nel, 2002, is also closely related to *Oligaeschna* and *Oplonaeschna*, but it is characterized by a pterostigma covering 5–6 cells (five in our fossils), and by five rows of cells in the area between IR2 and RP2 (four in our fossil and 3–4 in *Oligaeschna*) (Prokop and Nel, 2002).

Apart from weak differences in wing sizes and proportions, these wings are very similar and can be attributed to the same species, even if there is some uncertainty in the presence vs. absence of a fork of IR2 for the hind wing specimen PE 1995/9174-LS. Its preserved part of venation fits quite well with that of the hind wing of the type series of *Oligaeschna jungi* and with the complete hind wing from Céreste attributed to this species by Nel et al. (2005c). Thus, we propose to attribute these fossils to *Oligaeschna*, in accordance with Wedmann (2000: fig. 5) and Wedmann et al. (2010: fig. 6d) who indicated that it is 'probably *Oligaeschna jungi*'.

The genus *Oligaeschna* comprises nine described species from Oligocene and Miocene deposits in North American and Eurasia. *Oligaeschna bulgariensis* has much more postnodals (21). *Oligaeschna* cf. *jungi* shares with *O. palaeocoerulea* the presence of four rows of cells between IR2 and RP2, five cells below the pterostigma, 14 postnodal crossveins and 17 post-subnodals, close distances between nodus and pterostigma (25.2 mm in *Oligaeschna* cf. *jungi* and 28.3 mm in the type of *O. palaeocoerulea*). But *O. palaeocoerulea* has 10 rows of cells between IR2 and RP2 along wing margin, instead of five in *Oligaeschna* cf. *jungi*. *Oligaeschna kvaceki* is based on a hind wing of same length as our fossil and a pterostigma covering five cells, five rows of cells between IR2 and RP2 along wing margin, as in *Oligaeschna* cf. *jungi*. But it has 17 postnodals instead of 12–14 in *Oligaeschna* cf. *jungi* and a shorter pterostigmal brace (Prokop et al., 2007). *Oligaeschna lapidaria* has a pterostigma covering three cells and a shorter pterostigmal brace (Cockerell, 1913). *Oligaeschna saurai* also has a pterostigma covering three cells, a shorter pterostigmal brace, and five rows of cells between Rspl and IR2 (Peñalver et al., 1996). *Oligaeschna wedmanni* has a forewing of the same size as *Oligaeschna* cf. *jungi*, but five rows of cells between IR2 and RP2, and only three rows of cells between Mspl and MAa, unlike *Oligaeschna* cf. *jungi* (Nel and Fleck, 2014). *Oligaeschna ashutasica*, based on a hind wing, has three rows of cells between RP2 and IR2, and three rows of cells between MAa

and Mspl (Martynov, 1929). *Oligaeschna separata* has a forewing 44 mm long and 13 postnodals (Scudder, 1890).

Oligaeschna cf. *jungi* differs from the type series of *Oligaeschna jungi* in the presence of four rows of cells between IR2 and RP2 instead of five, pterostigma covering 3–5 cells instead of three, and wing lengths 45–50 mm instead of ca. 55–56 mm in *O. jungi*. These differences would hardly support a species separation between the two populations from France and Germany.

These fossil wings are of interest to show the intraspecific variability, which is rather important in the genus *Oligaeschna*. Nevertheless, the character ‘presence of three rows of cells in basal part of the forewing postdiscoidal area’ and ‘presence of 4–5 rows of cells in basal part of the hind wing postdiscoidal area’ appear stable enough to justify the separation between the two genera *Oligaeschna* and *Oplonaeschna*.

Genus *EPIAESCHNA* Hagen, 1877

Type species. *Aeshna heros* Fabricius, 1798 (Recent, Nearctic).

Other species. *Epiaeschna gossi* (Campion, 1916) (middle–late Eocene, UK), *Epiaeschna magnifica* (Martynov, 1929) (late Oligocene, Kazakhstan), *Epiaeschna wisseri* sp. nov. (late Oligocene, Germany), *Epiaeschna pseudoheros* Nel and Petrulevičius, 2010 (latest Oligocene, France), *Epiaeschna stauropolitana* Martynov, 1927 (middle Miocene, Crimea), *Epiaeschna matutina* (Zhang, 1989) (middle Miocene, China).

Epiaeschna wisseri sp. nov.

Figures 5–6

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Type material. Holotype PE 2000/5355-LS a, b (part and counterpart of a nearly complete hind wing, parts of basal fourth of wing missing), stored at the State Collection of Natural History of Rhineland-Palatinate.

Additional material. PE 1997/6211-LS a, b (part and counterpart of basal two-third of a hind wing), stored at the State Collection of Natural History of Rhineland-Palatinate.

Diagnosis. Hind wing characters only. Wing darkened; fork of IR2 far from pterostigma; base of IR1 opposite base of pterostigma; pterostigma covering four cells, 18 postnodals; area between Rspl and IR2 with three rows of cells.

Etymology. Named for Dieter Wisser, mayor of Enspel, for his continuous support of the excavations.

Description. Holotype PE 2000/5355-LS a (Figures 5.1, 6.1): Hind wing darkened, 58.1 mm long, 16.9 mm wide, ratio length/width 3.4; distance between base and arculus 5.4 mm, between arculus and nodus 18.0 mm, between nodus and pterostigma 23.0 mm, between pterostigma and apex 7.0 mm; pterostigma 5.3 mm long, 0.8 mm wide, covering four cells; pterostigmal brace present, distinctly oblique, and aligned with basal margin of pterostigma; primary antenodal crossveins not preserved, 11 secondary crossveins visible; 18 postnodal crossveins not aligned with 17 postsubnodals; median space free; CuP not visible; RP and MA meeting at their base in arculus; posterior part of arculus not aligned with anterior part; hypertriangle crossed by three veins, rather short, 7.3 mm long, 0.9 mm wide; discoidal triangle elongate but rather broad, 6.9 mm long, 1.1 mm wide, crossed by three transverse veins; trigonal planate not preserved; Mspl partly preserved, weakly zigzagged, without strong concave bend, and with three rows of cells between it and MAa; MAa and RP3/4 parallel and MAa with no concave bend before wing margin, two rows of cells between MA and RP3/4 in distal end; base of RP2 aligned with subnodus; oblique vein ‘O’ one cell distal of base of RP2; distal fork of IR2 symmetrical, 6.1 mm basal of level of pterostigma, with 4–5 rows of cells in area between its branches; RP2 parallel with anterior branch of IR2, making a distinct curve; base of IR1 one cell distal of pterostigmal brace; Rspl straight, with three rows of cells between it and IR2; anal loop only partly visible; CuA poorly preserved, probably with 5–6 posterior branches and 6–7 rows of cells between it and posterior wing margin.

Additional specimen PE 1997/6211-LS a (Figures 5.2, 6.2): Hind wing, apparently hyaline, 13.6 mm wide, preserved part 28.0 mm long; distance between base and arculus 4.2 mm, between arculus and nodus 12.8 mm, pterostigma not preserved; median space free; RP and MA meeting at their base in arculus; posterior part of arculus not aligned with anterior part; hypertriangle crossed; discoidal triangle elongate but rather broad, crossed by three transverse veins; trigonal planate weak; Mspl weakly curved, with two rows of cells between it and MAa; MAa and RP3/4 parallel and MAa with no concave bend before wing margin, two rows of cells between MA and RP3/4 in distal end; base of RP2 aligned with subnodus; oblique vein ‘O’ one cell distal of base of RP2; distal fork of IR2 not preserved; RP2 parallel with IR2; Rspl straight, with two rows of cells between it and IR2;

