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### Two new fossil dragonfly species (Insecta: Odonata: Panisoptera: Aeschnidiidae and Aktassiidae) from the Solnhofen Lithographic Limestones (Upper Jurassic, Germany)

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With 4 Figures

#### Summary

Two new dragonfly taxa are described from the Upper Jurassic Solnhofen Limestone (Bavaria, Germany). *Solnhofenia stobeneri* n. g. n. sp. is the sixth species of Aeschnidiidae from this locality and also the smallest one. *Aeschnogomphus kuempeli* n. sp. (Petalurida: Aktassiidae) is one of the biggest dragonflies known from this locality and even from the whole post-Triassic Mesozoic and Cenozoic.

#### Zusammenfassung

Zwei neue Libellen werden aus den oberjurassischen Solnhofener Plattenkalken (Bayern, Deutschland) beschrieben. *Solnhofenia stobeneri* n. g. n. sp. ist die sechste Art der Aeschnidiidae von dieser Fundstelle und auch die kleinste. *Aeschnogomphus kuempeli* n. sp. (Petalurida: Aktassiidae) ist eine der größten bekannten Libellen von dieser Fundstelle und sogar aus dem ganzen post-triassischen Mesozoikum und Känozoikum.

#### 1. Introduction

The extinct dragonfly family Aeschnidiidae belongs to the dominating elements of the Mesozoic odonate fauna. About 25 species are known from the Upper Jurassic to the Upper Cretaceous. Five species of Aeschnidiidae have been described from the famous Solnhofen Lithographic Limestones: *Aeschnidium densum* HAGEN, 1862, *Urogomphus eximius* HAGEN, 1862 (= *Lithoaeschnidium viohli* NEL, MARTÍNEZ-DELCLÒS & PAICHELER, 1993), *Urogomphus giganteus* (MÜNSTER in GERMAR, 1839), *Bergeriaeschnidia abscissa* (HAGEN, 1862) (= *Bergeriaeschnidia inexpectata* NEL, BECHLY & MARTÍNEZ-DELCLÒS, 1996), *Malmaeschnidium mayeri* NEL, MARTÍNEZ-DELCLÒS & PAICHELER, 1993. Here I describe a sixth species which

is the smallest representative of this group from this locality. Furthermore, I describe a new giant petalurid species of the genus *Aeschnogomphus* (Aktassiidae), which indeed proves to be one of the biggest known odonates from the whole post-Triassic Mesozoic and Cenozoic.

## 2. Material and methods

The drawing was made with a camera lucida, and the photos were made with a 35 mm SLR camera and macro lens. The nomenclature of the dragonfly wing venation is based on the interpretations of RIEK & KUKALOVÁ-PECK (1984), amended by NEL et al. (1993), NEL & MARTÍNEZ-DELCLÒS (1993), and BECHLY (1996). The systematic analysis is based on the principles of consequent Phylogenetic Systematics (sensu HENNIG 1966, 1969).

## 3. Systematic Palaeontology

Class Insecta LINNAEUS, 1758 (= Hexapoda LATREILLE, 1825)

Pterygota BRAUER, 1885

Order Odonata FABRICIUS, 1793

Panansoptera BECHLY, 1996

Family Aeschnidiidae HANDLIRSCH, 1906

(= Sonidae PRITYKINA, 1986; = Nothomacromiidae CARLE, 1995)

Genus *Solnhofenia* n. g.

Type species: *Solnhofenia stobeneri* n. sp., by present designation.

Derivation of name: After the city of Solnhofen in Bavaria (Germany).

Diagnosis. – See type species, since monotypic.

Phylogenetic position. – This genus shares four distinct synapomorphies with Aeschnidiidae and thus can be attributed to this taxon with great certainty: Discoidal triangles strongly transverse in both pairs of wings; presence of a well-defined M<sub>spl</sub> that originates and ends on MA; hypertrophied vein PsA and enlarged subdiscoidal triangle with an angled posterior side; fan-like anal area. Furthermore, there are several rare symplesiomorphies, such as the short and broad female abdomen, short abdominal segments, and widely separated compound eyes.

*Solnhofenia stobeneri* n. sp.

Figs 1–2

Holotype: Specimen no. SMNS 64274 in collection of the Staatl. Museum f. Naturkunde, Stuttgart, Germany. This specimen was kindly donated to this museum by the private collector Mr G. STÖBENER (Staufenberg). It is the only known specimen of this new taxon.

