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A revision of the fossil dragonfly genus *Urogomphus*, with description of a new species (Insecta: Odonata: Pananisoptera: Aeschnidiidae)

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With 34 Figures

Summary

The dragonfly genus *Urogomphus* from the Upper Jurassic of Germany is revised and its position in Aeschnidiidae is confirmed. *Urogomphus giganteus* and *U. eximius* are redescribed, and a lectotype for *U. eximius* is designated. *Lithoaeschnidium viohli* is considered as a synonym of *U. eximius*. A new species *Urogomphus nusplingensis* n. sp. is described from the Upper Jurassic Lithographic Limestone of Nusplingen, while the 20 other known specimens of this genus have been found in the Solnhofen Lithographic Limestone. *Urogomphus abscissus* is considered as conspecific with *Bergeriaeschnidia inexpectata*, and the holotype of the latter species is designated as neotype of *U. abscissus*, so that its valid name is now *Bergeriaeschnidia abscissa* comb. nov. The phylogenetic position of *Urogomphus* and Aeschnidiidae is discussed, a new taxon Neoanisoptera is introduced, and an explanation for the extinction of Aeschnidiidae is proposed.

Zusammenfassung

Die Libellengattung *Urogomphus* aus dem Oberjura Deutschlands wird revidiert und deren Zugehörigkeit zu den Aeschnidiidae bestätigt. *Urogomphus giganteus* und *U. eximius* werden wiederbeschrieben und ein Lectotypus für *U. eximius* festgelegt. *Lithoaeschnidium viohli* wird als Synonym von *U. eximius* angesehen. Eine neue Art, *Urogomphus nusplingensis* n. sp., wird aus den oberjurassischen Nusplinger Plattenkalken beschrieben, während die 20 übrigen bekannten Exemplare dieser Gattung in den Solnhofener Plattenkalken gefunden wurden. *Urogomphus abscissus* wird als artgleich mit *Bergeriaeschnidia inexpectata* angesehen, und der Holotypus dieser Art wird als Neotypus von *U. abscissus* festgelegt, so daß der gültige Name nun *Bergeriaeschnidia abscissa* comb. nov. ist. Die phylogenetische Stellung von *Urogomphus* und der Aeschnidiidae wird diskutiert, ein neues Taxon Neoanisoptera wird eingeführt, und eine Erklärung zum Aussterben der Aeschnidiidae wird vorgeschlagen.

1. Introduction

The specimens of the genus *Urogomphus* belong to the most famous and largest (besides *Isophlebia* and *Aeschnogomphus*) fossil dragonflies from the Solnhofen

Limestone. Since they are relatively rare (only 20 specimens are known to me), and are generally poorly preserved, they also belonged to the least known dragonflies from this locality.

In their large revision of Aeschnidiidae, Nel & Martínez-Delclòs (1993) remarked that next to nothing is known about the three species of the genus *Urogomphus*, including the type species *U. giganteus*, and that this genus therefore has to be regarded as a nomen dubium within Aeschnidiidae incertae sedis. The authors therefore suggested that the genus *Urogomphus* should not be used for the description of further new species.

With the present revision, *Urogomphus* may now be regarded as one of the best known genera of Aeschnidiidae. The new species described from Nusplingen Limestone is based on the first specimen of this genus that was not found in Solnhofen Limestone, and represents the oldest known member of Aeschnidiidae.

2. Material and methods

The results of this revision are based on my examination of 17 specimens of the genus *Urogomphus* in the collections of SMNS (Staatliches Museum für Naturkunde, Stuttgart, incl. coll. Ludwig), GPIT (Institut und Museum für Geologie und Paläontologie, Univ. Tübingen), Jura-Museum (Eichstätt), BSPGM (Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich), SMF (Naturmuseum Senckenberg, Frankfurt a.M.), MNHB (Museum für Naturkunde, Berlin), MCZ (Museum of Comparative Zoology, Cambridge/Mass.), and private coll. Kümpel (Wuppertal), as well as on the published descriptions and figures, and an unpublished photo of Frickhinger (Emmering). I also studied 2 specimens of the genus *Bergeriaeschnidia* in the collection of Museum Bergér (Eichstätt) and coll. Leich/Fossilium (Bochum), and a further specimen on the basis of an unpublished photo of Frickhinger (Emmering).

I could not find any specimens of the genus *Urogomphus* at "Bürgermeister Müller Museum" (Solnhofen), "Maxberg Museum" (Solnhofen), Museum Bergér (Eichstätt), coll. Leich/Fossilium (Bochum), and in private coll. Tischlinger (Stammham). According to literature information, there seem to be no specimens at NHM (Naturhistorisches Museum, Vienna) and Teyler Museum (Haarlem) either.

The holotype of the new species *U. nusplingensis* n. sp. described in this publication is deposited in the collection of the Staatl. Museum f. Naturkunde (SMNS) in Stuttgart. A few of the figured specimens (originals), but no types, are located in the mentioned private collections.

All drawings were made with camera lucida, and all 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 (1976) and Riek & Kukalová-Peck (1984), amended by Kukalová-Peck (1991), Nel et al. (1993), Nel & Martínez-Delclòs (1993), and Bechly (1995, 1996). The higher classification is based on the new phylogenetic system of fossil and extant odonates of Bechly (1996, 1997). The systematic analysis is based on the principles of consequent Phylogenetic Systematics (sensu Hennig 1966, 1969) rather than numerical cladism (also called "computer cladistics") which unfortunately still is mainstream, although it has more in common with phenetics than with genuine Hennigian methods (for the referring arguments see WÄGELE 1994, BORUCKI 1996, and BECHLY 1997). The assignment of formal categorial ranks has been omitted as far as possible because they are more or less arbitrary and superfluous (WILLMANN 1989).

3. Systematic Palaeontology

Class Insecta LINNAEUS, 1758 (= Hexapoda LATREILLE, 1825)
Pterygota BRAUER, 1885
Order Odonata FABRICIUS, 1793

Pananisoptera BECHLY, 1996
Family Aeschnidiidae HANDLIRSCH, 1906
(= Sonidae PRITYKINA, 1986; = Nothomacromiidae CARLE, 1995)

Genus *Urogomphus* HANDLIRSCH, 1906

Type species: *Urogomphus giganteus* (MÜNSTER in GERMAR, 1839), by subsequent designation of COWLEY (1934).

New diagnosis. – This genus shows all autapomorphies of Aeschnidiidae (see below). It can be distinguished from the other aeschnidiid genera by the following combination of characters: Anal margin of hindwing straight and parallel to body axis, and with a sharp rectangular curvature towards the posterior wing margin (autapomorphy); costal margin and posterior wing margin rather straight, so that the hindwing has the shape of an elongate triangle (autapomorphy); pterostigma well-defined (plesiomorphy), but short and in a basal position, with an oblique basal side and a more transverse distal side; pterostigmal brace well-defined (plesiomorphy), very oblique, and either aligned with the basal side of pterostigma, or slightly displaced distally; discoidal triangles transverse, but not extremely narrow (plesiomorphy), and with two "vertical" rows of cells (plesiomorphy); RP and MA not fused at arculus, but originating from the same place on RA (plesiomorphy; the drawings in NEL & MARTÍNEZ-DELCLÒS 1993, showing a different character state, are clearly incorrect); CuAa of hindwing with two or three well-defined distal posterior branches; wing venation dense, but not as dense as in most other aeschnidiid genera (e.g. *Aeschnidium*) (plesiomorphy); large size (wing length 68–94 mm).

Like in other Aeschnidiidae, the compound eyes are widely separated and the abdomen is relatively short (distinctly shorter than the wings). The female abdomen is very broad, equilateral, and has a strongly elongated ovipositor. The male abdomen is more slender, somewhat dilated distally, and the anal appendages seem to be very short.

Phylogenetic position. – Most authors classified *Urogomphus* within Aeschnidiidae (e.g. HANDLIRSCH 1906–1908, CARPENTER 1932, FRASER 1957, ROHDENDORF et al. 1962, HENNIG 1969, MALZ & SCHRÖDER 1979, NEL & MARTÍNEZ-DELCLÒS 1993), but CARPENTER (1992) and BRIDGES (1994) recently regarded this genus as too poorly known to permit assignment to a family within Anisoptera. However, according to this revision, there can be no longer any doubt about the aeschnidiid affinities of this genus, since it shares all important autapomorphies of Aeschnidiidae (see below).

Several plesiomorphies (relatively open cross-venation, well-defined pterostigma with strong and oblique brace vein, and relatively broad and straight discoidal triangles) indicate that *Urogomphus* is the most basal representative of Aeschnidiidae, as already suggested by Schlüter & Hartung (1982). However, the statement by Schlüter & Hartung (1982) that the distal side (MAb) of the discoidal triangle is primitively convex-curved is clearly incorrect, since it is mostly weakly concave-curved or rather straight, but only very rarely convex-curved in *Urogomphus*.

Urogomphus is certainly not closely related to the giant aeschnidiid *Gigantoaeschnidium ibericum* (nomen correct. pro *G. ibericus* Nel & Martínez-Delclòs, 1993) from the Lower Cretaceous of Spain, since the latter species shares derived character states (more dense cross-venation, reduced pterostigmal brace, and narrower and more oblique discoidal triangle) with some other "higher" Aeschnidiidae.

The autapomorphies of *Urogomphus*, mentioned in the diagnosis, are clearly absent in *Aeschnidium densum*. Therefore, the attribution of the latter genus and species to the genus *Urogomphus* by Carpenter (1932: 108) has to be regarded as unwarranted. The similarities between *Aeschnidium densum* and *Urogomphus giganteus* are all derived groundplan characters (autapomorphies) of Aeschnidiidae, thus symplesiomorphies for the two mentioned species.

Urogomphus giganteus (Münster in Germar, 1839)
Figs 1–14

*1839 *Aeschna gigantea* Münst. – Münster in Germar, p. 216, pl. 23, fig. 14, non fig. 13, 14a.
1848 *Anax giganteus*. – Hagen, p. 10.
1862 *Petalura gigantea*. – Hagen, p. 107.
1862 *Anax giganteus*. – Hagen, p. 142.
1862 *Petalura latialata*. – Hagen, p. 107.
1886 *Estemoa gigantea*. – Deichmüller, p. 35, pl. 3, fig. 1–3.
1890 *Aeschnidium giganteum*. – Kirby, p. 165.
1898 *Estemoa gigantea* Deichmüller. – Meunier, pp. 120–121.
1906 *Urogomphus giganteus* Germar. – Handlirsch, p. 595, pl. 47, fig. 18 (after Deichmüller's figure).
1932 *Urogomphus giganteus* (Germar). – Carpenter, pp. 107–109, fig. 4.
1934 *Urogomphus* Handlirsch, 1906 ... *Aeshna gigantea* Germar (1839). – Cowley, p. 253 (subsequent designation as type species of *Urogomphus*).
1979 *Urogomphus giganteus* (Germar 1839). – Malz & Schröder, p. 39, fig. 23.
1982 *Urogomphus giganteus* Handlirsch, 1908 [sic]. – Schlüter & Hartung, p. 301, fig. 3.
1985 *Urogomphus giganteus* Carpenter. – Frickhinger, p. 260 (below).
1992 "*Urogomphus* Handlirsch, 1906b, p. 594 [**Aeschna gigantea* Germar, 1839, p. 216; SD Cowley, 1934b, p. 253]". – Carpenter, p. 85.
1993 *Urogomphus giganteus* (Germar, 1839). – Nel & Martínez-Delclòs, pp. 54–56 (placed in Aeschnidiidae incertae sedis stat. nov.).
1994 *Palaeophlebia synlestoides* Brauer [sensu Frickhinger]. – Frickhinger, p. 138, fig. 255.
1994 *Urogomphus giganteus* (Germar) 1839. – Frickhinger, p. 138, fig. 263.
1996 *Urogomphus giganteus* (Germar, 1839). – Nel, Bechly & Martínez-Delclòs, p. 178.

Holotype: Specimen no. AS VII 791 in collection BSPGM, Munich.
Type locality: Eichstätt/Solnhofen, southern Frankonian Alb, Bavaria, Germany.
Type horizon: Upper Jurassic, Malm ζ 2b ("oberer Weißjura"), Lower Tithonian, Hybonotum-Zone, Solnhofen Lithographic Limestone.

Paratype: No paratype, since GERMAR's second specimen AS VII 795 (BSPGM) is indeed a male *Aeschnogomphus intermedius* (Petalurida) (NEL & MARTÍNEZ-DELCLÒS 1993).

Further material: Specimen no. 1951.21 at Jura-Museum, Eichstätt. Specimen no. 17593 at GPIT, Tübingen. Specimen MB.J. 1721 at Museum f. Naturkunde, Berlin. Specimens nos VI 98c, VI 98b1/b2, and VI 98a at Senckenberg Museum, Frankfurt. Specimen no. 6192 at MCZ, Cambridge/Mass. Specimens no. 3831 and nos 3829–3830 in coll. BAYET at Carnegie Museum, Pittsburgh (figured in CARPENTER 1932: fig. 4). The drawing of a complete pair of wings in SCHLÜTER & HARTUNG (1982: fig. 3) is not (!) based on an original drawing from a new specimen, but clearly is a combined redrawing from previous published figures, since the basal parts of the wings are absolutely identical with CARPENTER's figure (including the four posterior branches of CuAa in the hindwing). Specimen without number in coll. BECHLY (ex coll. LUDWIG) that will be acquired by SMNS, Stuttgart. Specimen without number in private coll. KÜMPEL, Wuppertal, and a specimen in private coll. KARIOPP (Regensburg). FRICKHINGER (1994: figs 255) provided a photo of a further complete specimen in coll. INTERFOSS (wing span 19 cm, probably female).The current location of the latter specimen is unknown. Two specimens labelled «*Urogomphus giganteus*» in exhibition of coll. LEICH at the Fossilium in Bochum, indeed are both specimens of *Aeschnogomphus intermedius* (Petalurida). MEUNIER (1898) mentioned five specimens in the Museum of Munich. These five specimens most likely represent the holotype of *U. giganteus* (AS VII 791 = no. 252 of MEUNIER), the misidentified specimen of *Aeschnogomphus* (AS VII 795 = no. 250 of MEUNIER ?), and HAGEN's three syntypes of *U. eximius* (nos 16, 17, and 18 = nos 251, 253, and 254 of MEUNIER ?). All these specimens are still present in this museum (BSPGM).

New diagnosis. – Nearly all known characters, except of size, are more or less identical with *U. eximius*. I here regard all specimens with a wing length above 80 mm as *U. giganteus*, although the minimum wing length of 81–85 mm is also very close to the maximum wing length of *U. eximius* (78 mm). However, the maximum wing length of 93–95 mm certainly excludes a conspecific status with small *U. eximius* specimens (wing length, 68 mm). Therefore, two distinct species of *Urogomphus* in the Solnhofen Limestone are certainly justified, even though they can only be distinguished by a very small gap of 3 mm between their size ranges.

A further distinction from *U. eximius* seems to be the number of rows of cells between ScP and costal margin in the antenodal area of the forewings: in *U. giganteus* there are four rows of cells between Ax1 and Ax2, and three rows of cells between Ax2 and nodus (visible in specimens SMF no. VI 98c and SMF no. VI 98b2), while in *U. eximius* there are only two rows of cells in these areas (visible in specimen BSPGM no. 17), just like in the hindwings of both species. Three rows of cells are also present in the costal part of the forewing antenodal area of *U. nusplingensis* n. sp. (also between Ax1 and Ax2), which could well represent a synapomorphy with *U. giganteus*.