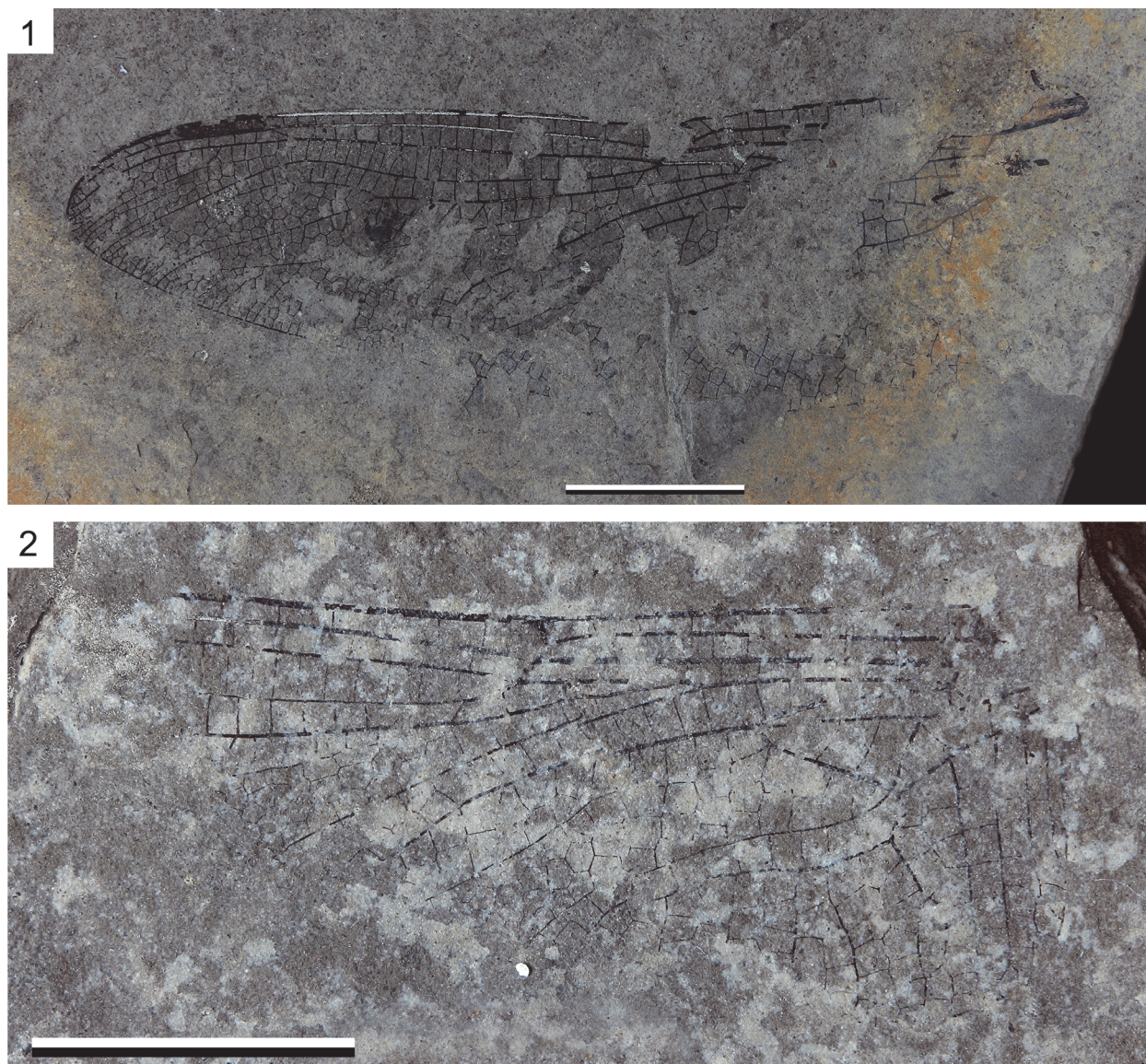


FIGURE 5. *Epiaeschna wisseri* sp. nov. **1**, holotype, PE 2000/5355-LS a; **2**, putative specimen PE 1997/6211-LS a, hind wing. Scale bars are 10 mm.

anal loop with two rows of cells; CuA with six posterior branches and seven rows of cells between it and posterior wing margin.

Remarks. Specimen PE 2000/5355-LS (Figures 5.1, 6.1; a hind wing because of the broad cubito-anal area) is extremely similar to those of the Oligocene-Miocene hawker dragonflies of Eurasia described or revised in Nel and Petrulevičius (2010) and Li et al. (2011), and attributed to the genus *Epiaeschna*. *Epiaeschna heros* differs from all fossil species in the shorter and less oblique pterostigmal brace and narrower area between IR2 and Rspl with only two rows of cells (Garrison et al., 2006). *Epiaeschna wisseri* sp. nov. differs from *Epiaeschna pseudoheros* in the base of IR1 being

opposite to the base of the pterostigma instead of being opposite to its middle, the pterostigma covering four cells instead of five, and the presence of only 18 postnodals instead of 20. The pterostigma of *Epiaeschna stauropolitana* covers seven cells, and its area between Rspl and IR2 has two rows of cells instead of three as in *Epiaeschna wisseri* sp. nov. *Epiaeschna magnifica* also has a pterostigma covering 7–8 cells, and its base of IR1 is well basal of the pterostigmal brace. *Epiaeschna gossi* has much more postnodals than *Epiaeschna wisseri* sp. nov. and a very long and oblique pterostigmal brace. *Epiaeschna matutina* has 21 postnodals in a slightly shorter wing (55.6 mm long, instead of 58.1 mm in *Epiaeschna wisseri* sp. nov.). Otherwise, the

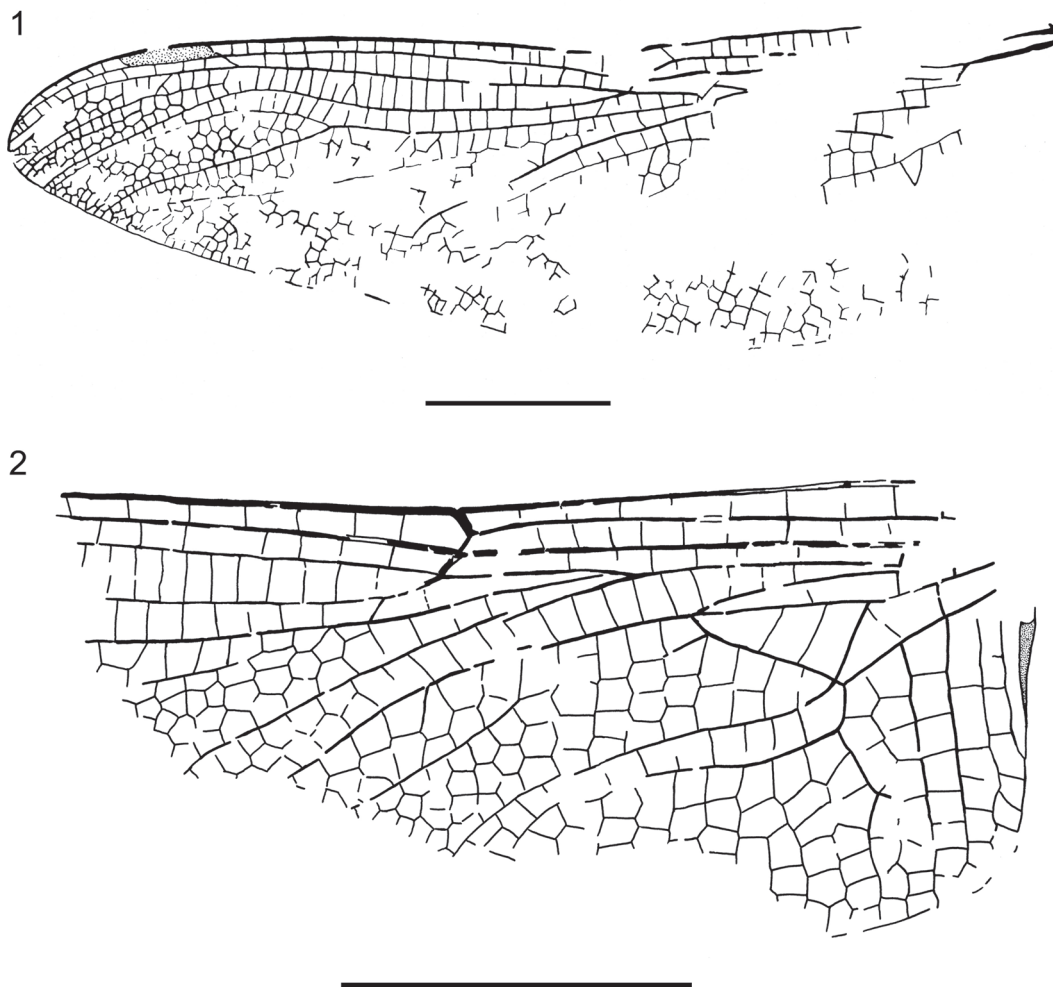


FIGURE 6. *Epiaeschna wisseri* sp. nov., interpretative drawings of hind wings. **1**, holotype, PE 2000/5355-LS a; **2**, putative conspecific specimen, PE 1997/6211-LS a, female hind wing. Scale bars are 10 mm.