Type locality: Blumenberg near Eichstätt, southern Frankonian Alb, Bavaria, Germany.

Type horizon: Solnhofen Formation (Solnhofen Lithographic Limestones, „Malm ζ 2b“). Upper Jurassic, Lower Tithonian, Hybonotum Zone, Rueppellianum Subzone.

Derivation of name: Named in honour of the collector Mr GERHARD STÖBENER (Staufenberg).

Diagnosis. – This new genus and species differs from all other Aeschniidae from the same locality by its distinctly smaller size (wing length 32.5 mm, compared to 40–95 mm in the five other species). Also considering other localities, it is distinguished from the few other Aeschniidae that are of comparably small size by the following hindwing characters: Discoidal triangle relatively broad (discoidal triangle very narrow in *Iberoaeschnidium conquensis*, *Lleidoaeschnidium valloryi*, and *Aeschnidiella kabanovi*); its distal side MAb straight (MAb distinctly bulged inwards in *Iberoaeschnidium conquensis*, *Lleidoaeschnidium valloryi*, *Aeschnidiella kabanovi*, and *Nannoaeschnidium pumilio*); subdiscoidal veinlet very long and transverse (short and/or oblique in all other species); subdiscoidal triangle very broad with angled posterior side (subdiscoidal triangle narrow with curved posterior side in *Lleidoaeschnidium valloryi*, *Aegyptidium aburasiensis*, and *Aeschnidiella kabanovi*); space between MA and Mspl broad (very narrow in *Iberoaeschnidium conquensis*, *Aegyptidium aburasiensis*, and *Aeschnidiella kabanovi*).

#### Description

A rather complete but very poorly preserved fossil dragonfly with all four wings in outstretched position. Only one pair of legs is visible, and the distal parts of the forewings and the right hindwing are hardly preserved. The main veins are visible due to the corrugation of the wing, but only few crossveins are preserved. Probable total wing span about 68 mm. It cannot be clearly recognized if it is a male or a female specimen, but within Aeschniidae such a broad abdomen always suggests that it is most likely a female specimen.

Body: Width of head 5.9 mm; compound eyes small and widely separated (distance 2.9 mm). Thorax is 9.6 mm long and max. 5.5 mm wide, but does not show any details. Length of abdominal segment I, 2.4 mm; of segment II, 3.4 mm; of segment III, 3.0 mm; of segment IV, 4.1 mm; of segment V, 2.9 mm; of segment VI, 3.2 mm; of segment VII, 2.4 mm; of segment VIII, 3.0 mm; of segment IX, 2.2 mm; visible length of segment X, 0.4 mm. Anal appendages well-preserved (cerci 2.2 mm long and 0.8 mm wide; epiproct 2.1 mm long and pointed); thus, the relative length of the anal appendages is much longer than for example in *Urogomphus* (BECHLY 1998). The median longitudinal „line“ that is visible on the abdomen probably is not a dorsal carina, but the ventral cleft. Auricles or secondary genital organs are not visible. The fore legs are well-preserved (visible length of femur 5.5 mm, length of tibia 5.6 mm, length of tarsus with claws 2.9 mm). The middle and hind legs are not visible.

Forewing: Only very poorly preserved. Even the total length is not visible. The only useful preserved character is the transverse discoidal triangle, which is somewhat broader than that of the hindwing; length of its anterior side, 2.2 mm; of its straight basal side, 3.6 mm; of its distal side MAb, 4.5 mm; MAb is slightly sigmoidally curved.

Hindwing: Length, 32.3 mm; max. width near wing base, 11.1 mm; width at nodus, 9.6 mm; distance from base to arculus, 3.2 mm; distance from base to nodus, 14.5 mm. Pterostigma not preserved. Nodus situated at about 45 % of wing length. Nodal transverse and subnodal veinlet oblique. It is not visible if ScP is prolonged distal of nodus by a pseudo-ScP. Only the two primary antenodal crossveins are preserved; they are aligned and strong. Ax1 is 0.7 mm basal of arculus, while Ax2 is not clearly preserved. Arculus angled with a less distinct posterior part. RP and MA not fused at arculus, but originating from one place on RA. First branching of RP (midfork) 5.9 mm basal of subnodus, and origin of IR2 only 0.5 mm distal of midfork.