Redescription

Holotype BSPGM no. AS VII 791 (Figs 1–2): A complete female dragonfly with poorly preserved wing venation that was regarded by NEL & MARTÍNEZ-DELCLÒS (1993) as not showing any usable characters. This redescription proves that this statement is not quite true. Very important is the lucky circumstance that the pterostigmal brace vein is still visible in the hindwing, since its position and shape demonstrates the relationship of the holotype of *U. giganteus* (type species!) with the other better preserved specimens of the three species of this genus. Otherwise a congeneric status of these aeschnidiids would have been solely based on the common large size and the common origin from the Upper Jurassic of southern Germany.

Body: Length from head to end of abdomen (without ovipositor), 84 mm. Width

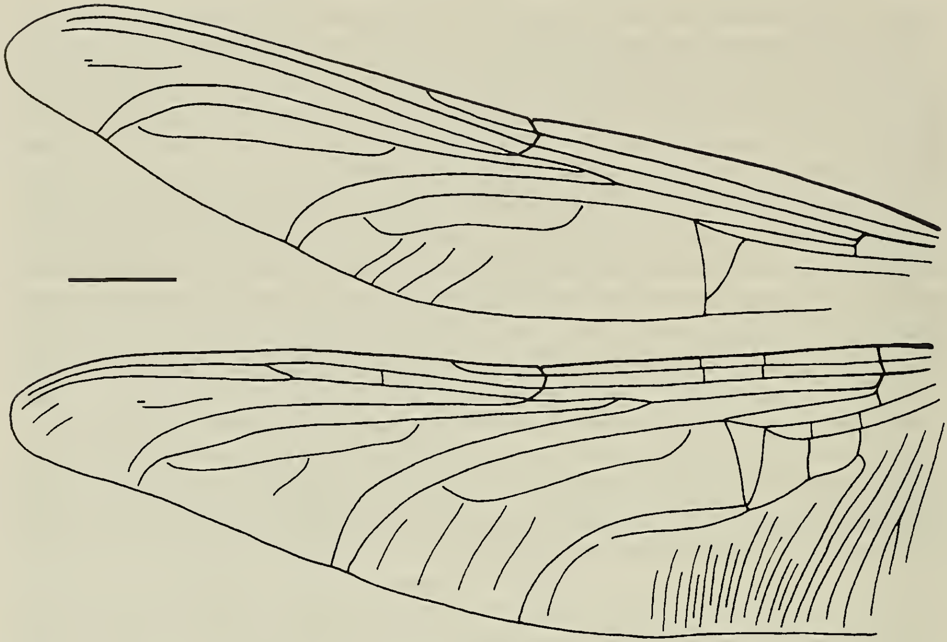

Fig. 1. *Urogomphus giganteus*, ♀ holotype BSPGM AS VII 791, left wings. Scale 10 mm.

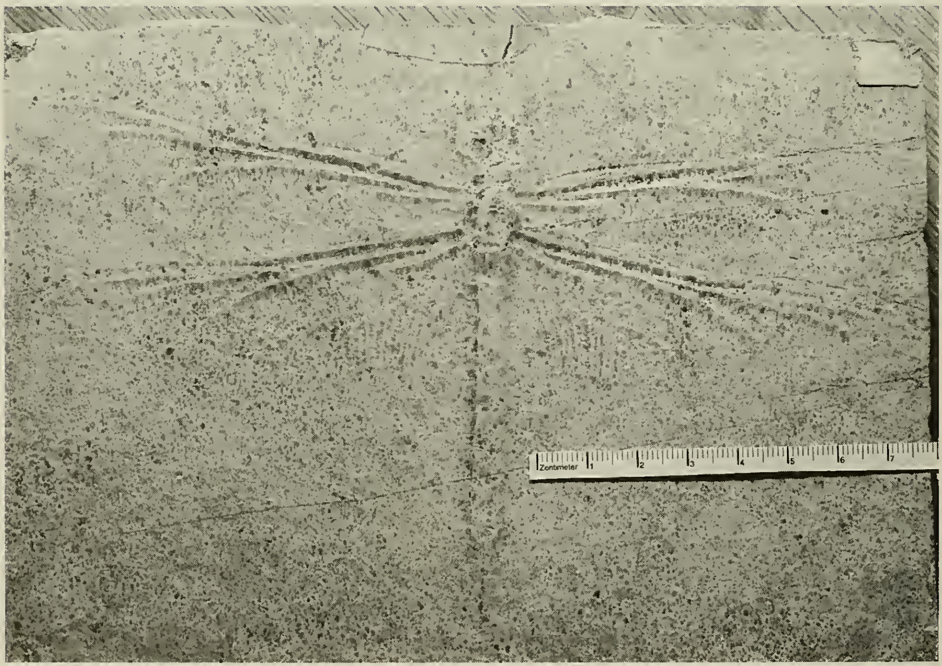

Fig. 2. *Urogomphus giganteus*, ♀ holotype BSPGM AS VII 791. Scale as indicated by rule.

of head, 11.8 mm. Compound eyes rather small and widely separated (min. distance, 4.2 mm). The abdomen is 60 mm long, broad (max. width, 5.9 mm), and has an ovipositor (length, 14 mm). Thus, it is a female specimen.

Forewing: Length, 91.8 mm; width at nodus, 18.7 mm; distance from base to arculus, 9.1 mm; from base to nodus, 42.1 mm. Nodus of Aeschnidiidae type and situated at about 46 % of wing length. Pterostigma not preserved. Nodal veinlet weakly oblique, but subnodal veinlet more oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 10.8 mm) in basal postnodal area. Postnodal and antenodal crossveins, including two primary antenodal crossveins, not preserved. Arculus weakly defined and angled. First branching of RP (midfork) 9.3 mm basal of subnodus, and origin of IR2 6.3 mm basal of subnodus. Base of RP2 aligned with subnodus. Oblique veins 'O' not preserved. Rspl well-defined, long (length about 23.9 mm), and parallel to IR2; Rspl not reaching posterior wing margin, but ending on IR2. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened, but again narrowed near wing margin. RP1 and RP2 divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2; pseudo-IR1 not preserved. Area between RP3/4 and MA distally widened, but again narrowed near wing margin. Mspl well-defined and long (length, 20.7 mm); Mspl not reaching posterior wing margin, but ending on MA. Several convex secondary veins originating on Mspl and reaching posterior wing margin. Hypertriangle very long and narrow (length, 15.4 mm; max. width, 1.0 mm); its costal margin is rather straight. Discoidal triangle transverse; length of its anterior side, 4.8 mm; of its basal side, 6.7 mm; of its distal side MAb, 7.3 mm; basal side sigmoidally curved, but distal side MAb straight. MP, CuA and distal part of AA not preserved. Anal area incompletely preserved.

Hindwing: Length, 90.7 mm (not 85.3 mm as incorrectly stated by NEL & MARTÍNEZ-DELCLÒS 1993); max. width near wing base, 26.8 mm; width at nodus, 24.3 mm; distance from base to arculus, 8.6 mm; distance from base to nodus, 40.5 mm; from nodus to pterostigma, about 25.3 mm (indicated by the pterostigmal brace vein). Nodus of Aeschnidiidae type and situated at about 45 % of wing length. Pterostigma not preserved, but the clearly preserved pterostigmal brace vein proves that it was in a basal position, and distinctly braced by a strong and very oblique brace vein. Nodal veinlet weakly oblique, but subnodal veinlet more oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 8.6 mm) in basal postnodal area. Postnodal and antenodal crossveins hardly preserved. Ax1 aligned with arculus, but Ax2 not preserved. Arculus weakly defined and angled. First branching of RP (midfork) 11.4 mm basal of subnodus, and origin of IR2 8.4 mm basal of subnodus. Base of RP2 aligned with subnodus. Oblique veins 'O' not preserved. Rspl well-defined, long (length, 23.9 mm), and parallel to IR2; Rspl not reaching posterior wing margin, but ending on IR2. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened, but again narrowed near posterior wing margin. RP1 and RP2 divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2. Area between RP3/4 and MA distally gently widened, but again narrowed near wing margin. Mspl well-defined and long (length, 23.9 mm); Mspl not reaching posterior wing margin, but ending on MA. Several convex secondary veins originating on Mspl and reaching posterior wing margin. Postdiscoidal area distally widened (width near discoidal triangle, 7.9 mm; width at posterior wing margin, 16.6 mm). Hypertriangle very long, but broader than in forewing (length, 14.6 mm; max. width, 1.6 mm); its costal margin is rather straight. Discoidal triangle transverse; length of its anterior side, 3.6 mm; of its basal side, 7.5 mm; of its distal side MAb, 8.0 mm; basal side sigmoidally curved, but distal side MAb straight. Anal vein divided into a well-defined anterior secondary branch PsA and an angled main branch AA, delimiting a very large subdiscoidal triangle. PsA ends on MP at basal angle of discoidal triangle. MP and CuA basally parallel, but diverging near posterior wing margin. MP reaches posterior wing margin on level of nodus. Basal posterior branches of CuA suppressed, and original cubito-anal area occupied by a concave secondary vein Aspl1 and its posterior branches, alternating with convex intercalary veins. Subdiscoidal veinlet distinct (length, 0.3 mm). Max. width of cubito-anal area (below discoidal triangle), 11.1 mm. Anal area broad (max. width, probably about 20 mm) and fan-like with numerous posterior branches of AA, alternating with concave intercalaries (Aspls). Anal loop completely absent, but one pseudo-anal loop basal of subdiscoidal triangle.

Specimen JME no. 1951.21. (Figs 3–4): A nearly complete but very poorly preserved female dragonfly (labelled «*Urogomphus giganteus*, Wintershof-Ost»).

Body: Length from head to end of abdomen (without ovipositor), about 84 mm. The abdomen is about 65 mm long and extended by an ovipositor (length, about 12–13 mm). Thus, it is a female specimen.

Forewing: Length, 94.5 mm. The wing venation is too incompletely preserved to be worth a detailed description, but the visible features completely agree with the holotype.

Hindwing: Length 93.5 mm; max. width near wing base, 26.4 mm; width at nodus, about 23.6 mm. Arculus and nodus not preserved. Pterostigma in a basal position, very short (max. length, 2.5 mm; max. width, 1.1 mm), and distinctly braced by a strong and very oblique brace vein that is slightly displaced distally (not aligned with basal side of pterostigma). Postnodal and antenodal crossveins not preserved. Oblique veins 'O' not preserved. Rspl well-defined, long (length, about 23.2 mm), and parallel to IR2; Rspl not reaching posterior wing margin, but ending on IR2. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened, but again narrowed near posterior wing margin. RP1 and RP2 divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2, accompanied by a long basal convex secondary vein (primary IR1 ?). Area between RP3/4 and MA distally widened, but again narrowed near wing margin. Mspl well-defined and very long (length, 32.1 mm); Mspl not reaching posterior wing margin, but ending on MA. Several convex secondary veins originating on Mspl and reaching posterior wing margin. Postdiscoidal area distally widened (width near discoidal triangle, 7.9 mm; width at posterior wing margin, 17.8 mm). Hypertriangle only partly preserved. Discoidal triangle transverse; length of its anterior side, 3.6 mm; of its basal side, 7.1 mm; of its distal side MAb, 7.7 mm; basal side sigmoidally curved, but distal side MAb straight. Anal vein divided into a well-defined and hypertrophied anterior secondary branch PsA and an angled main branch AA, delimiting a very large subdiscoidal triangle. PsA ends on MP at basal angle of discoidal triangle. MP and CuA basally parallel, but gently diverging near posterior wing margin. CuAa with three well-defined distal posterior branches in both hindwings; CuAb reduced to an "oblique crossvein" between CuA and Aspl (only preserved in right hindwing). Basal posterior branches of CuA suppressed, and original cubito-anal area occupied by a concave secondary vein Aspl1 and its posterior branches, alternating with convex

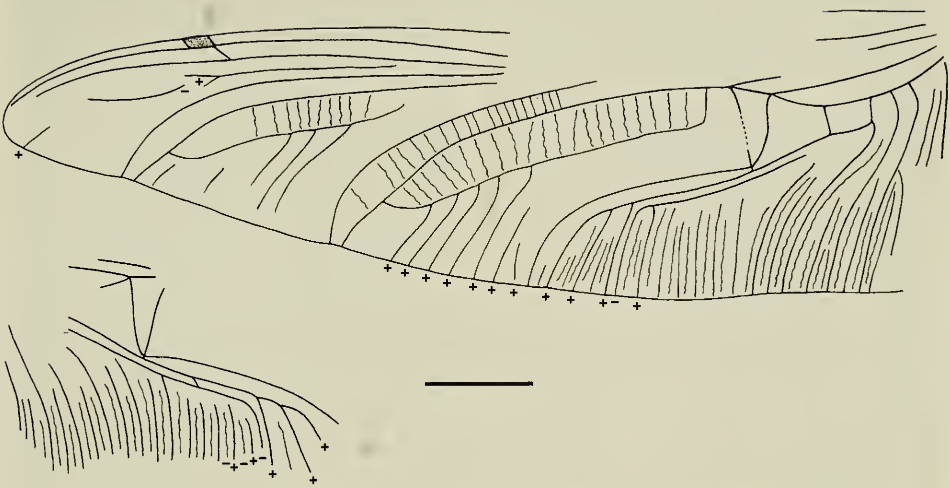

Fig. 3. *Urogomphus giganteus*, ♀ JME 1951.21, left hindwing and right hindwing base. Scale 10 mm.

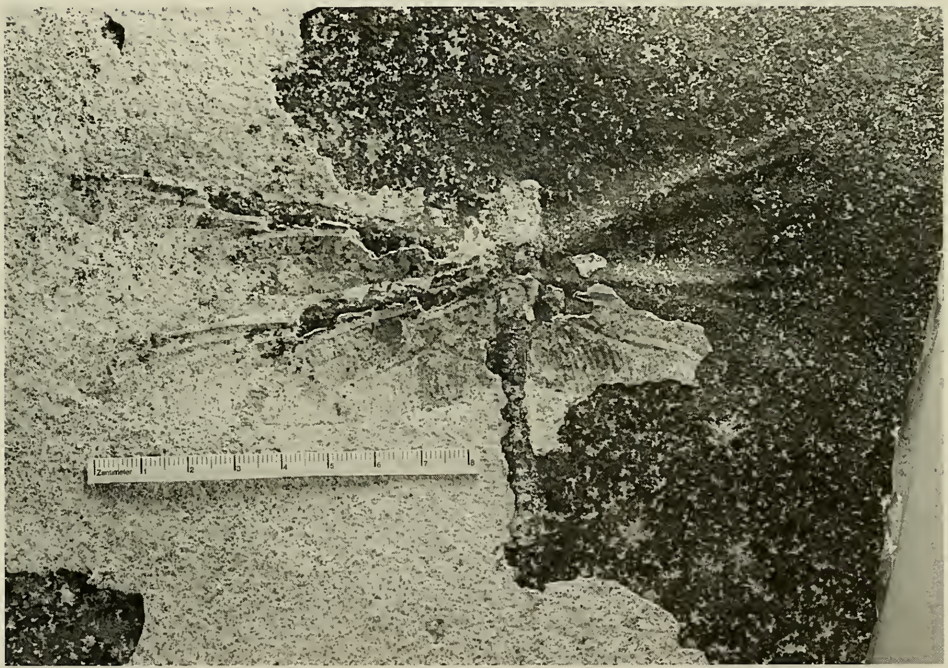

Fig. 4. *Urogomphus giganteus*, ♀ JME 1951.21. Scale as indicated by rule.

intercalary veins. Subdiscoidal veinlet distinct (length, 0.3 mm). Max. width of cubito-anal area (below discoidal triangle), 11.4 mm. Anal area broad and fan-like with numerous posterior branches of AA, alternating with concave intercalaries (Aspls). Anal loop completely absent, but one pseudo-anal loop basal of subdiscoidal triangle.