venations of *E. matutina* and *Epiaeschna wisseri* sp. nov. are very similar, even in their darkened wings and the ratios wing length/wing width (Li et al., 2011). The most significant difference is in the position of the fork of IR2, being farther from the pterostigma in *Epiaeschna wisseri* sp. nov. than in *E. matutina* [viz. 6.1 mm basal of level of base of pterostigma in *Epiaeschna wisseri* sp. nov., while it is 5.1 mm in *E. matutina*, that is ratio (wing length/distance between Pt and fork of IR2) = 9.5 in *Epiaeschna wisseri* sp. nov. vs. 10.9 in *E. matutina*].

Specimen PE 1997/6211-LS (Figures 5.2, 6.2) is also a hind wing (female, because of the absence of anal angle and triangle), smaller than holotype PE 2000/5355-LS and with a wing membrane apparently hyaline. But these differences are compatible with intraspecific variations and taphonomic biases. Despite the lack of information on the fork of IR2, the venation of the preserved part

fits well with that of the extant and fossil *Epiaeschna* spp., especially in the narrow anal loop with two rows of cells (see Garrison et al., 2006: fig. 247). Thus, we tentatively attribute it to *Epiaeschna wisseri* sp. nov., but with some doubt, so that we do not consider it as a paratype.

Family LIBELLULIDAE Leach, 1815 (stem group representative?)

Genus and species undetermined
Figures 7–8

Material. Specimen PE 2001/5195-LS (incomplete hind wing with only anterior half preserved), stored at the State Collection of Natural History of Rhineland-Palatinate.

Description. Hind wing, hyaline; length of preserved part 28.0 mm; width 7.0 mm; distance from base to arculus 4.0 mm, from arculus to nodus 9.0 mm, from nodus to pterostigma 13.6 mm;



FIGURE 7. Probably a stem-Libellulidae, PE 2001/5195-LS, hind wing. Scale bar is 10 mm.

pterostigma incomplete but rather elongate; pterostigmal brace weak and not aligned with basal side of pterostigma; Ax1, Ax2, and first secondary antenodal of same shape with a membrane between them, C, ScP, and RA; two more distal antenodals complete but without membrane, last antenodal apparently incomplete, only present between ScP and RA; arculus midway between Ax1 and Ax2; sectors of arculus not stalked but joined at base; four antensubnodal crossveins, the last one being distal of base of IR2; hypertriangle and discoidal triangle free; PsA not oblique and weak; eight postnodal crossveins, not aligned with the postsubnodals, the two basal postsubnodals absent; no 'libellulid oblique crossvein'; oblique crossvein 'O' two cells distal of subnodus (Figures 7–8).

Remarks. This hind wing is attributable to the clade Libellulida Bechly, 1996, because of the following characters: hind wing discoidal triangle recessed to the level of the arculus; the first secondary crossvein has a membrane between it, C,

ScP, and RA, as for the two primary antenodal crossveins Ax1 and Ax2. The absence of a 'libellulid oblique crossvein' between RP1 and RP2 excludes affinities with the Urothemistidae Lieftinck, 1954. But even if the two more distal secondary antenodals are complete (alignments of the antenodals of first row with those of second row), but they lack the membrane of the three more basal antenodals, and the sectors of arculus are not stalked but only joined at their base, which are symplesiomorphies of the Libellulidae. Even if they share the character 'sectors of arculus not stalked but basally joined', our new fossil does not fit well in the Eocene family Urolibellulidae, belonging to the stem Libellulida, because the new fossil has its third antenodal crossvein identical to Ax1 and Ax2, which is not the case in this last family (Zeiri et al., 2015; Nel, 2020). Also, the hind wing vein PsA of the new fossil is not oblique as in the extant Libellulidae, but also different from that in the Urolibellulidae.

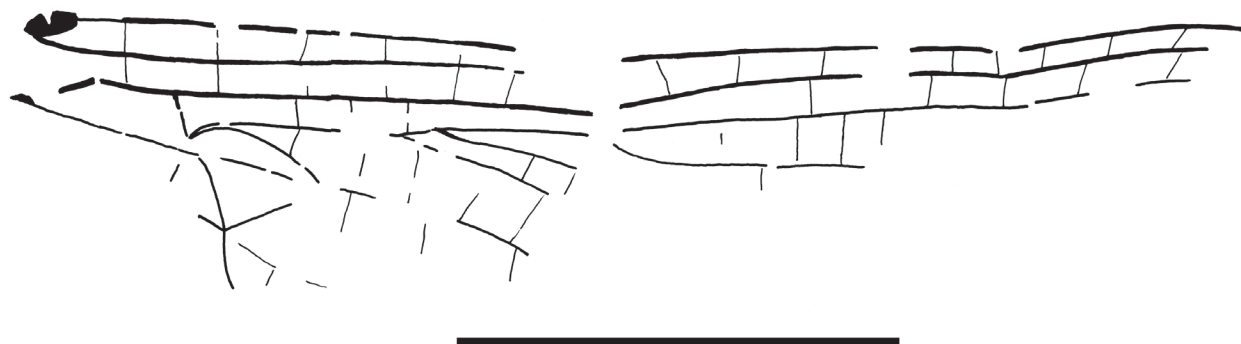


FIGURE 8. Probably a stem-Libellulidae, PE 2001/5195-LS, interpretative drawing of hind wing. Scale bar is 10 mm.