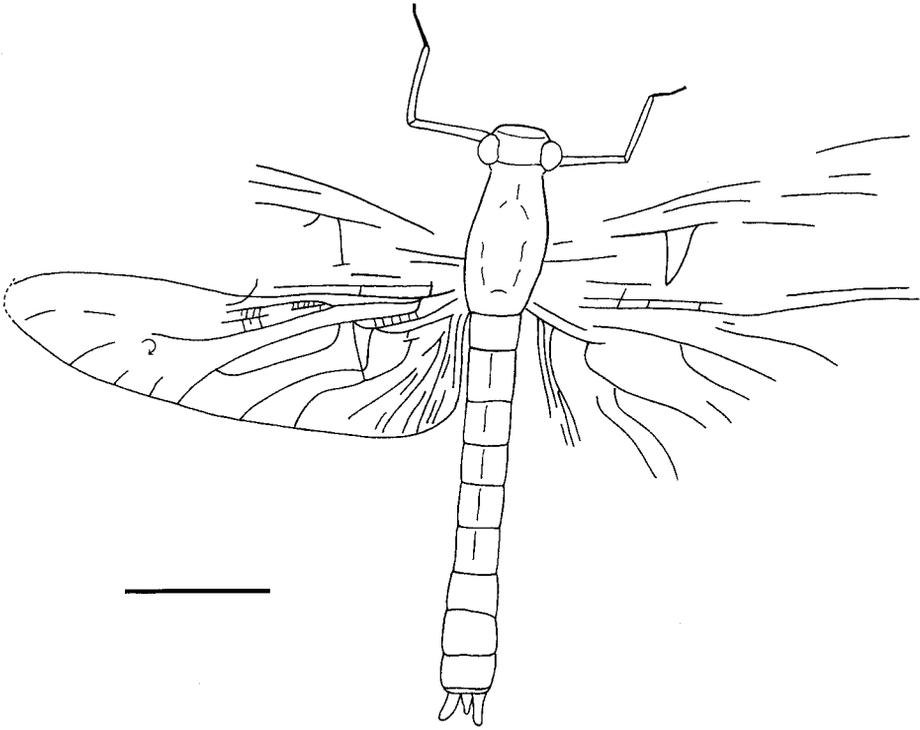


Fig. 1. *Solnhofenia stoebeneri* n. gen. n. sp., holotype SMNS 64274. Scale 10 mm.

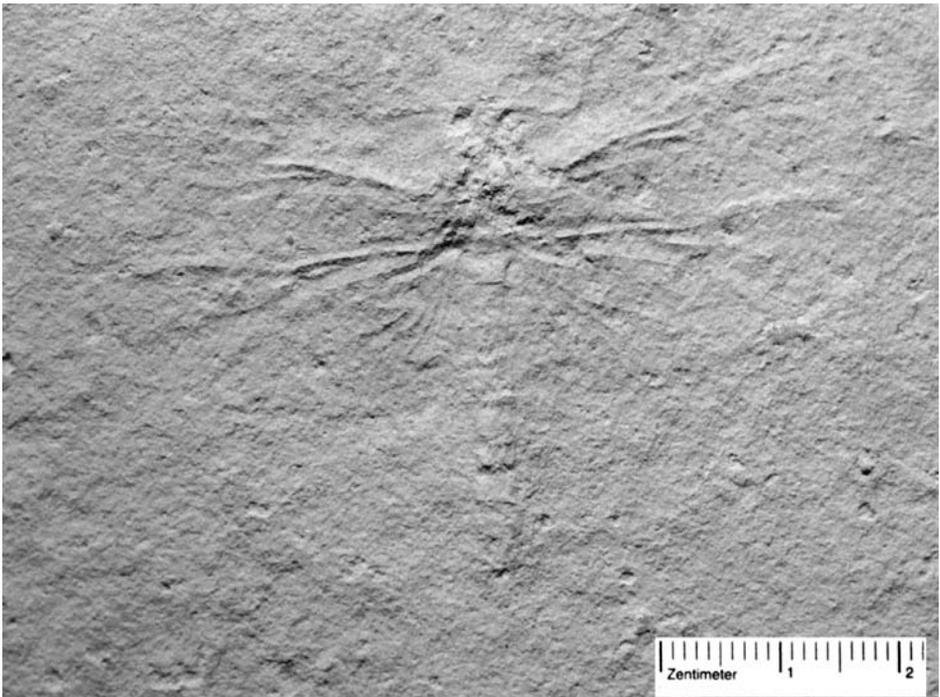


Fig. 2. *Solnhofenia stoebeneri* n. gen. n. sp., holotype SMNS 64274. Scale as indicated by rule.