Specimen no. 17593, GPIT, Tübingen: A complete but poorly preserved female dragonfly (labelled «*Urogomphus eximius* HAGEN, Libelle, Malm zeta, Solnhofen» and «21 *Petalia* spc. Solnhofen»).

Body: Length from head to end of abdomen (without ovipositor), 92 mm. Width of abdomen, 6 mm. Length of ovipositor, 15 mm.

Forewing: Length, 90.0 mm.

Specimen no. MB.J. 1721: Plate and counterplate of two forewings (labelled «*Aeschnogomphus charpentieri* HAGEN, REDENBACHER'sche Sammlung, Solenhofen»), of which only one is complete (length, 83.0 mm).

Specimen SMF no. VI 98c (Figs 5–7): A photo of this very well-preserved specimen (labelled «*Urogomphus giganteus* GERM., Alte Slg., Solnhofen») was published by MALZ & SCHRÖDER (1979: fig. 23). It definitely shows the best-preserved wing venation of all known specimens! The apex of the forewing and the distal halves of the right fore- and hindwing are missing, but the left hindwing is complete and about 85 mm long. The left hindwing shows the following characters: area between RP1 and RP2 with a basal convex secondary vein (IR1 ?), and a distal curved concave secondary vein (apical supplement); pterostigma in a basal position (basal end 67 mm distal of wing base), short (3 mm), and with a very oblique brace vein that is aligned with its basal margin; CuAa with three distal branches (also in the right hindwing); only two rows of cells in the costal part of

Fig. 5. *Urogomphus giganteus*, ♂ SMF VI 98c. Scale as indicated by rule.

Fig. 6. *Urogomphus giganteus*, ♂ SMF VI 98c, left wings. Without scale.

Fig. 7. *Urogomphus giganteus*, ♂ SMF VI 98c, right wings. Without scale.

Fig. 8. *Urogomphus giganteus*, ♂ SMF VI 98b1. Scale as indicated by rule.

the antenodal area (also in the right hindwing). In both forewings there are four rows of cells in the costal part (between ScP and costal margin) of the antenodal area between Ax1 and Ax2, and three rows of cells between Ax2 and nodus. All other visible characters of the wing venation agree with the other specimens of *Urogomphus giganteus* described here. The body is relatively poorly preserved (length of thorax & abdomen, about 77 mm). The abdomen is about 67.2 mm long and distally broadened (max. width, 7 mm). There is no ovipositor visible, thus it is probably a male specimen.

Specimen SMF no. VI 98b1/b2 (Fig. 8): A photo of no. VI 98b1 was published by Frickhinger (1994: fig. 263). It is a plate and counterplate of a complete, but not very well-preserved specimen (labelled «*Urogomphus giganteus* Germar ♂, det. Handlirsch»). The body is 77 mm long, and the abdomen is distally somewhat broadened (basal width, 3 mm; distal width, 5 mm). There is no ovipositor visible, thus it is probably a male specimen. The forewing is about 80–81 mm long, and the hindwing only about 79–80 mm long. The wing venation of the counterplate is better preserved and shows three to four rows of cells between ScP and costal margin in the antenodal area of the forewing, and only two rows in the same area of the hindwing.

Specimen SMF no. VI 98a (Fig. 9): An incomplete dragonfly (labelled «*Urogomphus giganteus* (Germ.), Prof. F. Richters, 1900, det. Handlirsch»). Head, thorax, both hindwings, and a part of the abdomen are preserved. The forewings and legs, and the distal part of the abdomen are missing. Both hindwings are folded to the left side of the fossil. The left hindwing is 81 mm long (the right hindwing appears to be shorter, only 78 mm long, but this is obviously due to its folding on the left side); the wing venation is poorly preserved, but shows the typical features of Aeschnidiidae (transverse triangle, etc.).

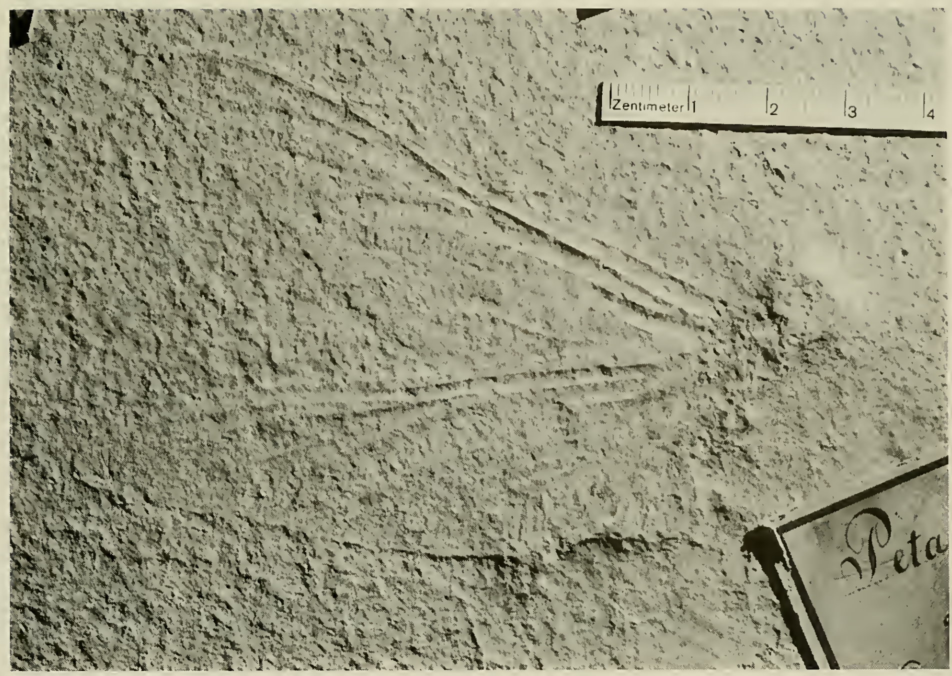

Fig. 9. *Urogomphus giganteus*, SMF VI 98a. Scale as indicated by rule.

Specimen MCZ no. 6192 (Figs 10–12): An incomplete dragonfly (labelled «*Urogomphus giganteus* Solnhofen») with rather well-preserved wing venation. The head, legs, distal halves of the left pair of wings, and the antero-distal part of the right forewing are missing. The abdomen is preserved, but does not show any details. Since it is rather slender, distally somewhat broadened, and does not have an ovipositor, it most likely is a male specimen.

Hindwing: Length, 83.5 mm; max. width near wing base, 26.4 mm; width at nodus, 22.5 mm; distance from base to arculus, 6.5 mm; from base to nodus, 37.6 mm; from nodus to pterostigma, 27.5 mm; from pterostigma to apex, 13.5 mm. Nodus of

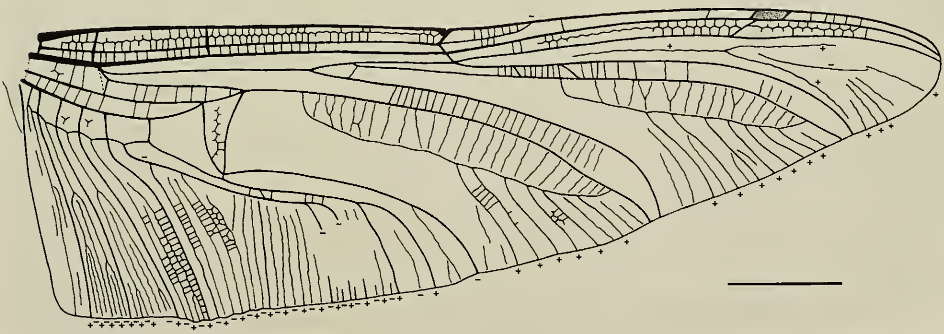

Fig. 10. *Urogomphus giganteus*, ♂ MCZ 6192, right hindwing. Scale 10 mm.

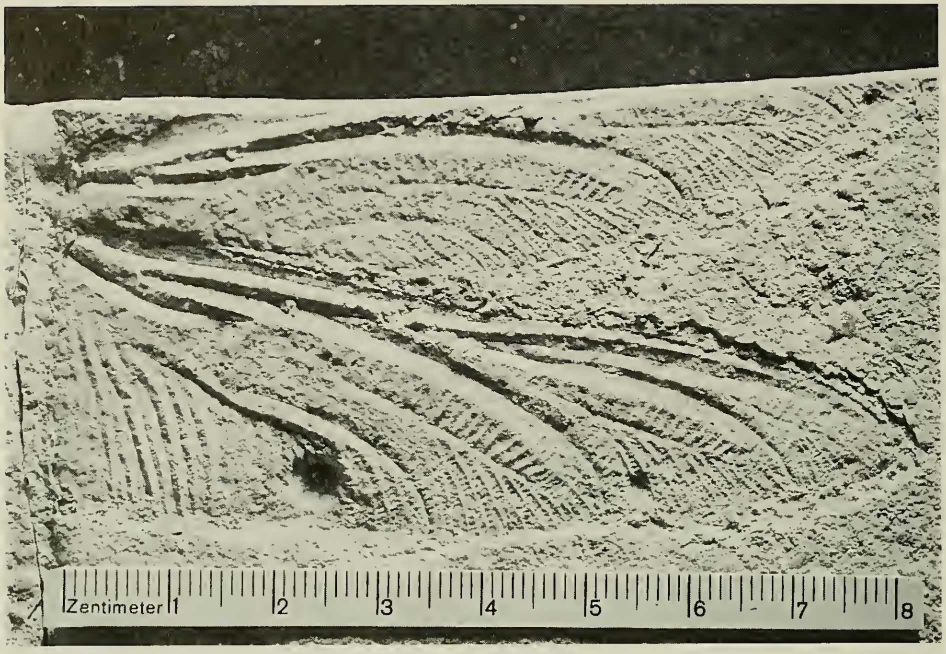

Fig. 11. *Urogomphus giganteus*, ♂ MCZ 6192, right wings. Scale as indicated by rule.

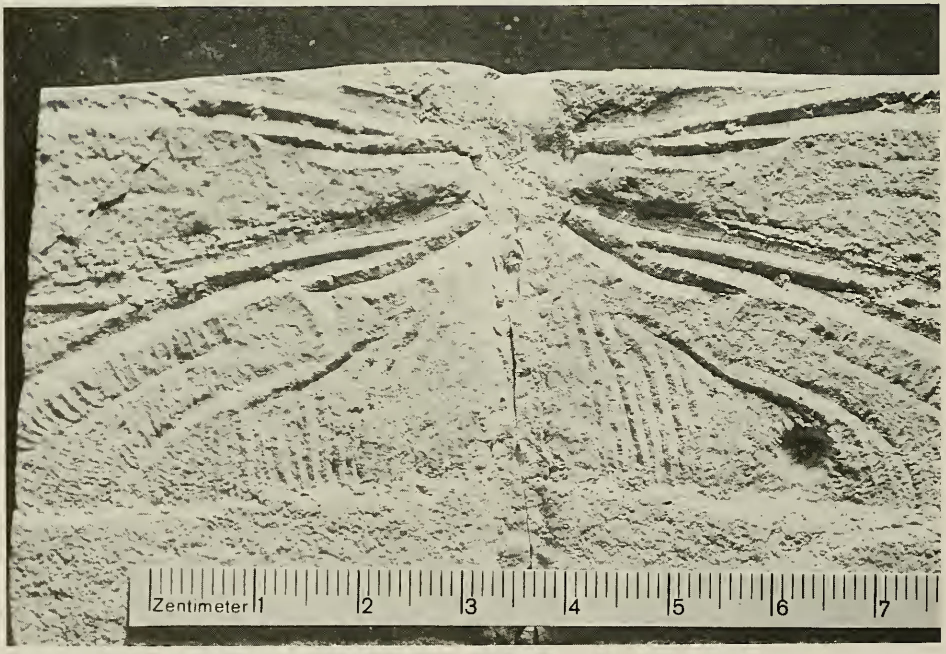

Fig. 12. *Urogomphus giganteus*, ♂ MCZ 6192. Scale as indicated by rule.

Aeschnidiidae type and situated at about 45 % of wing length. Pterostigma in a basal position (max. length, 3.1 mm; max. width, 1.1 mm), and distinctly braced by a strong and very oblique brace vein that is slightly displaced distally (not aligned with basal side of pterostigma). Nodal veinlet and subnodal veinlet oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 8.2 mm) in basal postnodal area. Numerous postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins. Two rows of cells in most part of area between RA and RP1 basal and distal of pterostigmal brace vein. Numerous antenodal crossveins between costal margin and ScP, not aligned with secondary antenodal crossveins between ScP and RA. Two rows of cells in complete antenodal area between costal margin and ScP, but only one row of cells in antenodal area between ScP and RA. Two primary antenodal crossveins aligned and distinctly stronger, with about fourteen or fifteen cells between them. Ax1 only 0.6 mm basal of arculus, and Ax2 10.2 mm distal of Ax1, on level of basal half of discoidal triangle. Basal brace Ax0 preserved, and several accessory antenodal crossveins between Ax0 and Ax1. Arculus weakly defined and angled. RP and MA not fused at arculus, but originating from one place on RA. First branching of RP (midfork) 12.9 mm basal of subnodus, and origin of IR2 9.0 mm basal of subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O', 5.4 mm and 9.7 mm distal of subnodus (the second one being more oblique than the first one). Rspl well-defined, long (length, 22.4 mm), and parallel to IR2; Rspl not reaching posterior wing margin, but ending on IR2. Several (about seven) convex secondary veins originating on Rspl and reaching posterior wing margin, alternating with concave intercalaries. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened, but again narrowed near posterior wing margin. RP1 and RP2 divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2, enclosed by a furcation of a long basal convex intercalary (primary IR1 ?). Area between RP3/4 and MA distally widened, but again narrowed near wing margin. Mspl well-defined and very long (length, 29.1 mm); Mspl not reaching posterior wing margin, but ending on MA. Several (about six) convex secondary veins originating on Mspl and reaching posterior wing margin, alternating with concave intercalaries. Postdiscoidal area distally widened (width near discoidal triangle, 7.2 mm; width at posterior wing margin, 16.1 mm). Hypertriangle very long, but not very narrow (length, 12.4 mm; max. width, 1.5 mm); its costal margin is rather straight. Discoidal triangle transverse and divided into numerous cells arranged in two "vertical" rows; length of its anterior side, 3.5 mm; of its basal side, 6.6 mm; of its distal side MAb, 7.5 mm; basal side sigmoidally curved, but distal side MAb somewhat concave-curved. Anal vein divided into a well-defined and hypertrophied anterior secondary branch PsA and an angled main branch AA, delimiting a very large subdiscoidal triangle. PsA ends on MP at basal angle of discoidal triangle. MP and CuA basally parallel, but distally diverging. MP reaches posterior wing on level of nodus. CuAa with two well-defined distal posterior branches; CuAb reduced to an "oblique crossvein" between CuA and Aspl. Basal posterior branches of CuA suppressed, and original cubito-anal area occupied by a concave secondary vein Aspl1 and its posterior branches, alternating with convex intercalary veins. Subdiscoidal veinlet distinct (length, 0.3 mm). Max. width of cubito-anal area (below discoidal triangle), 11.9 mm. Anal area broad (max. width, 19.3 mm) and fan-like with five posterior branches of AA, alternating with concave intercalaries (Aspls). Anal loop completely absent, but a row of five pseudo-anal loops basal of subdiscoidal triangle. Neither distinct anal angle, nor anal triangle, but anal margin makes rectangular bend near wing base. A small membranule seems to be visible.