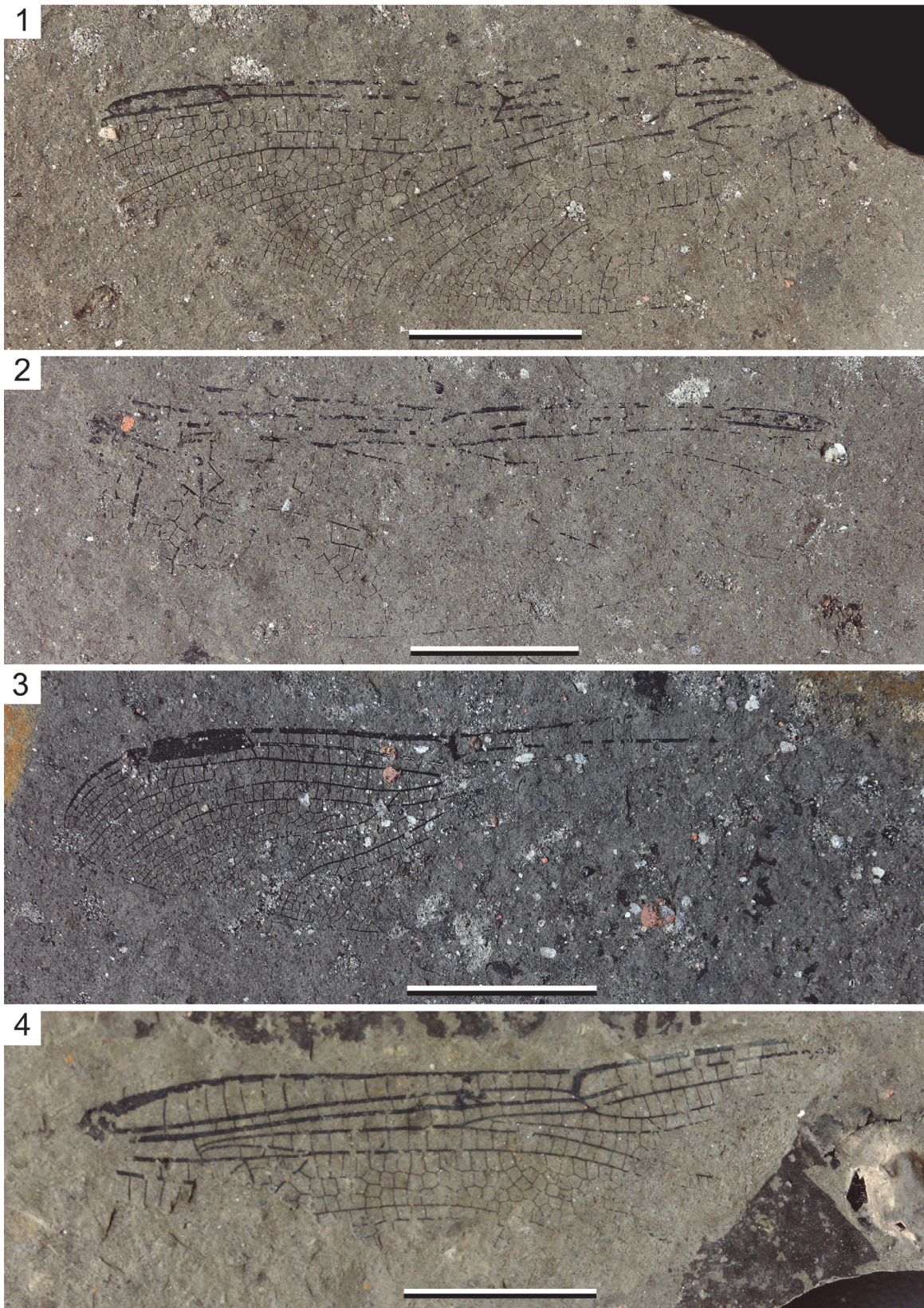


FIGURE 9. *Ictinogomphus engelorum* sp. nov. **1**, Holotype PE 2000/5006-LS a, hind wing; **2**, Counterpart of holotype, PE 2000/5006-LS b; **3**, Paratype, PE 2003/5039-LS a, distal part of wing; **4**, Paratype, PE 2003/5040-LS, part of forewing. Scale bars are 10 mm.

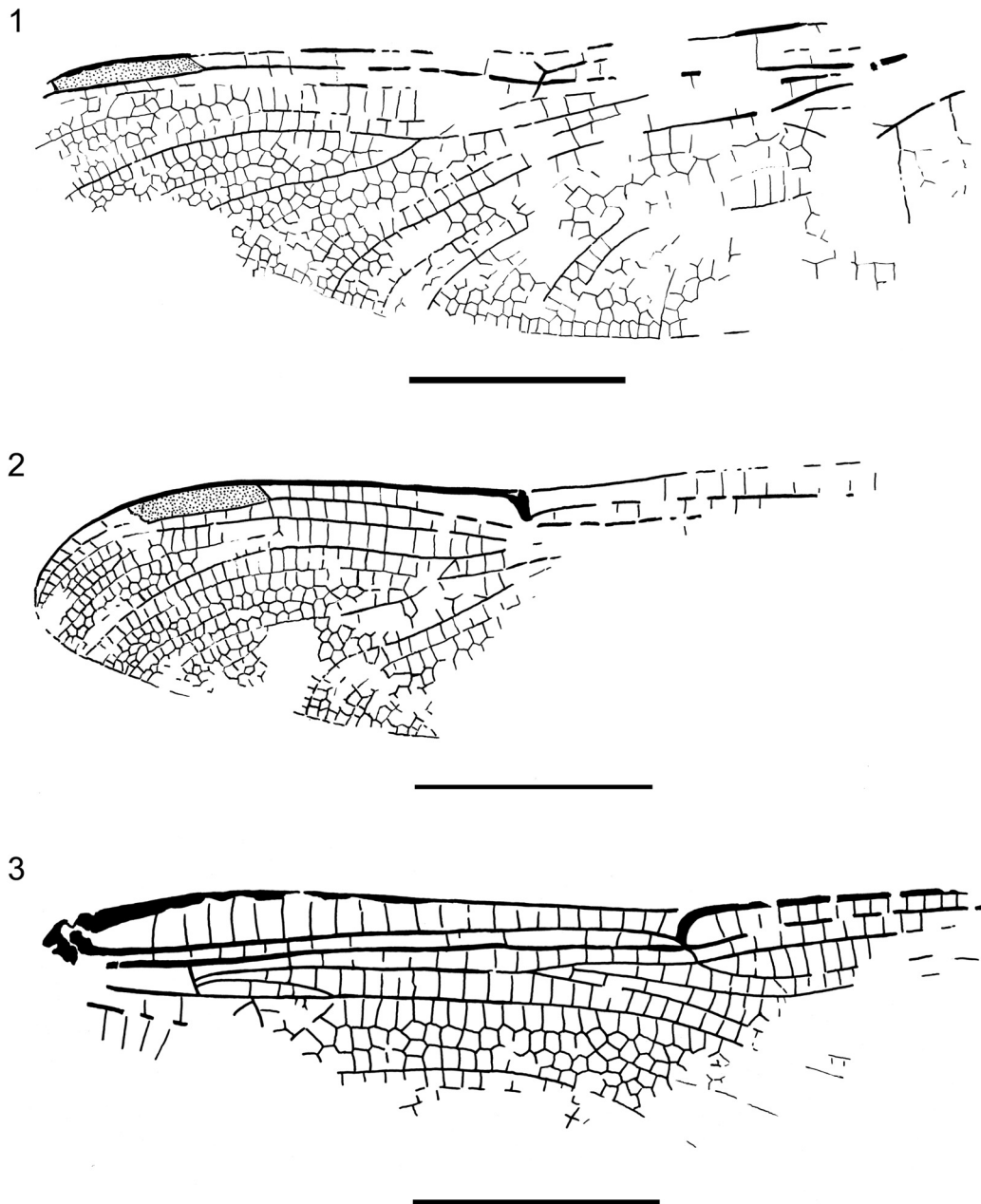


FIGURE 10. *Ictinogomphus engelorum* sp. nov., interpretative drawings of wings. **1**, Holotype PE 2000/5006-LS a, hind wing; **2**, Paratype, PE 2003/5039-LS a, distal part of wing; **3**, Paratype, PE 2003/5040-LS, part of forewing. Scale bars are 10 mm.

Thus, despite its incompleteness, that forbids us to name it, this new fossil probably belongs to the stem group of the Libellulidae.

Several representatives of the crown Libellulidae are recorded from the Oligocene of Europe (Nel and Paicheler, 1993; Nel et al., 1995, 1997, 2005), and the oldest record of the family is from the Late Cretaceous (Fleck et al., 1999). Nevertheless, the clade Libellulida is nearly unrecorded

from the Paleocene and the Eocene, with only one fossil found in the earliest Eocene amber of France (Fleck et al., 2000). Thus, the present fossil is of great interest because it shows that representatives of the stem group of the Libellulidae were still present in the Late Oligocene.

Family GOMPHIDAE Rambur, 1842
Subfamily LINDENIINAE Jacobson and Bianchi,
1905

Genus *ICTINOGOMPHUS* Cowley, 1934 (sensu lato, see below)

Ictinogomphus engelorum sp. nov.

Figures 9–10

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Type material. Holotype PE 2000/5006-LS a, b (part and counterpart of a nearly complete hind wing with extreme apex and base missing), paratype PE 2003/5040-LS (part only, basal two-third of a forewing), paratype PE 2003/5039-LS a, b (part and counterpart of distal half of a wing), stored at the State Collection of Natural History of Rhineland-Palatinate.