Base of RP2 aligned with subnodus. Oblique vein(s) ,O' not preserved. Rspl not clearly preserved. Distal part of wing poorly preserved, not showing useful details. Area between RP3/4 and MA distally widened. Mspl short (length 9.2 mm) but well-defined; Mspl originates and ends on MA. Postdiscoidal area distally gently widened (width near discoidal triangle, 3.2 mm; width at posterior wing margin, 4.5 mm). Hypertriangle long and narrow (length, 4.4 mm; max. width, 0.7 mm), and divided by several crossveins (at least five are visible); its costal margin is rather straight. Discoidal triangle transverse; length of its curved anterior side, 1.5 mm; of its bent basal side, 3.0 mm; of its straight distal side MAb, 3.5 mm. CuP-crossing and potential cubito-anal crossveins not preserved. Anal vein divided into a well-defined anterior secondary branch PsA and an angled main branch AA, delimiting a large subdiscoidal triangle that was certainly divided into multiple cells. PsA ends at basal angle of discoidal triangle. MP and CuA basally slightly diverging, but distally strongly divergent. MP reaches posterior wing margin on a level with subnodus. Posterior branches of CuAa not preserved or absent; CuAb not visible (reduced). Subdiscoidal veinlet very long (length, 0.7 mm). Max. width of cubito-anal area (below discoidal triangle), 3.7 mm. Anal area broad (max. width, 6.9 mm) and fan-like with several posterior branches of AA, alternating with concave intercalary veins. Anal loop absent. Pseudo-anal loop basal of subdiscoidal triangle not preserved or absent. Neither distinct anal angle, nor anal triangle, but anal margin makes rectangular bend near wing base. No membranule visible.

Anisoptera SELYS in SELYS & HAGEN, 1854

Petalurida BECHLY, 1996

Family Aktassiidae PRITYKINA, 1968

Subfamily Aktassiinae PRITYKINA, 1968

Genus *Aeschnogomphus* HANDLIRSCH, 1906

Type species: *Aeschnogomphus buchi* (HAGEN, 1848), by subsequent designation of COWLEY (1934: 249). *Aeschnogomphus charpentieri* (HAGEN, 1848) is a junior synonym of *A. buchi* according to NEL et al. (1998: 42).

Further species: *Aeschnogomphus intermedius* (MÜNSTER in GERMAR, 1839) and *Aeschnogomphus kuempeli* n. sp.

Phylogenetic position. – This genus belongs to Aktassiidae within the stem-group of Petaluridae according to NEL et al. (1998). The attribution of the new species to this genus is based on the following distinct synapomorphies and diagnostic similarities: giant size (wing span larger than 150 mm); wings falcate and very slender; posterior margin of hindwing rather straight between CuA and apex; postnodal space and bridge space (Bqs-area) very narrow; discoidal triangles longitudinally elongate in both pairs of wings; RP3/4 and MA undulated in both pairs of wings; long and strong IR1; characteristic shape of long and straight anal appendages.

*Aeschnogomphus kuempeli* n. sp.

Figs 3–4

Holotype (Fig. 3): Specimen without number in coll. KÜMPEL (Wuppertal); the specimen is deposited as permanent loan at the Jura Museum in Eichstätt, and a donation to this museum is already written in will.