Specimen nos 3829–3830 in Carnegie Museum: CARPENTER (1932: fig. 4) provided a drawing of the wing venation of the basal parts of right fore- and hindwing of this very well-preserved specimen. The visible characters agree with the other specimens of *Urogomphus giganteus* described here, except for the presence of four posterior branches of CuAa in the hindwing. Since the venation in the cubito-anal area is very complex, because of the numerous intercalary veins, I suppose that this unusual condition is rather based on a drawing error.

Specimen without number in coll. BECHLY: A relatively well-preserved dragonfly with both hindwings, fragments of the forewings, pterothorax, and abdomen with ovipositor, thus it is a female specimen.

Body: The thorax does not show any details, and the legs are not visible. The abdomen is 70 mm long and 5.5–7 mm wide. The ovipositor is visible, but its distal part is missing.

Hindwing: Length, about 95 mm, thus the biggest known specimen. The distal side MAb of the discoidal triangle is distinctly curved in a concave way.

Specimen without number in coll. KÜMPEL, Wuppertal (Fig. 13): A complete but poorly preserved dragonfly without ovipositor, thus it is probably a male specimen.

Body: The head is incomplete. The thorax does not show any details, and the legs are not visible. The abdomen is 63 mm long, distally somewhat dilated (male), and the anal appendages seem to be very small or incompletely preserved.

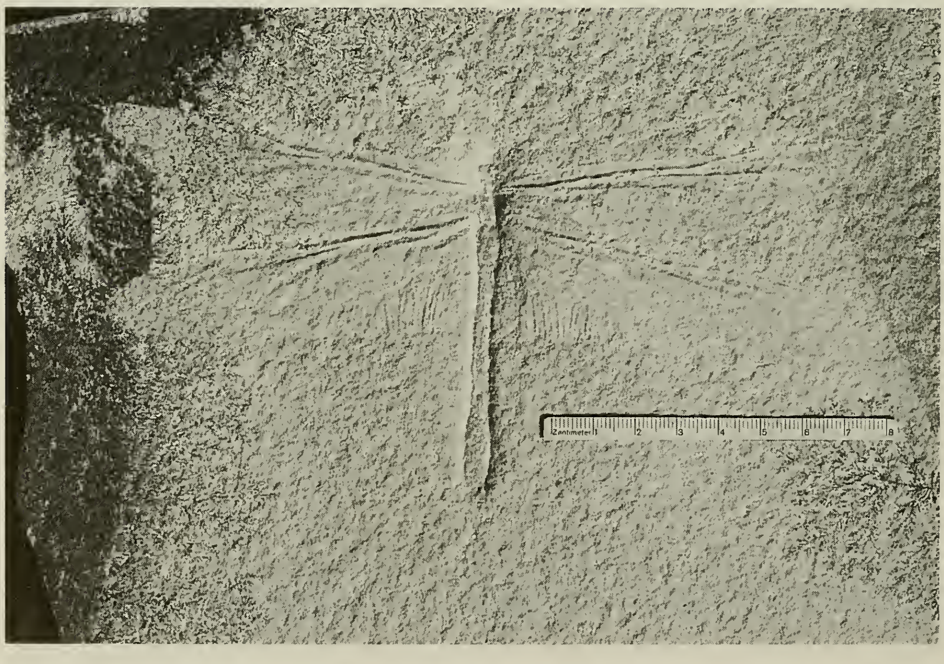

Fig. 13. *Urogomphus giganteus*, ♂ coll. KÜMPEL without no. Scale as indicated by rule.

Fig. 14. *Urogomphus giganteus*, ♂ coll. KARIOPP without no. Scale unknown (photo by K.A. FRICKHINGER).

Forewing: Length, 89.2 mm.

Hindwing: Length, 90.5 mm.

Specimen without number in coll. KARIOPP, Regensburg (Fig. 14): A complete dragonfly with well-preserved body. The compound eyes are distinctly separated; the abdomen is short; and the wing span is about 17 cm. Since there is no ovipositor visible it is probably a male specimen.

Urogomphus eximius (HAGEN, 1862)

Figs 15–25

*1862 *Petalura eximia*. – HAGEN, p. 107.
1869 *Petalura eximia*. – WEYENBERGH, p. 235.
1898 *Estemoa gigantea* [sensu MEUNIER]. – MEUNIER, pp. 120–121, pl. 7, fig. 13.
1906 *Urogomphus eximius* HAGEN. – HANDLIRSCH, p. 595.
1932 *Urogomphus eximius* (HAGEN). – CARPENTER, pp. 107–108.
1982 *Urogomphus eximius* (HAGEN, 1862). – SCHLÜTER & HARTUNG, p. 301.
1993 *Urogomphus eximius* (HAGEN, 1862) (HANDLIRSCH, 1906–1908). – NEL & MARTÍNEZ-DELCLÒS, p. 56 (placed in Aeschnidiidae genus incertae sedis stat. nov.).
1993 *Lithoaeschnidium viohli*. – NEL & MARTÍNEZ-DELCLÒS, pp. 57–60, figs 33–40 (new synonymy, as junior subjective synonym).
1996 *Urogomphus eximius* (HAGEN, 1862). – NEL, BECHLY & MARTÍNEZ-DELCLÒS, p. 178.

Lectotype: HAGEN (1862) described three syntypes at BSPGM (Munich), but did not designate a holotype. I here designate the male specimen no. 16 as lectotype.

Type locality: Solnhofen, southern Frankonian Alb, Bavaria, Germany.

Type horizon: Upper Jurassic, Malm ζ 2b ("oberer Weißjura"), Lower Tithonian, Hybonotum-Zone, Solnhofen Lithographic Limestone.

Paratypes: Because of the present lectotype designation, female specimen no. 17 and female specimen without number (no. 18 ?) at BSPGM (Munich) are paralectotypes.

Further material: Specimens no. 63717 and no. 63718 at SMNS (Stuttgart), and a specimen without number in coll. BECHLY (ex coll. LUDWIG) that will be acquired by SMNS, too.

New diagnosis. – Nearly all known characters, except of size, are more or less identical with *U. giganteus*. I here regard all specimens with a wing length of less than 80 mm as *U. eximius*, although the maximum wing length of 78 mm is rather close to the minimum wing length of *U. giganteus* (81–85 mm). However, the minimum wing length of 68 mm certainly excludes a conspecific status with large *U. giganteus* specimens (wing length, 93–95 mm). Therefore, two distinct species of *Urogomphus* in the Solnhofen Limestone are certainly justified, even though they can only be distinguished by a small gap of 3 mm between their size ranges.

A further distinction from the other two species seems to be the number of rows of cells between ScP and costal margin in the antenodal area of the forewings: in *U. eximius* there are only two rows of cells in this area of the forewing, just like in the hindwings of all three species, while there are three or four rows of cells in the referring area of the forewing in the other two species.

Redescription

Lectotype BSPGM no. 16 (Figs 15–16): A complete and rather well-preserved male dragonfly (labelled «No. 16 *Petalura eximia* ♂, *Aeschna eximia* M.M. XI., H., Solenhofen»), of which only the legs are not visible. All the main wing veins are visible, but the cross-venation is hardly preserved. Wing span 161.9 mm.

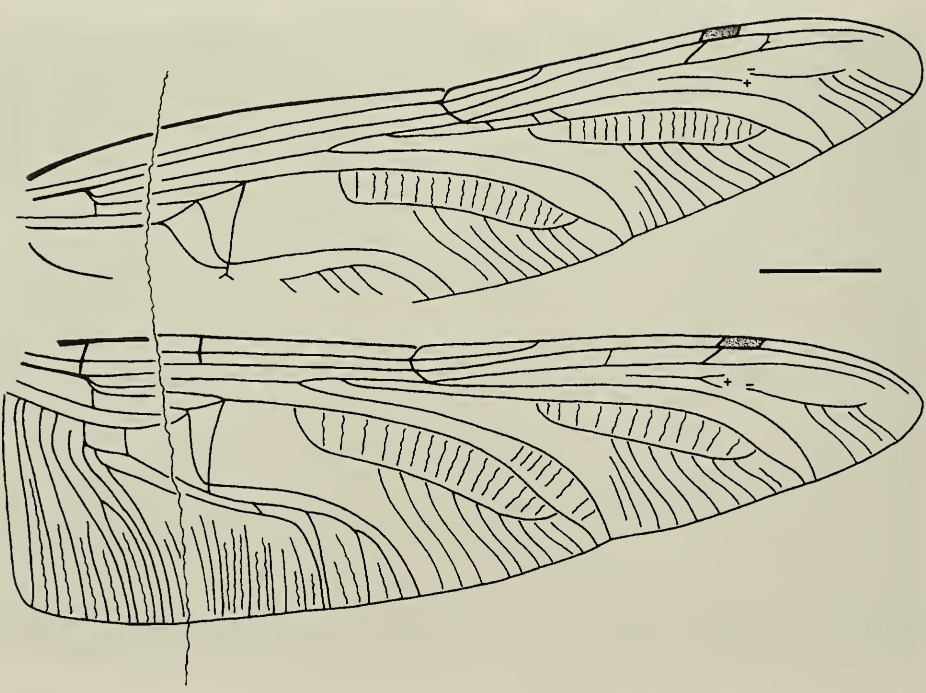

Fig. 15. *Urogomphus eximius*, ♂ lectotype BSPGM 16, right wings. Scale 10 mm.

Fig. 16. *Urogomphus eximius*, ♂ lectotype BSPGM 16. Scale as indicated by rule.

Body: Length from head to end of abdomen, 78.6 mm. Width of head, 11.3 mm. Compound eyes rather small and widely separated (min. distance, 2.4 mm). The abdomen is about 55 mm long, relatively slender (width, about 3 mm), but distally somewhat broadened (max. width, 4.9 mm), and lacks an ovipositor. Thus, it is most likely a male specimen (females have a broad abdomen, without distal dilation, but with a long ovipositor).

Forewing: Length, 76.3 mm; width at nodus, 17.2 mm; distance from base to arculus, 5.2 mm; from base to nodus, 36.1 mm; from nodus to pterostigma, 21.8 mm; from pterostigma to apex, 15.4 mm. Nodus of Aeschnidiidae type and situated at about 47 % of wing length. Pterostigma in a basal position, relatively short (max. length, 3.4 mm; max. width, 1.0 mm), and distinctly braced by a strong and very oblique brace vein that is slightly displaced distally (not aligned with basal side of pterostigma). Nodal veinlet weakly oblique, but subnodal veinlet more oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 8.8 mm) in basal postnodal area. Postnodal and antenodal crossveins, including two primary antenodal crossveins, not preserved. Arculus weakly defined and angled. RP and MA not fused at arculus, but originating from one place on RA. First branching of RP (midfork) 11.6 mm basal of subnodus, and origin of IR2 6.5 mm basal of subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O', 1.9 mm and 7.4 mm distal of subnodus. Rspl well-defined, long (length about 20 mm), and parallel to IR2; Rspl not reaching posterior wing margin, but ending on IR2. Six convex secondary veins originating on Rspl and reaching posterior wing margin. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened, but again narrowed near wing margin. RP1 and RP2 divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2, accompanied by a basal longitudinal convex intercalary (primary IR1 ?); several convex secondary veins originating on apical supplement and reaching posterior wing margin; pseudo-IR1 not preserved. Area between RP3/4 and MA distally widened, but again narrowed near wing margin. Mspl well-defined and long (length, 20.4 mm); Mspl not reaching posterior wing margin, but ending on MA. Several convex secondary veins originating on Mspl and reaching posterior wing margin, alternating with concave intercalaries. Postdiscoidal area distally widened (width near discoidal triangle, 6.7 mm; width at posterior wing margin, 14.7 mm). Hypertriangle very long and narrow (length, 12.7 mm; max. width, 1.2 mm); its costal margin is rather straight. Discoidal triangle transverse; length of its anterior side, 4.0 mm; of its basal side, 5.9 mm; of its distal side MAb, 6.8 mm; basal side sigmoidally curved, but distal side MAb straight. Anal vein divided into a well-defined anterior secondary branch PsA and an angled main branch AA, delimiting a large subdiscoidal triangle. PsA ends on MP at basal angle of discoidal triangle. MP and CuA parallel up to posterior wing margin. MP reaches posterior wing margin somewhat basal of level of nodus. CuA with at least five well-defined posterior branches. Subdiscoidal veinlet distinct (length, 0.2 mm). Max. width of cubito-anal area, about 3.2 mm. Anal area broad (max. width, about 5 mm).

Hindwing: Length, 77.6 mm; max. width near wing base, 24.1 mm; width at nodus, 20.9 mm; distance from base to arculus, 6.2 mm; distance from base to nodus, 33.8 mm; from nodus to pterostigma, 25.2 mm; from pterostigma to apex, 13.8 mm. Nodus of Aeschnidiidae type and situated at about 44 % of wing length. Pterostigma in a basal position, hardly longer than in forewing (max. length, 3.7 mm; max. width, 1.1 mm), and distinctly braced by a strong and very oblique brace vein that is slightly displaced distally (not aligned with basal side of pterostigma). Nodal veinlet weakly oblique, but subnodal veinlet more oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 10.8 mm) in basal postnodal area. Two primary antenodal crossveins aligned and stronger. Ax1 aligned with arculus, and Ax2 9.8 mm distal of Ax1. Arculus weakly defined and angled. RP and MA not fused at arculus, but originating from one place on RA. First branching of RP (midfork) 10.8 mm basal of subnodus, and origin of IR2 7.1 mm basal of subnodus. Base of RP2 aligned with subnodus. Oblique veins 'O' not preserved. Rspl well-defined, long (length, 18.9 mm), and parallel to IR2; Rspl not reaching posterior wing margin, but ending on IR2. Several convex secondary veins originating on Rspl and reaching posterior wing margin, alternating with concave intercalaries. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened, but again narrowed near posterior wing margin. RP1 and RP2 divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2, enclosed by a furcation of a long basal convex intercalary (primary IR1 ?). Area between RP3/4 and MA distally widened, but again narrowed near wing margin. Mspl well-defined and very long (length, 23.8 mm); Mspl not reaching posterior wing margin, but ending on MA. Several convex secondary veins originating on Mspl and reaching posterior wing margin, alternating with concave intercalaries. Postdiscoidal area distally widened (width near discoidal triangle, 7.2 mm; width at posterior wing margin, 15.5 mm). Hypertriangle very long, but broader than in forewing and hindwing of other specimens (length, 10.9 mm; max. width, 1.5 mm); its costal margin is rather straight. Discoidal triangle transverse; length of its anterior side, 3.0 mm; of its basal side, 6.5 mm; of its distal side MAb, 7.0 mm; basal side sigmoidally curved, but distal side MAb straight. Anal vein divided into a well-defined and hypertrophied anterior secondary branch PsA and an angled main branch AA, delimiting a very large subdiscoidal triangle (maybe "fused" with adjacent pseudo-anal loop). PsA ends on MP at basal angle of discoidal triangle. MP and CuA more or less parallel. MP reaches posterior wing margin slightly basal of level of nodus. CuAa with three well-defined distal posterior branches; CuAb reduced to an "oblique crossvein" between CuA and Aspl. Basal posterior branches of CuA suppressed, and original cubito-anal area occupied by a concave secondary vein Aspl1 and its posterior branches, alternating with convex intercalary veins. Subdiscoidal veinlet distinct (length, 0.5 mm). Max. width of cubito-anal area (below discoidal triangle), 10.5 mm. Anal area broad (max. width, 17.2 mm) and fan-like with numerous posterior branches of AA, alternating with concave intercalaries (Aspls). Anal loop completely absent, but one pseudo-anal loop basal of subdiscoidal triangle. Neither distinct anal angle, nor anal triangle, but anal margin makes rectangular bend near wing base. No membranule visible.