Diagnosis. Wing characters only. A broad area between posterior branch of IR2 and RP3/4 with three rows of cells in the narrowest part: broad area between two branches of IR2 with three rows of cells basal of secondary longitudinal vein; a long well-defined secondary vein between branches of IR2; hind wing subtriangle free; forewing one probably two-celled; forewing discoidal triangle five-celled, with costal side distinctly longer than basal side; in hind wing, one row of cells between IR2 and RP2 below pterostigma.

Etymology. Named after Carmen Engel and the entire Engel family from Enspel, for their continuous interest in and support of the excavations.

Description. Holotype PE 2000/5006-LS a, b (Figures 9.1-2, 10.1): Hind wing, hyaline, 46.7 mm long, wing 13.3 mm wide; pterostigma 7.1 mm long, 1.1 mm wide, covering six cells; pterostigmal brace strong and oblique; 12 postnodals; distance between nodus and pterostigma 15.6 mm, between nodus and arculus 15.6 mm; Ax2 at level of distal angle of discoidal triangle; possibly one crossvein in hypertriangle; discoidal triangle elongate, crossed by a vein, with distal side MAb slightly angled at base of trigonal planate tspl; tspl rather weak and short; 4–5 crossveins in area between RP and MAa basal of RP3/4; probably numerous antenodals, but many are not preserved; 4–5 Bqs crossveins; oblique crossvein 'O' four cells distal of subnodus; IR1 basally zigzagged, and straight in distal part; base of RP2 aligned with subnodus, RP2 regularly curved without marked concavity; main branch of IR2 parallel to RP2; posterior branch of IR2 well-defined with four rows of cells and a well-defined secondary longitudinal vein between it and main branch; three rows of cells between posterior branch of IR2 and RP3/4 in narrower part; RP3/4 smoothly curved but with a more pronounced curve apically; one row of cells between RP3/4 and MAa, but near their apices a zigzagged vein and two rows of cells in-between;

MAa smoothly curved; a posterior branch of MAa similar to that of IR2; postdiscoidal area with two rows of cells basally and distally greatly broadened; mostly one row of cells between MP and CuAa, but two rows near posterior wing margin; cubito-anal area broad with 6–7 rows of cells between CuAa and posterior wing margin and 4–5 posterior branches of CuAa; anal area poorly preserved, anal loop apparently subdivided into four cells; subtriangle free; PsA well-defined and oblique; median area free; submedian crossed by CuP and another vein.

Paratype PE 2003/5039-LS a (Figures 9.3, 10.2): As the basal third is missing, it is not possible to determine if it is a fore- or a hind wing. Preserved parts are very similar to those of specimen PE 2000/5006-LS. Only IR1 is slightly shorter than in PE 2000/5006-LS, only four rows of cells between the branches of IR2, and 11 postnodals. Pterostigma 6.7 mm long, 1.1 mm wide, distance between nodus and pterostigma 10.5 mm.

Paratype PE 2003/5040-LS (Figures 9.4, 10.3): Forewing, hyaline; length of fragment 38.6 mm; wing ca. 9.8 mm wide; distance from base to arculus 4.5 mm, from arculus to nodus 19.8 mm, from base to Ax1 2.7 mm, from Ax1 to Ax2 6.3 mm; Ax2 slightly basal to distal angle of discoidal triangle; five crossveins between Ax1 and Ax2, 15 secondary antenodal crossveins distal of Ax2; 14 preserved postnodals; 12 crossveins between RP and MAa basal of RP3/4; seven Bqs veins; oblique vein 'O' five cells distal of subnodus; hypertriangle with two crossveins; discoidal triangle subdivided into five cells, with costal side 3.2 mm long, basal side 2.5 mm long, distal side MAb 3.2 mm long, MAb with a slight angle at base of tspl; RP3/4 and MAa weakly curved and parallel in preserved parts, with one row of cells in-between; three rows of cells in basal part of postdiscoidal area, broadened distally; a distinct posterior branch of MAa, with four rows of cells between it and MAa; median area free; submedian area crossed by CuP and two other veins; PsA strong and oblique; subtriangle possibly crossed by a vein (fragment visible).

Remarks. The preserved parts of these three wings are very similar, and the forewing and the hind wing fit well with a Gomphidae of the genus *Ictinogomphus* Cowley, 1934. Probably all wings are of the same species. The attribution to the family Gomphidae is suggested by the following synapomorphies: distinct PsA; slight angle in the posterodistal side of the discoidal triangle caused by the presence of the tspl; anterior side of the hypertriangle distinctly curved; straight arculus

(Bechly, 1996, 2003). *Ictinogomphus engelorum* sp. nov. shows an elongated discoidal triangle with a distinct tspl, which is a feature only known within Gomphidae from the Hageniinae and Lindeniinae. The Hageniinae have the veins MP and CuAa strongly divergent towards the wing margin in their hind wings; IR1 is secondarily elongated in both wings; costal margin and RA is not widened along pterostigmata. All these characters are not present in *Ictinogomphus engelorum* sp. nov. Also, the Hageniinae have the discoidal triangles distinctly longitudinal elongate in both pairs of wings, which is not the case for the forewing. The Lindeniinae are characterized by the following synapomorphies: secondary branch of IR2 very distinct, therefore IR2 appears to be dichotomously forked distal of the lestine oblique vein; hind wing discoidal triangle longitudinal elongate with a strongly sigmoidal and angulated distal side, caused by the development of a distinct tspl in the postdiscoidal area; discoidal triangles divided into more than two cells in both pairs of wings; in forewings the basal part of the subdiscoidal cell (between CuP-crossing and pseudo-anal vein PsA) is traversed by supplementary cubito-anal-crossveins; pseudo-anal vein PsA is less distinct in the hind wing, correlated with the elongated hind wing discoidal triangle; hypertriangle divided by at least two or more crossveins.

Among the Recent lindenine genera, *Diastatomma* Burmeister, 1839, has a pronounced angle in the forewing distal side (MAb) of discoidal triangle, strongly curved distal halves of main longitudinal veins, and many more cells covered by the pterostigmata, unlike *Ictinogomphus engelorum* sp. nov. (Schouteden, 1934; Dijkstra and Clausnitzer, 2014). *Lindenia* De Haan, 1826, has also a pronounced angle of MAb, a more elongate discoidal triangle of forewing, and a narrower apical part of the area between RP3/4 and MAa than *Ictinogomphus engelorum* sp. nov. *Gomphidictinus* Fraser, 1942, differs from *Ictinogomphus engelorum* sp. nov. in the absence of the pterostigmal brace, in numerous small cells covered by the pterostigmata and in the three-celled hind wing subtriangle (Carle, 1986; Zhang et al., 2017). The venation of *Gomphidia* Selys, 1854 (incl. *Mitragomphus* Needham, 1944), resembles that of *Ictinogomphus engelorum* sp. nov., but the pterostigmal braces are reduced, and the forewing discoidal triangle is more equilateral than in *Ictinogomphus engelorum* sp. nov., although subject to some variation (Needham, 1944; Garrison et al., 2015; Zhang et al., 2017; Babu and Subramanian, 2019). *Cacoides*

Cowley, 1934 shares with *Ictinogomphus engelorum* sp. nov. the presence of three rows of cells between RP3/4 and posterior branch of IR2, several crossveins in the area between RP and MAa basal of RP3/4, but it differs from *Ictinogomphus engelorum* sp. nov. in the equilateral forewing discoidal triangle, a marked concavity of the vein RP2, and a longer pterostigma, covering much more cells (Schmidt, 1935: pl. 17, fig. 5; Garrison et al., 2010). *Melanocacus* Belle, 1986, also differs from *Ictinogomphus engelorum* sp. nov. in the equilateral forewing discoidal triangle and a longer pterostigma, covering many more cells (Belle, 1986).