Paratype (Fig. 4): Specimen no. SOS 4653, Jura Museum in Eichstätt. The counterplate is

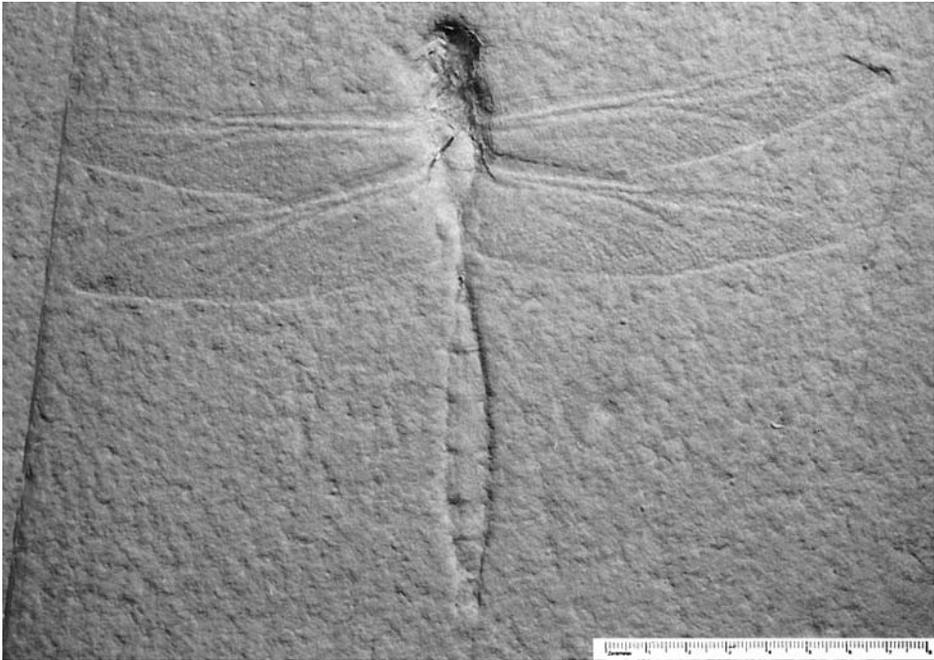


Fig. 3. *Aeschnogomphus kuempeli* n. sp., holotype JME without no. (in coll. KÜMPEL). Scale as indicated by rule.

in private possession. A further specimen that might belong to this species or another new species is a large *Aeschnogomphus* with broadened abdomen that was found as first fossil insect from the Öchselberg quarry near Breitenhill (Malm  $\zeta$  1 or 2a according to VIOHL, pers. comm.) and is now deposited at the Bürgermeister Müller Museum in Solnhofen.

Type locality: „Kinderdorf“ quarry, Blumenberg near Eichstätt, southern Franconian Alb, Bavaria, Germany.

Type horizon: Solnhofen Formation (Solnhofen Lithographic Limestones, „Malm  $\zeta$  2b“). Upper Jurassic, Lower Tithonian, Hybonotum Zone, Rueppellianum Subzone.

Derivation of name: Named in honour of the collector Mr DIETER KÜMPEL (Wuppertal).

Diagnosis. – This new species differs from the other two species of the same genus by its larger size (wing span 205–220 mm) and the strong expansion of the distal part of the abdomen.

#### Description

Holotype: A complete male dragonfly with all four wings in outstretched position. Only one pair of legs is visible, and the apex of the left forewing is reconstructed. The wing venation is rather poorly preserved, but some of the main veins are visible due to the corrugation of the wing. Total wing span about 220 mm!

Body: The head is only preserved as a calcite-filled hollow; max. width of head, 14 mm; the compound eyes apparently have been large. The thorax does not show any useful details and none of the legs is visible. Length from head to apex of abdomen (incl. appendages) 143 mm; the basal part of the abdomen is strongly constricted (min. width only 2 mm), while the distal part is very much dilated (max. width