Discussion: NEL & MARTÍNEZ-DELCLÒS (1993) regarded the type series (three specimens at BSPGM) of HAGEN (1862) as lost, although they mentioned that they found specimen no. 17 at BSPGM, which probably belongs to this type series. They designated this specimen no. 17 as holotype of a new genus and species (*Lithoaeschnidium viohli*), because it does not precisely agree in size with HAGEN's original description. On the other hand, SCHWEIGERT et al. (1996) mentioned that only two of the three syntypes of HAGEN (1862) are still present in the collection of BSPGM.

I could find three specimens of *Urogomphus eximius* at BSPGM that are all marked with a "H", which indicates that they belong to coll. HAEBERLEIN (MAYR pers. comm.). This collection was already present in this museum in the time of HAGEN. The conclusion that these three specimens represent the type series of HAGEN is also supported by the information of MEUNIER (1898) that five specimens of *Urogomphus* are present in the Museum of Munich (including the holotype of *U. giganteus*, and a specimen of *Aeschnogomphus* that was misidentified as *U. giganteus*). The three *U. eximius* specimens represent two females with ovipositor (specimen no. 17, and a specimen without number), and one putative male specimen without ovipositor (specimen no. 16). HAGEN (1862) mentioned that his type series includes two female and one male specimen in this museum. In his original description he stated a body length of 80 mm and a wing span of 160 mm. This description exactly agrees with the size of specimen no. 16, but neither with specimen no. 17, nor with the female specimen without number. The latter specimen might indeed be the third syntype of HAGEN (no. 18), since I found a separate label «Nr. 18 *Petalura eximia* ♀ *Aeschna eximia* MÜNST. H. Solenhofen» [sic]. I regard the three mentioned specimens as representing the complete type series of HAGEN, and here designate specimen no. 16 as lectotype, because of its agreement in size with the original description. The other two specimens therefore have to be regarded as paralectotypes.

Paralectotype (and holotype of *Lithoaeschnidium viohli*) BSPGM no. 17 (Figs 17–18): A complete and well-preserved female dragonfly (wing span of forewings, 151 mm).

Body: Length from head to end of abdomen, 77 mm. Head and thorax do not show any details, but the segmentation of the abdomen is still visible. Length of abdomen (without ovipositor), 55 mm. The valves (length, about 16.5 mm) of the ovi-

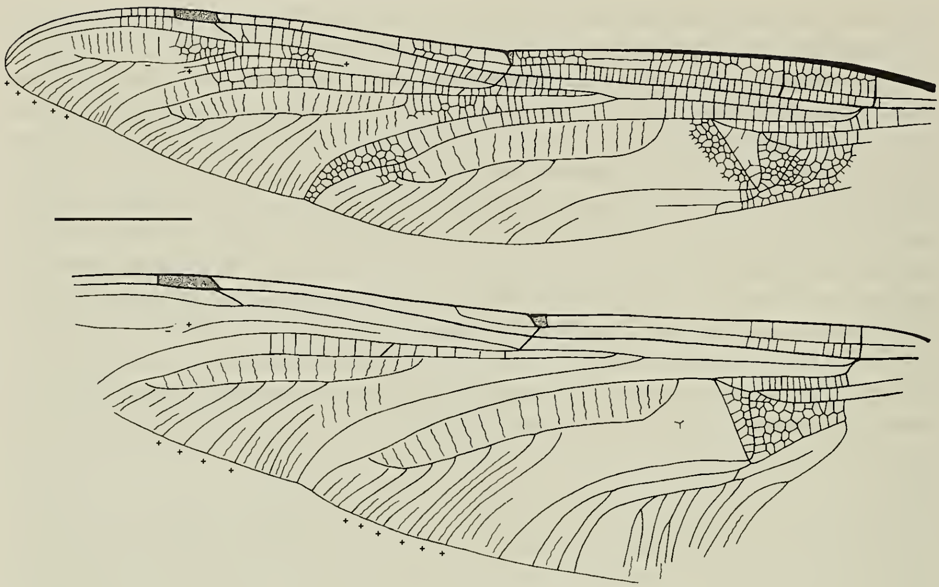

Fig. 17. *Urogomphus eximius*, ♀ paralectotype BSPGM 17 (holotype of *Lithoaeschnidium viohli*), left wings (original drawing combined with detail drawings of NEL & MARTÍNEZ-DELCLOS 1993). Scale 10 mm.

Fig. 18. *Urogomphus eximius*, ♀ paralectotype BSPGM 17 (holotype of *Lithoaeschnidium viohli*). Scale as indicated by rule.

positor are far spread, one being direct backwards, and one slanted obliquely forwards (see Nel & Martínez-Delclòs 1993: fig. 40; with incorrect scale!).

Forewing: Length, 69.4 mm (length incorrectly stated as 73–74 mm in Nel & Martínez-Delclòs 1993); width at nodus, 14.4 mm; distance from base to arculus, 5.5 mm; from base to nodus, 32.1 mm; from nodus to pterostigma, 21.6 mm; from pterostigma to apex, 12.5 mm. Nodus of Aeschnidiidae type and situated at about 46 % of wing length. Pterostigma in a basal position, relatively short (max. length, 3.3 mm; max. width, 0.8 mm), and distinctly braced by a strong and very oblique brace vein that is slightly displaced distally (not aligned with basal side of pterostigma). Small part of distal antenodal area near nodus sclerotized ("accessory pterostigma" ?). Nodal veinlet weakly oblique, but subnodal veinlet more oblique. ScP apparently prolonged through nodus by a long zigzagged pseudo-ScP (length, 7.4 mm) in basal postnodal area. Numerous postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins. Apparently only one row of cells in distal half of area between RA and RP1 basal and distal of pterostigmal brace vein. Numerous antenodal crossveins between costal margin and ScP, not aligned with secondary antenodal crossveins between ScP and RA (more than 45). Two rows of cells in complete antenodal area between costal margin and ScP, but only one row of cells in antenodal area between ScP and RA. Two primary antenodal crossveins aligned and distinctly stronger, with eleven cells between them. Ax1 only 0.8 mm basal of arculus, and Ax2 6.8 mm distal of Ax1, even basal of level of basal side of discoidal triangle. Antesubnodal area with numerous crossveins, but without any gap of crossveins near nodus. Arculus weakly defined and angled. RP and MA not fused at arculus, but originating from one place on RA. Ten bridge-crossveins (Bqs) visible basal of subnodus. Numerous antefurcal crossveins between RP and MA basal of midfork. First branching of RP (midfork) 8.3 mm basal of subnodus, and origin of IR2 6.8 mm basal of subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O', five cells (2.2 mm) and eleven cells (6.6 mm) distal of subnodus. Rspl well-defined, long (length about 17.8 mm), and parallel to IR2; Rspl not reaching posterior wing margin, but ending on IR2. Six convex secondary veins originating on Rspl and reaching posterior wing margin, alternating with concave intercalaries. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened with two or more rows of cells, but again narrowed near wing margin. RP1 and RP2 divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2, accompanied by a basal longitudinal convex intercalary (primary IR1 ?); several convex secondary veins originating on apical supplement and reaching posterior wing margin; pseudo-IR1 not clearly preserved. Area between RP3/4 and MA distally widened with three rows of cells, but again narrowed near wing margin. Mspl well-defined and very long (length, 20.3 mm); Mspl not reaching posterior wing margin, but ending on MA. About five convex secondary veins originating on Mspl and reaching posterior wing margin, alternating with concave intercalaries. Postdiscoidal area distally widened (width near discoidal triangle, 5.2 mm; width at posterior wing margin, 14.7 mm) with numerous rows of cells (about ten rows near discoidal triangle). Hypertriangle very long and narrow (length, 11.1 mm; max. width, 0.8 mm), and divided by numerous crossveins (at least thirteen are visible); its costal margin is rather straight. Discoidal triangle transverse and divided into numerous cells; length of its anterior side, 3.6 mm; of its basal side, 4.1 mm; of its distal side MAb, 6.1 mm; basal side sigmoidally curved, but distal side

MAb straight. Median space divided by several parallel crossveins (at least three); submedian space traversed by numerous parallel crossveins, so that CuP-crossing cannot be distinguished. Anal vein divided into a well-defined anterior secondary branch PsA and an angled main branch AA, delimiting a large subdiscoidal triangle that is divided into twenty-three cells. PsA ends on MP at basal angle of discoidal triangle. MP and CuA basally parallel, but distally diverging. MP reaches posterior wing margin on level of nodus. Posterior branches of CuA not preserved. Subdiscoidal veinlet distinct (length, 0.3 mm). Max. width of cubito-anal area, 1.8 mm. Anal area broad (max. width, 3.5 mm) with about five rows of cells between AA and posterior wing margin; anal area with at least three well-defined, closed, and multicellular pseudo-anal loops basal of subdiscoidal triangle.

Hindwing: Length, about 68 mm; max. width near wing base, about 19.9 mm; width at nodus, 18.3 mm; distance from base to arculus, 5.3 mm; distance from base to nodus, 29.9 mm; from nodus to pterostigma, 23.3 mm; from pterostigma to apex, 10.6 mm. Nodus of Aeschnidiidae type and situated at about 44 % of wing length. Pterostigma in a basal position, longer than in forewing (max. length, 4.6 mm; max. width, 1.1 mm), and distinctly braced by a strong and very oblique brace vein that is slightly displaced distally (not aligned with basal side of pterostigma); basal side of pterostigma more oblique than distal side. Antenodal area near nodus sclerotized ("accessory pterostigma" ?). Nodal veinlet and subnodal veinlet oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 5.9 mm) in basal postnodal area. Numerous antenodal crossveins between costal margin and ScP, not aligned with secondary antenodal crossveins between ScP and RA. Apparently only one row of cells in complete antenodal area between costal margin and ScP and between ScP and RA (very uncertain and dubious character state, because of rather poor preservation of cross-venation). Ax1 aligned with arculus, and Ax2 not preserved. Arculus weakly defined and angled. RP and MA not fused at arculus, but originating from one place on RA. First branching of RP (midfork) 9.2 mm basal of subnodus, and origin of IR2 7.1 mm basal of subnodus. Base of RP2 aligned with subnodus. Only one distal oblique vein 'O' visible, 9.4 mm distal of subnodus (basal oblique vein not preserved). Rspl well-defined, long (length about 20.6 mm), and parallel to IR2; Rspl not reaching posterior wing margin, but ending on IR2. Five or six convex secondary veins originating on Rspl and reaching posterior wing margin, alternating with concave intercalaries. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened. RP1 and RP2 divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2, accompanied by a basal longitudinal convex intercalary (primary IR1 ?); pseudo-IR1 not preserved. Area between RP3/4 and MA distally widened, but again narrowed near wing margin. Mspl well-defined and very long (length, 23.6 mm); Mspl not reaching posterior wing margin, but ending on MA. About six convex secondary veins originating on Mspl and reaching posterior wing margin, alternating with concave intercalaries. Postdiscoidal area distally widened (width near discoidal triangle, 6.0 mm; width at posterior wing margin, 14.7 mm). Hypertriangle very long and narrow (length, 9.9 mm; max. width, 1.1 mm), and divided by sixteen crossveins; its costal margin is rather straight. Discoidal triangle transverse and divided into sixteen cells, arranged in two "vertical" rows; length of its anterior side, 2.7 mm; of its basal side, 5.0 mm; of its distal side MAb, 6.4 mm; basal side sigmoidally curved, but distal side MAb straight. Submedian space traversed by numerous parallel crossveins, so that CuP-crossing cannot be distinguished. Anal vein divided into a well-defined and hypertrophied anterior secondary branch PsA and an angled main branch AA, delimiting a very large subdiscoidal triangle that is divided into numerous cells (the elongate shape mentioned by NEL & MARTÍNEZ-DELCLÒS 1993, is based on an apparent fusion of subdiscoidal triangle and a pseudo-anal loop, due to the zigzagged and weak posterior side of subdiscoidal triangle). PsA ends on MP slightly basal of discoidal triangle. MP and CuA basally parallel, but distally diverging. MP reaches posterior wing margin slightly distal (!) of level of nodus. CuAa with only two well-defined distal posterior branches; CuAb reduced to an "oblique crossvein" between CuA and Aspl. Basal posterior branches of CuA suppressed, and original cubito-anal area occupied by a concave secondary vein Aspl1 and its posterior branches, alternating with convex intercalary veins. Subdiscoidal veinlet distinct (length, 0.2 mm). Anal area broad and fan-like with numerous posterior branches of AA, alternating with concave intercalaries (Aspls) (anal area of right hindwing only partly preserved, but well-preserved in left hindwing and figured by NEL & MARTÍNEZ-DELCLÒS 1993: fig. 34). Anal loop completely absent, but at least two pseudo-anal loop basal of subdiscoidal triangle (the posterior margin of subdiscoidal triangle is zigzagged, so that one pseudo-anal loop next to subdiscoidal triangle seems to be fused with it).

Paralectotype? specimen BSPGM without number (no. 18 ?) (Figs 19–20): A complete but poorly preserved female *Urogomphus* specimen without number, that is indicated to belong to coll. HAEBERLEIN, too. This specimen probably represents the third paralectotype (no. 18) of HAGEN (1862). The apices of the wings are hardly preserved, and only the main veins are visible.

Body: The body is poorly preserved, but the segmentation of the abdomen is still visible and shows short segments. The head does not show any details. The abdomen is about 58 mm long (without ovipositor), very broad (width, 7–8 mm), distally not dilated. A long ovipositor is faintly visible, thus it is a female specimen (also indicated by the broad abdomen).

Forewing: Length, probably about 77.7 mm (estimated from distance of base to nodus which is about 47 % of wing length in other specimens); distance from base to arculus, 5.9 mm; from base to nodus, 36.5 mm; from nodus to pterostigma, 21.1 mm. Only the basal side of the pterostigma with the pterostigmal brace is preserved. Nodus of Aeschnidiidae type. Pterostigma in a basal position, and distinctly braced by a strong and oblique brace vein that is slightly displaced distally (not aligned with basal side of pterostigma). Nodal veinlet weakly oblique, but subnodal veinlet more oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 7.5 mm) in basal postnodal area. Two primary antenodal crossveins aligned and distinctly stronger. Ax1 only 0.6 mm basal of arculus, and Ax2 8.8 mm distal of Ax1, on level of basal side of discoidal triangle. Arculus weakly defined. RP and MA not fused at arculus, but originating from one place on RA. First branching of RP (midfork) 9.8 mm basal of subnodus, and origin of IR2 8.1 mm basal of subnodus. Base of RP2 aligned with subnodus. Rspl well-defined, long (length about 18.8 mm), and parallel to IR2; Rspl not reaching posterior wing margin, but ending on IR2. RP2 and IR2 smoothly curved. RP1 and RP2 strongly divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2, accompanied by convex intercalaries. Primary IR1 indistinct. Area between RP3/4 and MA distally widened. Mspl well-defined and very long (more than 22.5 mm). Postdiscoidal area

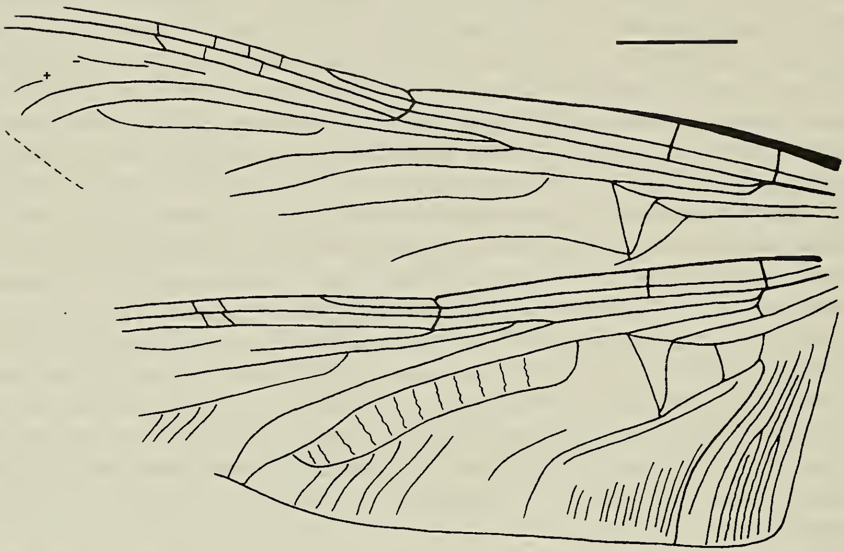

Fig. 19. *Urogomphus eximius*, ♀ paralectotype BSPGM 18 ?, left wings. Scale 10 mm.