The four Recent genera *Ictinogomphus*, *Austrictinogomphus* Fraser, 1940, *Sinictinogomphus* Fraser, 1939, and *Indictinogomphus* Fraser, 1939, can be accurately separated on the basis of the genitalia only (Fraser, 1939). Carle (1986: 320) indicated that *Austrictinogomphus*, *Cinitogomphus* Pinhey, 1964, *Indictinogomphus*, and *Sinictinogomphus* could be subgenera of *Ictinogomphus*. Only this group of genera would greatly resemble *Ictinogomphus engelorum* sp. nov. Nevertheless, *Ictinogomphus engelorum* sp. nov. differs from the African genus *Cinitogomphus* in the forewing discoidal triangle with the costal side longer than the basal side, not right angled isosceles (Pinhey, 1964, 1970). In *Ictinogomphus engelorum* sp. nov., this triangle is isosceles in having costal and distal sides of the same lengths, not the basal and costal sides. The monotypic genus *Austrictinogomphus* has only two rows of cells in the postdiscoidal area, but the variability of this character remains unknown (Fraser, 1940). It is not possible to discriminate among the three other genera *Ictinogomphus*, *Sinictinogomphus*, and *Indictinogomphus*. We can only indicate that *Ictinogomphus engelorum* sp. nov. corresponds to an *Ictinogomphus* sensu lato. The presence of three rows of cells in area between RP3/4 and posterior branch of IR2 in *Ictinogomphus engelorum* sp. nov. seems to be unusual in the genus *Ictinogomphus*. At least *Cinitogomphus dundoensis*, *Ictinogomphus alaquopterus*, *I. angulosus*, *I. australis*, possibly *I. distinctus*, *I. kishori* and *I. celebensis*, *I. decoratus*, *I. dobsoni*, *I. ferox*, *I. fraseri*, *I. paulini*, *I. pertinax*, *I. pugnovittatus*, *I. rapax*, *I. regis-alberti*, and *I. tenax* have only two rows of cells in this area (Schmidt, 1935; Ram, 1985).

Among the fossil Lindeniinae, the oldest representative *Cratolindenia knuepfae* Bechly, 2000, is from the Early Cretaceous of Brazil. It strongly differs from *Ictinogomphus engelorum* sp. nov. in a

more distal position of the posterior branch of IR2, in a strongly oblique pterostigmal brace and in having a very broad area between RP2 and RP1 below the pterostigma. Schädel and Bechly (2016) described *Burmalindenia imperfecta* based on the basal parts of hind wings from the 'mid'-Cretaceous Burmese amber, and attributed it to the 'subfamily cf. Lindeniinae'. It differs from *Ictinogomphus engelorum* sp. nov. in the strongly curved veins AA1b and CuAb.

Hagen (1863) described *Ictinogomphus fur* from the Oligocene of Rott am Siebengebirge (Germany), on the basis of the basal third of a wing. The elongate vein CuAb would suggest it is a hind wing; but if this is correct, the presence of three cells in the subdiscoidal area does not fit with an *Ictinogomphus* in which this area is unicellular (Frazer, 1957). Indeed, the shape of the discoidal triangle better corresponds to that of a forewing. Nel and Paicheler (1994a) already indicated that it is an Anisoptera of uncertain family that should be revised.

Nel and Paicheler (1994a) described an undetermined Lindeniinae from the latest Oligocene of Bes-Konak (Turkey). Also Prokop et al. (2016) described an *?Ictinogomphus* species indet. from the early Oligocene of Seifhennersdorf (Saxony, Germany) on the basis of the distal two-third of a forewing. *Ictinogomphus engelorum* sp. nov. differs from these two fossils in the broader area between posterior branch of IR2 and RP3/4 with three rows of cells in the narrowest part, instead of two, the broader area between the two branches of IR2 with three rows of cells basal of the secondary longitudinal vein instead of two, and the longer and better defined secondary vein between the branches of IR2.

Schädel and Lechner (2017) described *Ictinogomphus hassleri* from the early Miocene of Carinthia (Austria), on the basis of the distal two-third of a hind wing. *Ictinogomphus engelorum* sp. nov. differs from *I. hassleri* in the presence of three rows of cells between RP3/4 and posterior branch of IR2 instead of two, and in the presence of only one row of cells between IR2 and RP2, instead of two, below the pterostigma.

Schädel and Lechner (2017: 157) indicated that *Ictinogomphus hassleri* can be separated from the other lindeniiinae genera, except *Ictinogomphus* and *Sinictinogomphus* Fraser, 1939, by the 'shape of the triangulum and the position of the Tspl-origin', without being more precise. But the preserved parts of the wing of *I. hassleri* are nearly identical to those of the Recent *Gomphidia podhigai* Babu and

Subramanian, 2019, without perceptible differences in the discoidal triangle, position of the angle of MAb and shape of the trigonal planate (Babu and Subramanian, 2019: fig. 9).

Yasuno (1990) attributed an abdomen with characteristic lateral expansions from the Miocene of Japan to the genus *Ictinogomphus*. It is not possible to compare it to *Ictinogomphus engelorum* sp. nov., and its attribution to a lindeniiinae genus is not possible.

Suborder ZYGOPTERA Selys, 1854 or
EPIPROCTOPHORA Bechly, 1996

Stem group of family SIEBLOSIIDAE Handlirsch,
1907

Genus *OLIGOLESTES* Schmidt, 1958

Type species. *Lestes grandis* Statz, 1935 (Oligocene, Rott am Siebengebirge, Germany).

Other species. *Oligolestes stoeffelensis* sp. nov. (Oligocene, Enspel, Germany).

Oligolestes stoeffelensis sp. nov.

Undetermined Zygoptera (Wedmann, 2000: 15, pl.
9, fig. 1)

Figure 11

zoobank.org/3D348180-21EC-4BA1-871F-D994E84952F4

Type material. Holotype PE 1995/9164-LS (compression fossil of a rather well-preserved body with the three basal abdominal segments and bases of the four wings), stored at the State Collection of Natural History of Rhineland-Palatinate.

Diagnosis. Wing with a narrow area between CuA and posterior wing margin with two rows of cells.

Etymology. Named after the mined and now disappeared Stöffel hill, that once covered the sediments of paleolake Enspel.

Description. Head visible from frontal, hammer-shaped, with globular eyes well-separated, 4.6 mm wide, dark; meso-metathorax 9.3 mm long, 4.7 mm high, dorsally green-blue metallic; abdomen dorsally green-blue metallic, ventrally dark; second segment with secondary male genital apparatus; only parts of the wings between their bases and nodi preserved, 19.1 mm long, petiole of wings 4.8 mm long; distance from base to arculus 5.8 mm, from arculus to nodus 4.8 mm; estimated distance between nodus and wing apex 21.3 mm; estimated wing length 32.0 mm; wing 4.9 mm wide at level of nodus; Ax1 and Ax2 2.1 mm apart; Ax2 aligned with arculus; discoidal cells of fore- and hind wings identical, basal side 0.5 mm long, costal side 0.9 mm long, distal side (MAb) 0.9 mm long, ventral side 13.8 mm long; ScP kinked at nodus; nodal crossing and subnodus perpendicular to RA and RP1/2, respectively; bases of RP3/4 and IR2 mid-