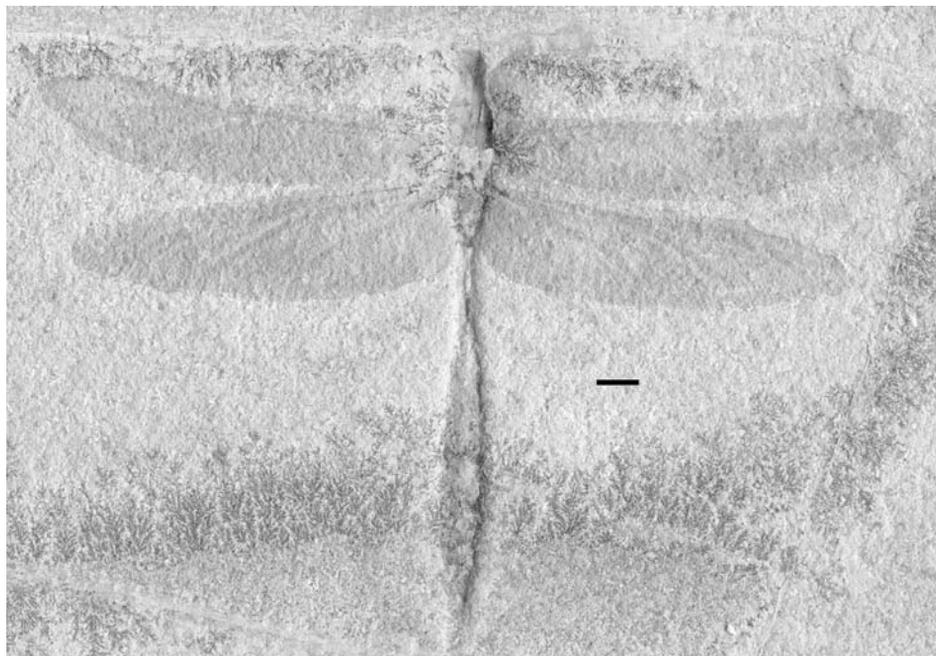


Fig. 4. *Aeschnogomphus kuempeli* n. sp., paratype JME SOS 4653. Scale 10 mm.

11 mm). Anal appendages long (cerci 8–9 mm long), straight and strong, but poorly preserved. Auricles or secondary genital organs are not visible.

Forewings: Total length 106 mm; width at nodus 19.5 mm; distance from base to nodus about 50 mm. The only useful preserved characters are the longitudinally elongate discoidal triangles and the undulation of RP3/4 and MA.

Hindwings: Total length 96 mm; width at nodus 23 mm; distance from base to nodus 42 mm; nodus situated at about 44 % of wing length. A long vein IR1 seems to be present. The discoidal triangle are longitudinally elongate. RP3/4 and MA somewhat undulated. An anal angle and a large anal triangle are visible in the right hindwing, thus it is a male specimen.

Paratype: A complete dragonfly with all four wings in outstretched position. Head and thorax are only preserved as a hollow, and not show any useful details. Length from head to apex of abdomen (incl. appendages) about 130 mm; the basal part of the abdomen is strongly constricted (min. width only 3 mm), while the distal part is very much dilated (max. width 10.5 mm). Anal appendages not distinctly preserved. Length of hindwings 91 mm and total wing span 205 mm! The wing venation is rather poorly preserved, but the visible parts of the wing venation agree with an attribution to *Aeschnogomphus* (long IR1, no Rspl and Mspl, elongate discoidal triangle especially in hindwing). The sex of the specimen is not clearly recognizable, but the shape of the right hindwing base suggests that it could be a male specimen.

Discussion. – Even though there are only two differences that distinguish this new species from the two other known species of this genus, these differences are present in the holotype and paratype and absent in all other specimens of this genus.

Especially the curious dilation of the abdomen is a distinct character that warrants a separate species. It cannot be a sexual dimorphism, since both sexes are known from the two other species and they do never show such a dilation. Therefore, an artifact of preservation is highly unlikely as well.

There are only few other dragonflies from this locality that reach a similar size as the present new species. NEL et al. (1993: 247) measured 11 specimens of *Isophlebia aspasia* and mentioned that the forewings are 100–110 mm long and the hindwings are 94–110 mm long. However, only five of these specimens are actually larger than the holotype of *Aeschnogomphus kuempeli* n. sp. The average forewing size of eight specimens of *Isophlebia aspasia* is 105 mm, thus slightly smaller. The two other species of *Aeschnogomphus* are distinctly smaller (max. forewing length 96 mm; NEL et al. 1998) and *Urogomphus giganteus* also does not exceed 200 mm wing span (max. wing length 93–95 mm). There are no other Mesozoic or Tertiary dragonfly species that reach a similar large size, except for the Triassic genus *Triadotypus* with a probable wing length of about 13 cm. The only extant odonate that reaches a similar size is the Neotropical helicopter damselfly *Megaloprepus coerulatus* with a maximum wing span of 200 mm, but it has much more slender wings and a very delicate abdomen. Consequently, the new species *Aeschnogomphus kuempeli* n. sp. is one of the largest dragonfly species from the post-Triassic Mesozoic and Cenozoic.

#### 4. Acknowledgements

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