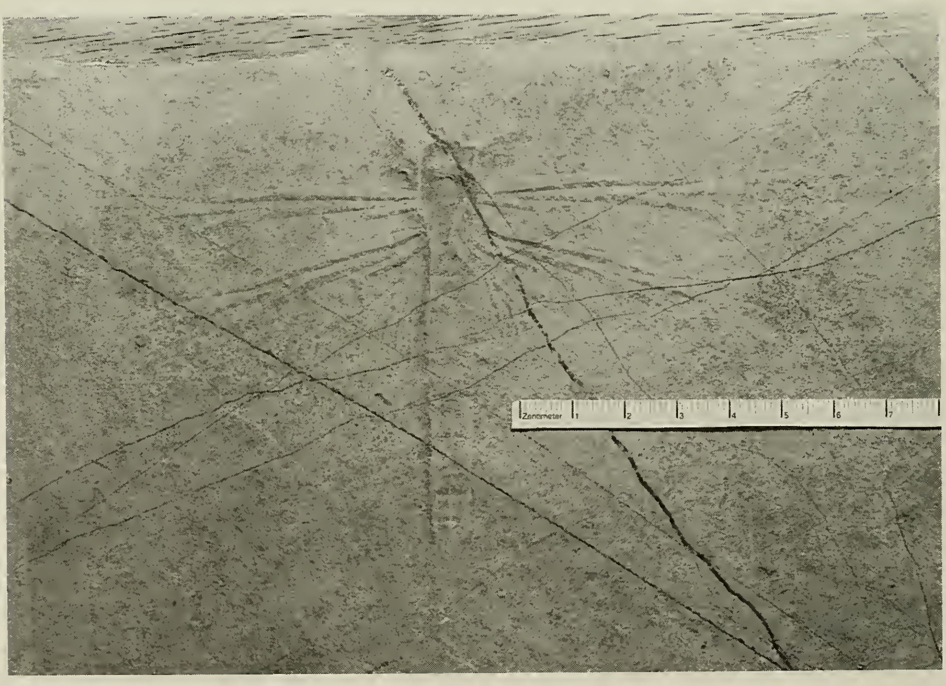

Fig. 20. *Urogomphus eximius*, ♀ paralectotype BSPGM 18 ?. Scale as indicated by rule.

distally widened (width near discoidal triangle, 5.1 mm). Hypertriangle very long and narrow; its costal margin is rather straight. Discoidal triangle transverse; length of its anterior side, 3.9 mm; of its basal side, 5.1 mm; of its distal side MAb, 5.9 mm; basal side sigmoidally curved, but distal side MAb straight. Anal vein divided into a well-defined anterior secondary branch PsA and an angled main branch AA, delimiting a large subdiscoidal triangle. PsA ends on MP slightly below basal angle of discoidal triangle. MP reaches up to level of nodus. Subdiscoidal veinlet distinct (length, 0.3 mm).

Hindwing: Length, probably about 74.4 mm (estimated from distance of base to nodus which is about 44 % of wing length in other specimens); max. width near wing base, 23.6 mm; width at nodus, 19.4 mm; distance from base to arculus, 5.9 mm; distance from base to nodus, 32.7 mm. Nodus of Aeschnidiidae type. Pterostigma not preserved. Nodal veinlet weakly oblique, but subnodal veinlet more oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 9.7 mm) in basal postnodal area. Two primary antenodal crossveins are aligned and distinctly stronger. Ax1 aligned with arculus, and Ax2 9.6 mm distal of Ax1, on level of middle of discoidal triangle. Arculus weakly defined and angled. First branching of RP (midfork) 10 mm basal of subnodus, and origin of IR2 6.7 mm basal of subnodus. Base of RP2 aligned with subnodus. Rspl well-defined, long, and parallel to IR2. Several convex secondary veins originating on Rspl and reaching posterior wing margin. Area between RP2 and IR2 distally gently widened. RP1 and RP2 divergent. Area between RP3/4 and MA distally distinctly widened, but again narrowed near wing margin. Mspl well-defined and long (length, 25.3 mm); Mspl not reaching posterior wing margin, but ending on MA. Several convex secondary veins originating on Mspl and reaching posterior wing margin. Postdiscoidal area distally widened (width near discoidal triangle, 7.6 mm). Hypertriangle very long and narrow (length, 11.1 mm; max. width, 1.3 mm); its costal margin is rather straight. Discoidal triangle transverse; length of its anterior side, 3.6 mm; of its basal side, 5.9 mm; of its distal side MAb, 6.9 mm; basal side sigmoidally curved, but distal side MAb straight. Anal vein divided into a well-defined anterior secondary branch PsA and an angled main branch AA, delimiting a very large subdiscoidal triangle. PsA ends on MP at basal angle of discoidal triangle. MP and CuA distally diverging. Basal posterior branches of CuA suppressed, and original cubito-anal area occupied by a concave secondary vein Aspl1 and its posterior branches, alternating with convex intercalary veins. Subdiscoidal veinlet distinct (length, 0.3 mm). Max. width of cubito-anal area (below discoidal triangle), 10.3 mm. Anal area broad (max. width, 17.0 mm) and fan-like with several posterior branches of AA, alternating with concave intercalary veins. Anal loop completely absent, but one well-defined pseudo-anal loop basal of subdiscoidal triangle. Neither distinct anal angle, nor anal triangle, but anal margin makes rectangular bend near wing base. No membranule visible.

Specimen SMNS no. 63717 (Figs 21–22): The specimen is labelled «hinterer Libellenflügel, *Urogomphus*?, Malm zeta, Untertithonium, Hybonotum Zone, Eichstätt/Bayern, Solnhofener Plattenkalke, Slg. W. Ludwig 1992». An isolated hindwing, of which the basal part is missing. The wing venation is poorly preserved, only the main veins being visible.

Hindwing: Probable total length, about 70.5 mm; max. width, 20.5 mm; width at nodus, 18.9 mm. Nodus of Aeschnidiidae type. Nodal veinlet and subnodal veinlet only weakly oblique. ScP apparently prolonged through nodus by a long pseudo-

Fig. 21. *Urogomphus eximius*, SMNS 63717, left hindwing. Scale 10 mm.

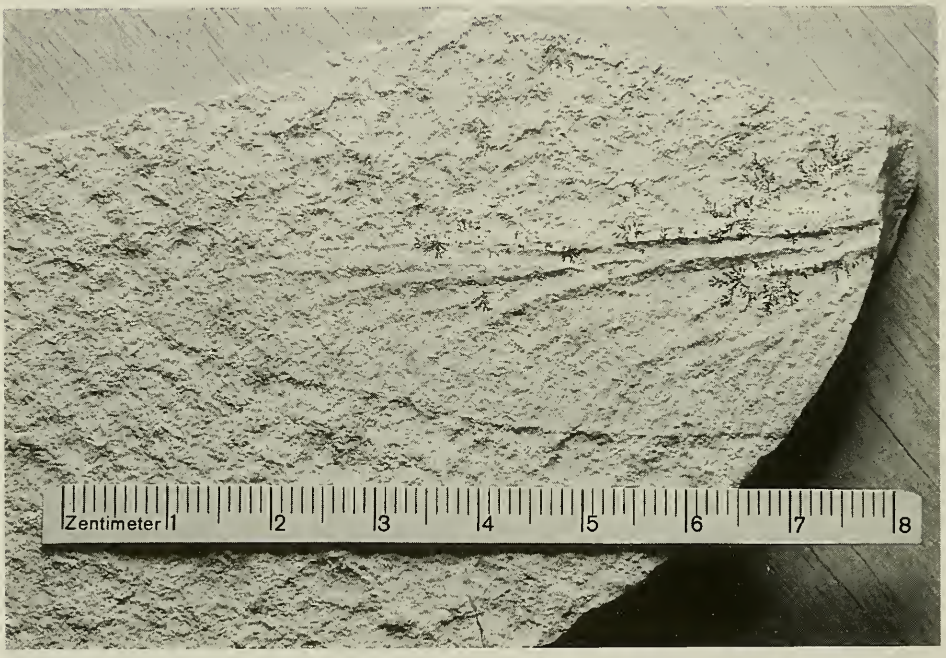

Fig. 22. *Urogomphus eximius*, SMNS 63717, left hindwing. Scale as indicated by rule.

ScP (length, 7.0 mm) in basal postnodal area. Arculus weakly defined and angled. First branching of RP (midfork) 11.3 mm basal of subnodus, and origin of IR2 8.2 mm basal of subnodus. Base of RP2 aligned with subnodus. Rspl well-defined. RP1 and RP2 divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2. Hypertriangle long and narrow (length, 9.7 mm; max. width, 1.1 mm); its costal margin is rather straight. Discoidal triangle transverse; length of its anterior side, 2.8 mm; of its basal side, 4.9 mm; of its distal side MAb, 6.0 mm; basal side sigmoidally curved, but distal side MAb straight. Anal vein divided into a well-defined anterior secondary branch PsA and an angled main branch AA, delimiting a very large subdiscoidal triangle. PsA ends on MP at basal angle of discoidal triangle. Basal posterior branches of CuA are suppressed, and original cubito-anal area occupied by a concave secondary vein Aspl1. Subdiscoidal veinlet distinct (length, 0.3 mm). Max. width of cubito-anal area (below discoidal triangle), 9.6 mm. Anal area broad. Anal loop completely absent, but at least one or two well-defined pseudo-anal loops basal of subdiscoidal triangle.

Specimen SMNS no. 63718 (Figs 23–25): The specimen is labelled «Libelle, *Urogomphus giganteus*, Malm zeta, Untertithonium, Hybonotum Zone, Langenaltheim, Solnhofener Plattenkalke, Slg. W. Ludwig 1992». Body and both hindwings of a dragonfly. The forewings are missing, and the apex of the right hindwing is destroyed. The main wing veins are well-preserved, but the cross-venation is hardly visible.

Body: Head and thorax are poorly preserved, and there are no legs visible, but the segmentation of the abdomen is still visible. Body length from head to end of abdomen, about 64 mm; width of abdomen, 5–6 mm; no ovipositor visible.

Hindwing: Length, 68.6 mm; max. width near wing base, 18.8 mm; width at nodus, 16.5 mm; distance from base to arculus, 5.6 mm; distance from base to nodus, 29.6 mm; from nodus to pterostigma, 22.6 mm; from pterostigma to apex, 13.3 mm. Nodus of Aeschnidiidae type and situated at about 43 % of wing length. Pterostigma in a rather basal position, short (max. length, 2.8 mm; max. width, 0.9 mm), and distinctly braced by a strong and oblique brace vein that is aligned with its basal side (not displaced distally!); basal side of pterostigma more oblique than distal side. Nodal veinlet weakly oblique, but subnodal veinlet strongly oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 7.7 mm) in basal postnodal area. Two rows of cells in distal half of area between RA and RP1 basal and distal (!) of pterostigmal brace vein. Two primary antenodal crossveins are aligned and dis-

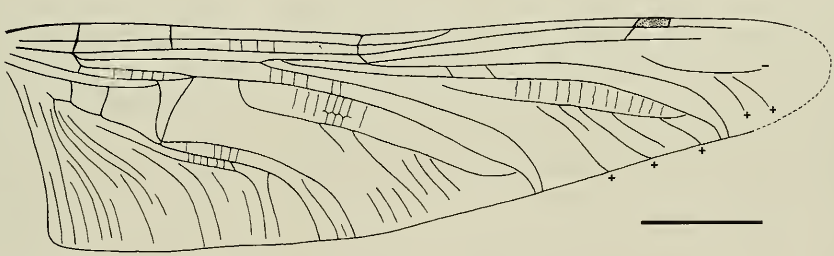

Fig. 23. *Urogomphus eximius*, SMNS 63718, left hindwing (ventral aspect). Scale 10 mm.

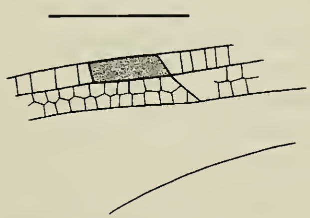

Fig. 24. *Urogomphus eximius*, SMNS 63718, right hindwing pterostigma (ventral aspect). Scale 5 mm.

Fig. 25. *Urogomphus eximius*, SMNS 63718, right hindwing (ventral aspect). Scale as indicated by rule.

tinctly stronger. Ax1 aligned with arculus, and Ax2 7.8 mm distal of Ax1, on level of middle of discoidal triangle. Arculus weakly defined and angled. RP and MA not fused at arculus, but originating from one place on RA. First branching of RP (midfork) 8.9 mm basal of subnodus, and origin of IR2 7.1 mm basal of subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O' visible, 6.6 mm and 9.8 mm distal of subnodus. Rspl well-defined, very long (length about 20.8 mm), and parallel to IR2; Rspl not reaching posterior wing margin, but ending on IR2. Several (at least five) convex secondary veins originating on Rspl and reaching posterior wing margin. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened, but again narrowed near wing margin. RP1 and RP2 strongly divergent. Curved concave secondary vein (apical supplement) between RP1 and RP2. Primary IR1 indistinct; pseudo-IR1 not preserved. Area between RP3/4 and MA distally widened, but again strongly narrowed near wing margin. Mspl well-defined and very long (length, 24.2 mm); Mspl not reaching posterior wing margin, but ending on MA. Several convex secondary veins originating on Mspl and reaching posterior wing margin. Postdiscoidal area distally widened (width near discoidal triangle, 5.4 mm; width at posterior wing margin, 15.3 mm). Hypertriangle very long and narrow (length, 9.4 mm; max. width, 0.8 mm), and divided by numerous crossveins (at least five are visible); its costal margin is rather straight. Discoidal triangle transverse; length of its anterior side, 3.0 mm; of its basal side, 5.0 mm; of its distal side MAb, 5.8 mm; basal side sigmoidally curved, but distal side MAb straight. Anal vein divided into a well-defined anterior secondary branch PsA and an angled main branch AA, delimiting a very large subdiscoidal triangle. PsA ends on MP slightly below basal angle of discoidal triangle. MP and CuA basally parallel with only one row of cells between them, but distally diverging. MP reaches posterior wing margin slightly basal of level of nodus. CuAa with two well-defined distal posterior branches; CuAb reduced to an "oblique crossvein" between CuA and Aspl. Basal posterior branches of CuA suppressed, and original cubito-anal area occupied by a concave secondary vein Aspl1 and its posterior branches, alternating with convex intercalary veins. Subdiscoidal veinlet distinct (length, 0.2 mm). Max. width of cubito-anal area (below discoidal triangle), 8.8 mm. Anal area broad (max. width, 13.6 mm) and fan-like with several posterior branches of AA, alternating with concave intercalary veins. Anal loop completely absent, but at least one or two well-defined pseudo-anal loops basal of subdiscoidal triangle. Neither distinct anal angle, nor anal triangle, but anal margin makes rectangular bend near wing base. No membranule visible.