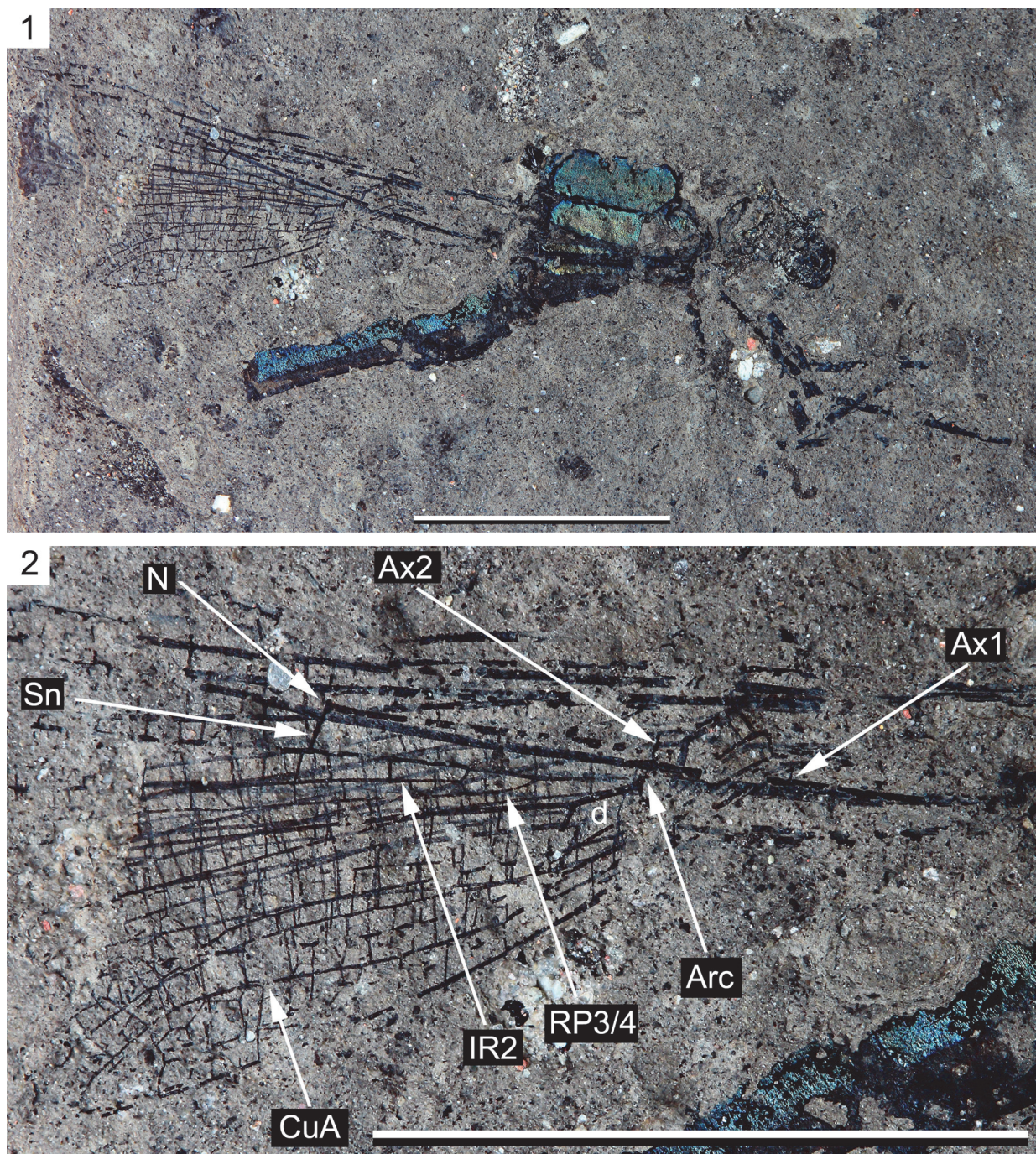


FIGURE 11. *Oligolestes stoeffelensis* sp. nov., holotype PE 1995/9164-LS. 1, Photograph of habitus; 2, Hind wing, Arc arcus, d discoidal cell, N nodus, Sn subnodus. Scale bar is 10 mm.

way between nodus and arcus, that of RP3/4 3.0 mm distal of arcus, that of IR2 1.5 mm of that of RP3/4; one row of cells between RP3/4 and MAa and in postdiscoidal area in preserved parts; CuA strongly curved, ending on posterior wing margin well distal of level of nodus; two rows of cells between CuA and posterior wing margin.

Remarks. The wing venation of this fossil, although incompletely preserved, is very similar to that of the Oligocene genus *Oligolestes* in the shape of the discoidal cells, subnodus being perpendicular to RP1/2 and RA, bases of IR2 and RP3/4 located midway between arcus and nodus, arcus opposite Ax2, curved CuA with three rows of cells between it and posterior wing

margin, base of RP2 well distal to subnodus, narrow area between RP3/4 and MAa (Schmidt, 1958: fig. 2). Statz (1935: 12) indicated that the arculus of *O. grandis* is 5.5 mm from the wing base but, after the photograph of Schmidt (1958: 3, pl. 1, fig. 1), the wing is broken at base, and thus the petiole is certainly longer than the estimation of Statz. Schmidt added that the wing is 39.0 mm long, and proposed a reconstruction with an elongate petiole figured with dotted lines. The ratio (wing width at level of nodus/distance nodus to arculus) is 1.05 for the two fossils, suggesting that the other main proportions are also similar. We calculate the estimated distance between the nodus and the wing apex of *Oligolestes stoeffelensis* sp. nov. after its ratio with the distance between arculus and nodus compared to that of *O. grandis*; and thus we could establish an estimation of the total wing length of *O. stoeffelensis* sp. nov., which would be ca. 32 mm, thus it is distinctly smaller than *O. grandis*. The ratio (distance nodus to arculus/width cubital area) is 3.3 for *O. grandis* while it is 4.3 in *O. stoeffelensis* sp. nov., corresponding to a narrower cubital area in the latter.

The exact phylogenetic position of the genus *Oligolestes* remains somewhat enigmatic, although Nel et al. (2005a) considered it as belonging to the stem group of the Cenozoic family Sieblosiidae. The Sieblosiidae sensu stricto are characterized by the presence of a highly specialised nodus apparently traversed by ScP, as the terminal kink of CP is shifted basally together with the nodal and subnodal veinlets and the nodal membrane sclerotisation is reduced. Such structure is only present, among the Odonata, in the Mesozoic anisopteran family Aeschnidiidae. Our fossil, *O. grandis*, and *Italolestes* Nel et al., 2005, have a ScP making a kink in the nodus as in the other Odonata. *Italolestes* differs from our fossil and *O. grandis* in the nodal crossing and subnodus of 'normal' obliquity (Nel et al., 2005a-b; Nel and Fleck, 2012). The Miocene sieblosiid genera *Paraoligolestes* Nel and Escuillie, 1993 and *Miostenolestes* Nel et al., 2005 have a venation also very similar to that of our fossil and *O. grandis*, especially in the rather narrow discoidal cells (compared to those of the Oligocene *Sieblosia* Handlirsch, 1906, *Stenolestes* Scudder, 1895, *Parastenolestes* Nel and Paicheler, 1994b, or the Miocene *Germanolestes* Nel and Fleck, 2012), but their ScP cross through the nodus (Nel and Escuillie, 1993; Nel and Paicheler, 1994b).

Notice that the current phylogenetic relationships of the Sieblosiidae remain uncertain, being either related to the Epiproctophora (the so-called

'Anisozygoptera' + Anisoptera) or to the Zygoptera (see discussion in Fleck et al., 2004).

Oligolestes stoeffelensis sp. nov. is of great interest for the head morphology in Sieblosiidae. In the few sieblosiid specimens with the head preserved, it is deformed due to the projection of the mouthparts and the crushing of the frons (Nel et al., 2005: fig. 11). This phenomenon is quite frequent among the fossil Zygoptera (Nel and Papazian, 1985: figs. 1-4; but see also <http://mediaphoto.mnhn.fr/media/15184399435421FO8gTE-JGLR9en8s> or <http://mediaphoto.mnhn.fr/media/15184399443786A3TS35X0Rz2fEVq>) or even in the Tarsophlebiidae (sister-group of Odonata) (Fleck et al., 2014: fig. 1). In the case of *Oligolestes stoeffelensis* sp. nov., the lateral position of the body together with the rotation of the head have led to the absence of frontal projection of the mouthparts and to a minimal deformation of the head. It clearly confirms that the head of the Sieblosiidae is of zygopteran hammer-type.

Oligolestes stoeffelensis sp. nov. is also of great interest because it has the dorsal surface of the thorax and abdomen green-blue metallic (probably physical colors, as it can be frequently observed in fossil insects preserved in diatomites), a character that was unknown for the other Sieblosiidae. Preservation of metallic structural colors in Enspel insects was hitherto primarily known from exceptionally well-preserved beetle fossils (e.g., Wedmann, 2000, Wedmann et al., 2010, McNamara, 2013; Penney and Jepson, 2014: figs 46–48).