Specimen without number in coll. BECHLY: Fragmentary hindwing of a dragonfly labelled «Hinterer Libellenflügel, Malm zeta, Eichstätt/Bayern». The wing base is missing and the wing venation is poorly preserved, but it is clearly a specimen of *Urogomphus eximius* (length of fragment, 60 mm).

Urogomphus nusplingensis n. sp.

Figs 26–31

1995 *Urogomphus* sp. – DIETL, KAPITZKE & RIETER, p. 120, pl. 6.
1995 *Urogomphus*. – DIETL, KAPITZKE & RIETER, unnumbered text-fig. on p. 171 (above).
1995 "Libelle". – DIETL, unnumbered text-fig. on p. 218 (above).
1996 *Urogomphus giganteus* [sensu SCHWEIGERT et al.]. – SCHWEIGERT, DIETL, KAPITZKE, RIETER & HUGGER, p. 6–9, figs 5–6, 7c.
1996 *Urogomphus giganteus*. – TISCHLINGER, p. 294, fig. 12 (erroneously indicated as SMNS Nr. 62744)

Holotype: Specimen no. SMNS 62602 in collection of the Staatl. Mus. f. Naturk., Stuttgart, Germany. This specimen was discovered during an excavation by SMNS in September 1994, and represents the first fossil insect discovered in the Jurassic of Swabia. It was found and prepared by M. KAPITZKE.

Type locality: Nusplingen quarry (property of Ges. Naturk. Württ.), Westerberg/Großer Heuberg, "Gewann Taubenloch", SW Swabian Alb, Baden-Württemberg, Germany.

Type horizon: Upper Jurassic, Malm ζ ("oberer Weißjura"), Upper Kimmeridgian, Beckeri-Zone, Ulmense-Subzone, Nusplingen Lithographic Limestone (layer "D" – 15 cm from above).

Derivation of name: After the type locality Nusplingen.

Diagnosis. – This new species differs from *U. giganteus* by its smaller size, and can be distinguished from *U. giganteus* and *U. eximius* by the following wing venational characters: Forewing with three rows of cells in the basal half of antenodal area between costal margin and ScP (also between Ax1 and Ax2); Ax2 on level of basal side of discoidal triangle in hindwing (generally on level of middle of discoidal triangle in the other two species); "accessory pterostigma" developed in front of nodus (autapomorphy); Rspl shorter than in all other species of Aeschnidiidae (autapomorphy); concave and convex secondary veins between RP1 and RP2 less distinct.

Description

Holotype SMNS no. 62602 (Figs 26–31): A very well-preserved and nearly complete dragonfly with all four wings in outstretched position. Only the end of the abdomen is missing, and most legs are not visible (except the fore legs). The speci-

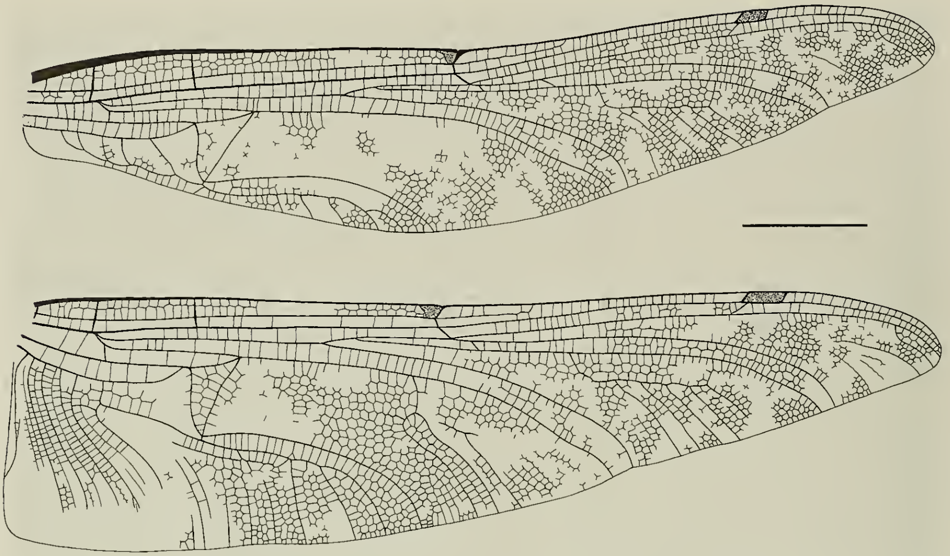

Fig. 26. *Urogomphus nusplingensis* n. sp., ♀ holotype SMNS 62602, right wings. Scale 10 mm.

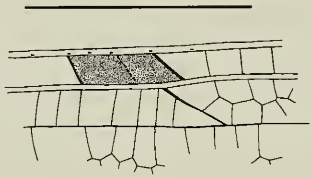

Fig. 27. *Urogomphus nusplingensis* n. sp., ♀ holotype SMNS 62602, left forewing pterostigma. Scale 5 mm.

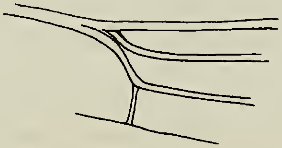

Fig. 28. *Urogomphus nusplingensis* n. sp., ♀ holotype SMNS 62602, right forewing arculus. Without scale.

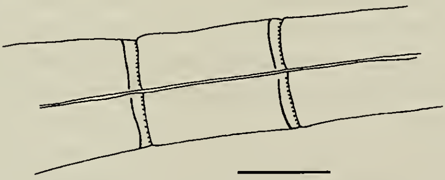

Fig. 29. *Urogomphus nusplingensis* n. sp., ♀ holotype SMNS 62602, abdominal segments. Scale 5 mm.

Fig. 30. *Urogomphus nusplingensis* n. sp., ♀ holotype SMNS 62602, right wings. Scale 10 mm.

Fig. 31. *Urogomphus nusplingensis* n. sp., ♀ holotype SMNS 62602. Scale 10 mm.

men is organically preserved in ventral aspect, and even the tiny spines on the longitudinal wing veins are visible, as well as the colour pattern of the wings. The anal area and the basal costal area are dark coloured. Since this colour pattern is absolutely symmetrical in both pairs of wings, it clearly is not an artifact of the fossilisation process. The antenodal area near the nodus is sclerotized and dark, looking like a second pterostigma. The wings are flattened without any trace of the original corrugation. The wing venation is dense with numerous cells, but not as dense as in most other aeschnidiid genera (contra fig. 6 in Schweigert et al. 1996, which does not feature the wing venation correctly), e.g. *Aeschnidium*. Wing span of forewings, 156.7 mm. Even though the specimen is clearly preserved in ventral aspect, the wing articulation is visible (impressed through the thorax). Since no genital organs are visible, and the male and female hindwings have the same shape in Aeschnidiidae (no male anal angle and anal triangle, thus probably also no auricles), it cannot be clearly recognized if it is a male or a female specimen. However, the secondary male genital apparatus should be visible on the referring abdominal segments, especially since they are well-preserved in ventral aspect, and the very broad abdomen also suggests that it is most likely a female specimen.

Body: The head is poorly preserved, but a median cleft of the labium seems to be visible; max. width of head, 10.0 mm; the compound eyes are relatively small and widely separated (but this separation is to be expected in a ventral aspect anyway). The pterothorax is about 9 mm long, but does not show any details. Length of abdominal segment I, 2.3 mm; of segment II, 5.4 mm; of segment III, 12.6 mm (!); of segment IV, 6.1 mm; of segment V, 5.5 mm; of segment VI, 7.5 mm; of segment VII, 6.8 mm; of segment VIII, 5.0 mm; segment IX is only incompletely preserved and segment X with the anal appendages is missing. The hind margins of the abdominal segments and the antecostal sutures bear a row of denticles. The median longitudinal "line" that is visible on the abdomen is not a dorsal carina, but the ventral cleft. Auricles or secondary genital organs are not visible. The fore legs are folded close to the head and only the tarsi are freely visible in front of the head (therefore misidentified as "short antennae" by Schweigert et al. 1996). The middle and hind legs are not visible.

Forewing: Length, 73.9 mm; width at nodus, 14.5 mm; distance from base to arculus, 5.8 mm; from base to nodus, 34.8 mm; from nodus to pterostigma, 22.7 mm; from pterostigma to apex, 13.6 mm. Nodus of Aeschnidiidae type and situated at about 47 % of wing length. Pterostigma in a very basal position, short (max. length, 2.4 mm; max. width, 0.9 mm), covering four cells, and distinctly braced by a strong and very oblique brace vein that is slightly displaced distally (not aligned with basal side of pterostigma); basal side of pterostigma more strongly oblique than distal side; pterostigma maybe traversed by one or two weak crossveins. Antenodal area near nodus sclerotized and dark ("accessory pterostigma"). Nodal veinlet weakly oblique, but subnodal veinlet strongly oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 9.2 mm) in basal postnodal area. Thirty-one postnodal crossveins visible between nodus and pterostigma (total number probably about 33), not aligned with corresponding postsubnodal crossveins. Two rows of cells in distal half of area between RA and RP1 basal of pterostigmal brace vein. Numerous (about 50) antenodal crossveins between costal margin and ScP, not aligned with secondary antenodal crossveins between ScP and RA. Three rows of cells in basal half of antenodal area between costal margin and ScP, but two rows of cells in distal half of this area. Only one row of cells in antenodal area between ScP and RA (except in basal area between Ax0 and Ax1). Two primary antenodal crossveins aligned and distinctly stronger, with about ten or eleven cells between them. Ax1 only 0.6 mm basal of arculus, and Ax2 8.2 mm distal of Ax1, on level of basal side of discoidal triangle. Basal brace Ax0 preserved, and several accessory antenodal crossveins between Ax0 and Ax1 (two rows of cells between costal margin and ScP, and between ScP and RA). Antesubnodal area with numerous crossveins, but without any gap of crossveins near arculus or nodus. Arculus weakly defined and angled. RP and MA not fused at arculus, but originating from one place on RA. Nine bridge-crossveins (Bqs) visible (total number probably ten). Numerous antefurcal crossveins between RP and MA basal of midfork. First branching of RP (midfork) 10.2 mm basal of subnodus, and origin of IR2 7.6 mm basal of subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O', one cell (0.8 mm) and eight cells (5.7 mm) distal of subnodus; second oblique vein more strongly oblique than basal one. Rspl well-defined, but short (length about 9.7 mm), and parallel to IR2, with up to four rows of cells between it and IR2; Rspl not reaching posterior wing margin, but ending on IR2. Five convex secondary veins originating on Rspl and reaching posterior wing margin. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened with two to four rows of cells, but again narrowed near wing margin. RP1 and RP2 strongly divergent. Primary IR1 indistinct; pseudo-IR1 very short, originating on RP1 near wing apex, far distal of pterostigma. Area between RP3/4 and MA distally widened with two to three rows of cells, but again narrowed near wing margin. Mspl not preserved. Postdiscoidal area distally widened (width near discoidal triangle, 5.2 mm; width at posterior wing margin, 14.6 mm) with numerous rows of cells. Hypertriangle very long and narrow (length, 11.7 mm; max. width, 1.1 mm), and divided by numerous crossveins (at least eleven are visible); its costal margin is rather straight. Discoidal triangle transverse and divided into numerous cells; length of its anterior side, 4.8 mm; of its basal side, 4.8 mm; of its distal side MAb, 6.9 mm; basal side sigmoidally curved, but distal side MAb straight. Median space divided by several parallel crossveins (at least five); submedian space traversed by numerous parallel crossveins (at least fourteen), so that CuP-crossing cannot be distinguished. Anal vein divided into a well-defined anterior secondary branch PsA and an angled main branch AA, delimiting a large subdiscoidal triangle that is divided into numerous cells. PsA ends on MP at basal angle of discoidal triangle. MP and CuA distally diverging, separated by two rows of cells (three or four cells near wing margin). MP reaches posterior wing margin slightly basal of level of nodus. CuA with about five well-defined distal posterior branches. Subdiscoidal veinlet distinct (length, 0.3 mm). Max. width of cubito-anal area, 2.1 mm, with probably up to five or six rows of cells. Anal area broad (max. width, 3.2 mm) with about four or five rows of cells between AA and posterior wing margin; anal area with four well-defined, closed, and multicellular pseudo-anal loops basal of subdiscoidal triangle. No membranule visible.

Hindwing: Length, 75.1 mm; max. width near wing base, 20.5 mm; width at nodus, 17.6 mm; distance from base to arculus, 5.8 mm; distance from base to nodus, 33.9 mm; from nodus to pterostigma, 24.2 mm; from pterostigma to apex, 12.7 mm. Nodus of Aeschnidiidae type and situated at about 45 % of wing length. Pterostigma in a very basal position, short but longer than in forewing (max. length, 3.2 mm; max. width, 0.9 mm), probably covering four cells, and distinctly braced by a strong and very oblique brace vein that is slightly displaced distally (not aligned with basal side of pterostigma); basal side of pterostigma more oblique than distal side. Antenodal area near nodus sclerotized and dark ("accessory pterostigma"). Nodal veinlet weakly oblique, but subnodal veinlet strongly oblique. ScP apparently prolonged through nodus by a long pseudo-ScP (length, 7.8 mm) in basal postnodal area. Numerous postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins. Two rows of cells in distal half of area between RA and RP1 basal of pterostigmal brace vein. Numerous (about 40) antenodal crossveins between costal margin and ScP, not aligned with secondary antenodal crossveins between ScP and RA. Two rows of cells in complete antenodal area between costal margin and ScP, but only one row of cells in antenodal area between ScP and RA. Two primary antenodal crossveins are aligned and distinctly stronger, with about eleven or twelve cells between them. Ax1 aligned with arculus, and Ax2 8.0 mm distal of Ax1, on level of basal side of discoidal triangle. Basal brace Ax0 preserved, and several accessory antenodal crossveins between Ax0 and Ax1. Antesubnodal area with numerous crossveins, but without any gap of crossveins near arculus or nodus. Arculus weakly defined and angled. RP and MA not fused at arculus, but originating from one place on RA. Two bridge-crossveins (Bqs) visible (total number certainly much higher). Numerous antefurcal crossveins between RP and MA basal of midfork. First branching of RP (midfork) 10.3 mm basal of subnodus, and origin of IR2 7.6 mm basal of subnodus. Base of RP2 aligned with subnodus. Only one oblique vein 'O' visible, two cells (1.7 mm) distal of subnodus; second oblique vein more strongly oblique than basal one. Rspl well-defined, short (length about 11.5 mm), and parallel to IR2, with three rows of cells between it and IR2; Rspl not reaching posterior wing margin, but ending on IR2. Five convex secondary veins originating on Rspl and reaching posterior wing margin. RP2 and IR2 smoothly curved; area between RP2 and IR2 distally gently widened with two to three rows of cells, but again narrowed near wing margin. RP1 and RP2 strongly divergent. Primary IR1 indistinct; pseudo-IR1 very short, originating on RP1 near wing apex, far distal of pterostigma. Area between RP3/4 and MA distally widened with two to four rows of cells, but again narrowed near wing margin. Mspl short but well-defined with up to four or five rows of cells between it and MA. At least three convex secondary veins originating on Mspl and reaching posterior wing margin. Postdiscoidal area distally widened (width near discoidal triangle, 6.0 mm; width at posterior wing margin, 16.0 mm) with numerous rows of cells. Hypertriangle very long and narrow (length, 10.8 mm; max. width, 1.2 mm), and divided by numerous crossveins (at least four are visible); its costal margin is rather straight. Discoidal triangle transverse and divided into sixteen cells, arranged in two "vertical" rows; length of its anterior side, 4.0 mm; of its basal side, 5.3 mm; of its distal side MAb, 7.0 mm; basal side curved, but distal side MAb straight. Median space divided by several parallel crossveins (at least two are visible); submedian space traversed by numerous parallel crossveins (at least seven are visible), so that CuP-crossing cannot be distinguished. Anal vein divided into a well-defined anterior secondary branch PsA and an angled main branch AA, delimiting a very large subdiscoidal triangle that is divided into numerous cells (the apparently very elongate shape is caused by an apparent fusion of subdiscoidal triangle with a pseudo-anal loop, due to the zigzagged and weak posterior side of subdiscoidal triangle). PsA ends on MP slightly basal of discoidal triangle. MP and CuA basally parallel with only one row of cells between them, but distally diverging, being separated by seven small cells along wing margin. MP reaches posterior wing margin slightly basal of level of nodus. CuAa with three well-defined distal posterior branches; CuAb reduced to an "oblique crossvein" between CuA and Aspl. Basal posterior branches of CuA suppressed, and original cubito-anal area occupied by a concave secondary vein Aspl1 and its posterior branches, alternating with convex intercalary veins. Subdiscoidal veinlet distinct (length, 0.3 mm). Max. width of cubito-anal area (below discoidal triangle), 8.6 mm, with up to twelve rows of cells. Anal area broad (max. width, 14.5 mm) with numerous rows of cells between AA and posterior wing margin; anal area fan-like with several (about six) posterior branches of AA, alternating with concave intercalary veins. Anal loop completely absent, but at least one well-defined pseudo-anal loop basal of subdiscoidal triangle (plus the pseudo-anal loop that is probably fused with subdiscoidal triangle). Neither distinct anal angle, nor anal triangle, but anal margin makes rectangular bend near wing base. No membranule visible.