NAIADS FROM PALEOLAKE ENSPEL

Brockhaus et al. (2020) described several naiads attributed to the Lindeniinae from paleolake Enspel, being likely more closely related to *Gomphidia* or *Ictinogomphus* than to any other genera of the subfamily. The present discovery of an adult *Ictinogomphus* confirms the presence of this group in this paleolake, and the probable correspondence between these naiads and the adult of *I. engelorum* sp. nov. These dragonflies were probably autochthonous in this paleolake. This new species also confirms the presence and diversity of the Lindeniinae in the Oligocene–Miocene of Europe.

Wedmann et al. (2010: fig. 6a) figured a naiad of a 'possibly Aeshnidae' from Enspel. This naiad clearly belongs to the Aeshnidae because of the long terminal spine-like abdominal appendages, long abdomen with lateral spines on the last segments, shape of the eyes and head very similar to

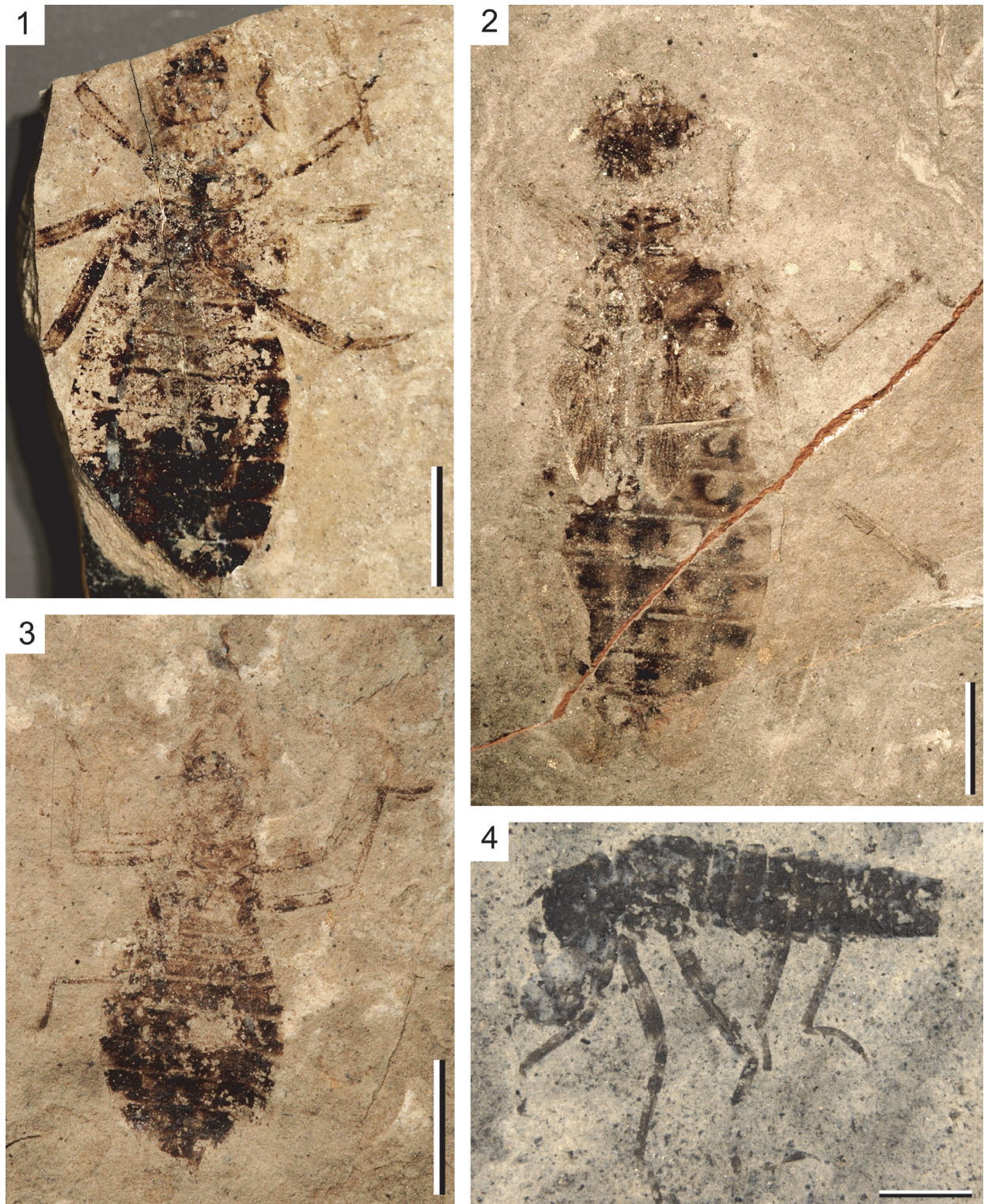


FIGURE 12. Naiads of Odonata from paleolake Enspel. **1–3**, Naiads attributable to the libelluloid clade. **1**, PE 2006/5022-LS; **2**, PE 2010/5637-LS; **3**, PE 2010/5657-LS; **4**, PE 2010/5637-LS, a zygopteran naiad. Scale bars are 5 mm (**1–3**), 2 mm (**4**).

those of extant *Aeshna*. Unfortunately, the wing pad trachea are too poorly preserved to allow an attribution to a precise genus. It can only be considered as an aeshnid naiad, possibly of the last stage, because of the long wing pads.

Several naiads (PE 2006/5022-LS, PE 2010/5657-LS, PE 2010/5637-LS) are attributable to the libelluloid clade (Figure 12.1–3). Their masks are too poorly preserved to be studied. Only the wing pads of PE 2010/5637-LS show very well-preserved trachea (Figure 12.2). The anal loop is clearly visible, elongate toe-shape, typical of the crown group of the Libellulidae. This naiad seems to have a dorsal aperture on the thorax, suggesting it could be an exuvia.

One undescribed naiad is attributable to the suborder Zygoptera (PE 2013/5018-LS, Figure 12.4). Although incomplete, the shape of the mask and body remind of Lestidae. In addition to the remains of the adult specimen of *Oligolestes stoef-felensis* sp. nov., this naiad is the only record of damselflies from paleolake Enspel.

CONCLUSION

The specimens described herein significantly add to the biodiversity of the Odonata fauna of the late Oligocene paleolake of Enspel, which is shown to be quite diverse comprising at least two species of Aeshnidae, one Gomphidae (adult and naiads), one Macromiidae (Brockhaus et al., 2020), a stem Libellulidae, a crown Libellulidae (naiad), a stem Sieblosiidae of the genus *Oligolestes*, and a zygopteran naiad possibly of the families Lestidae or Sieblosiidae. The genera *Oligaeschna*, *Epi-aeschna*, and *Ictinogomphus* were already recorded from other European outcrops. The presence of a stem Sieblosiidae is especially interest-

ing because this family is currently only known from Eurasian Oligocene–Miocene paleolakes and seems to be typical of these periods and paleogeographical area (Nel et al., 2005a; Nel et al., 2016). They are not present among the odonatan fauna of the Eocene of Messel or North America, where they seem to be ‘replaced’ by other large, damselfly-like Odonata (Garrouste and Nel, 2015).

This high diversity and the presence of many naiads suggest the presence of an autochthonous fauna with both naiads and adults of the same species and thus a water oxygenated enough for these nymphs, at least in the shallow water zones near the shores of the paleolake, that was frequently and long enough (several years with respect to Gomphidae) suitable to allow the development of these insects. Furthermore, extant Aeshnidae and Macromiidae are fast and enduring fliers and thus the representatives of these families were potential ‘hawker predators’ patrolling the open spaces along the shores of palaeolake Enspel when foraging. In contrast, Sieblosiidae, Libellulidae, and Gomphidae tend to be less persistent fliers and preferentially represent the ‘percher’ type of predator. This suggests that there was some niche partitioning among the dragonflies of paleolake Enspel indicating a well-structured ecosystem.

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