Discussion: Since this species has all autapomorphies of Aeschnidiidae, and all autapomorphies and diagnostic symplesiomorphies of *Urogomphus*, its attribution to this genus can be regarded as certain. The similar derived pattern of subdiscoidal triangle and pseudo-anal loops in the hindwing, and further derived similarities ("accessory pterostigma" at nodus ?), as well as the similar size, might suggest a sistergroup relationship of *U. nusplingensis* n. sp. and *U. eximius*. But this hypothesis is only supported by relatively weak evidence. On the other hand, the presence of more than two rows of cells between ScP and costal margin in the antenodal area of the forewings represents a rather unique and highly derived similarity (strong putative synapomorphy) with *U. giganteus*.

Genus *Bergeriaeschnidia* NEL, BECHLY & MARTÍNEZ-DELCLÒS, 1996

Type species: *Bergeriaeschnidia inexpectata* NEL, BECHLY & MARTÍNEZ-DELCLÒS, 1996, by original designation.

Bergeriaeschnidia abscissa (HAGEN, 1862) comb. nov.

Figs 32–33

*1862 (*Libellula*) *abscissa*. – HAGEN, p. 107.
1906 ? *Urogomphus abscissus* HAGEN. – HANDLIRSCH, p. 595.
1932 *Urogomphus abscissus* (HAGEN). – CARPENTER, pp. 107–108.
1982 *Urogomphus abscissus* (HAGEN, 1862). – SCHLÜTER & HARTUNG, p. 301.
1993 *Urogomphus abscissus* (HAGEN, 1862) (HANDLIRSCH, 1906–1908). – NEL & MARTÍNEZ-DELCLÒS, p. 56 (placed in Aeschnidiidae? incertae sedis stat. nov.).
1996 *Urogomphus abscissus* (HAGEN, 1862). – NEL, BECHLY & MARTÍNEZ-DELCLÒS, p. 178.
1996 *Bergeriaeschnidia inexpectata* (HAGEN, 1862). – NEL, BECHLY & MARTÍNEZ-DELCLÒS, p. 178 (new synonymy, as junior objective synonym).

Neotype: The holotype must be regarded as lost, since I could neither find it at BSPGM (Munich) where the specimen should be, nor among HAGEN's specimens at SMF (Frankfurt), nor in coll. HAGEN at MCZ (Cambridge/Mass.). For the reasons discussed below, I here designate specimen no. 6 in coll. Museum BERGÉR (Eichstätt) as neotype (Fig. 32). This specimen also is the holotype of *Bergeriaeschnidia inexpectata*. A cast is at MNHN (Paris).

Type locality: Solnhofen, southern Frankonian Alb, Bavaria, Germany.

Type horizon: Upper Jurassic, Malm ζ 2b ("oberer Weißjura"), Lower Tithonian, Hybonotum-Zone, Solnhofen Lithographic Limestone.

Further material: Specimen in coll. LEICH of the Fossilium (Bochum), figured in

FRICKHINGER (1994: fig. 245). A third specimen with a wing span of 110 mm is located in the private coll. BÜRGER (Bad Hersfeld); it is a female with ovipositor and well-preserved head (Fig. 33).

Diagnosis and description. – See NEL, BECHLY & MARTÍNEZ-DELCLÒS (1996).

Discussion: According to the brief original description of HAGEN (1862), *U. abscissus* has a wing span of about 110 mm. HANDLIRSCH (1906) added that it is certainly an Aeschnidiidae and that the wing length is about 60 mm, but that the attribution to the genus *Urogomphus* is questionable. Since the wings of Aeschnidiidae have numerous unique diagnostic features, it can be regarded as highly probable that Handlirsch's attribution, which was obviously based on a re-examination of the type specimen, is correct. Except *U. abscissus* there are five species of Aeschnidiidae known from the Solnhofen Limestone. *Aeschnidium densum* has a forewing length of about 40–45 mm; *Malmaeschnidium mayeri* has a forewing length of 68 mm; *Urogomphus eximius* (= *Lithoaeschnidium viohli*) has a forewing length of 68–78 mm; and *Urogomphus giganteus* has a forewing length of about 93 mm. Since the wing span of *Malmaeschnidium mayeri* is about 140 mm (instead of 110 mm), the statement by NEL & MARTÍNEZ-DELCLÒS (1993: 62), that these two taxa shall be of similar size and might be conspecific, has to be regarded as dubious. The only known aeschnidiid genus from this locality that indeed has a compatible wing length is *Bergeriaeschnidia inexpectata*. With a forewing length of 56 mm the holotype exactly corresponds to the stated wing span in the original description of *U. abscissus*.

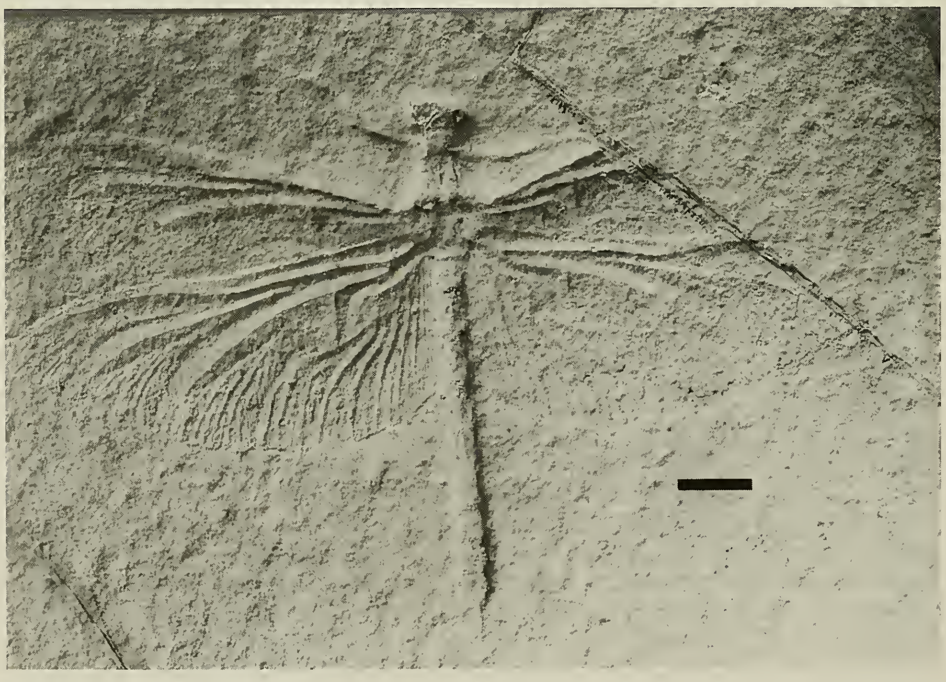

Fig. 32. *Bergeriaeschnidia abscissa* comb. nov., ♀ neotype Mus. BERGÉR no. 6. Scale 10 mm (photo by X. MARTÍNEZ-DELCLÒS).

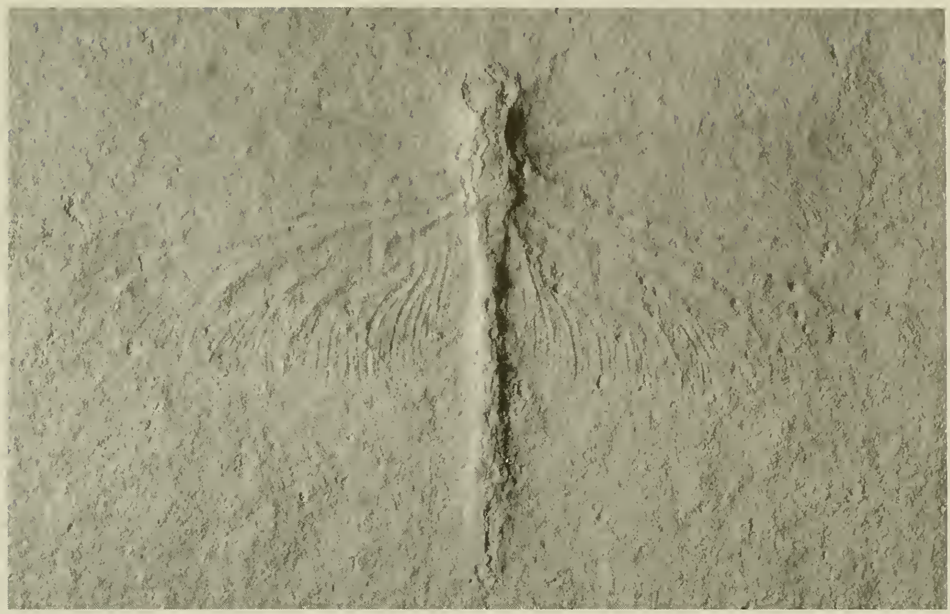

Fig. 33. *Bergeriaeschnidia abscissa* comb. nov., ♀ coll. BÜRGER without no. Scale unknown (photo by K.A. FRICKHINGER).

Most likely these two taxa are indeed conspecific. Since the holotype of *U. abscissus* is lost, and the original description is consistent with such a decision (Art. 75 IRZN), I here designate the holotype of *Bergeriaeschnidia inexpectata* as neotype of *U. abscissus*, to prohibit future taxonomic confusion. According to this revision of the genus *Urogomphus* and the original description of *Bergeriaeschnidia*, there can be no doubt that these two genera are distinct and justified. They are not even closely related within Aeschnidiidae, since *Urogomphus* has several plesiomorphies that are absent in *Bergeriaeschnidia* and some other aeschnidiid genera (e.g. broader discoidal triangles and a less dense cross-venation). Consequently, the valid name for *Urogomphus abscissus* is *Bergeriaeschnidia abscissa* comb. nov.

4. Phylogenetic position of Aeschnidiidae

Until recently, the aeschnidiids have been classified as a subfamily of Cordulegastridae. This classification was suggested by FRASER (1957), but was only based on the similar elongated ovipositor (clearly a convergence). CARPENTER (1992) also regarded Aeschnidiidae as closely related to Cordulegastridae.

CARLE & WIGHTON (1990) suggested a separate superfamily Aeschnidioidea, which they regarded to be the sistergroup of extant Anisoptera. However, their conclusion was mainly based on invalid arguments, since they incorrectly regarded the weakly developed arculus, nodus, and pterostigmata as plesiomorphies of Aeschnidiidae with "protodonates". BECHLY (1996, 1997) demonstrated that this conclusion is not tenable, since it would imply numerous convergent developments of these complex structures in the stemgroup of Odonata, in Zygoptera, in Epiophlebiidae, and in several groups of fossil "anisozygopteres".

Nel & Martínez-Delclòs (1993) made a preliminary numerical cladistic analysis of Anisoptera, which could not convincingly resolve the position of Aeschnidiidae. Trueman (1996) also made a numerical cladistic analysis, in which Aeschnidiidae (represented by *Wightonia*) were resolved within crowngroup Anisoptera (between Petaluridae and the remaining Anisoptera). Lohmann (1996) attributed Aeschnidiidae to the stemgroup of Anisoptera, but did not mention any arguments.

Bechly (1996, 1997) recently demonstrated several flaws in these previous phylogenetic analyses, which were mostly based on incorrectly polarised and homologised characters without appropriate character weighting. Based on a thorough phylogenetic systematic analysis of many characters, Bechly (1996) suggested a sistergroup relationship of Liassogomphidae and Aeschnidiidae (= Aeschnidioptera Bechly, 1996) with crowngroup Anisoptera. Bechly (1997) slightly modified this hypothesis, and placed Aeschnidiidae closer to crowngroup Anisoptera than Liassogomphidae. This position is also confirmed by this study.

Synapomorphies of Liassogomphidae, Aeschnidiidae and crowngroup Anisoptera (autapomorphies of Pananisoptera Bechly, 1996): Sharp Z-like kink of [M + Cu] at the basal side of the discoidal triangle in both wings; the origin of the RP1/2 on the RP is of the secondary type of junction (no equal bifurcation but a suture), at least on the dorsal surface of the hindwings; primary IR1 shortened and less straight and distinct in both pairs of wings (reversed in Petalurida and Austropetaliida); short convex secondary vein pseudo-IR1 developed that is originating as apparent branch on RP1 near the distal end of the pterostigma (fused with the vestigial primary IR1 in many recent Anisoptera of different families); the cubito-anal area of the hindwings is further expanded; distinct pseudo-anal vein PsA delimits a subdiscoidal triangle in both wings (in the groundplan); male hindwings with the anal triangle narrowed (transverse elongate in contrary to Heterophlebioptera); presence of a secondary posterior branch AA1b of the anal vein between the distal side of the anal triangle (AA2b) and CuAb; RP2 strictly aligned with subnodus; the adult insects are resting with the wings strictly horizontally outstretched (except the two highly derived extant libelluloid genera *Cordulephya* and *Zenithoptera*).

Synapomorphies of Aeschnidiidae and crowngroup Anisoptera (autapomorphies of Neoanisoptera taxon nov.; plesiomorphic absent in Liassogomphidae): Discoidal triangles are strictly triangular in both wings, since the triangular vein which divides the discoidal cell into triangle and hypertriangle ends precisely at the distal angle of the triangle (convergent to Stenophlebiidae; reversed in a few derived species of extant gomphids, cordulephyids and libellulids); well-defined pseudo-anal vein PsA delimits a subdiscoidal triangle in both wings (in the groundplan); presence of a second accessory oblique vein 'O' between RP2 and IR2 distal of the lestine oblique vein (convergent to *Selenothemis*, *Oreophlebia*, and *Xanthohypsa*; suppressed in most extant Anisoptera).

Synapomorphies of all crowngroup Anisoptera (plesiomorphic absent in Liassogomphidae and Aeschnidiidae): Hindwings with a well-defined anal loop (divided into four or five cells in the groundplan) that is posteriorly closed and basally limited by a secondary branch of AA (AA1b) and distally by CuAb; pterostigmata more strongly elongated in the groundplan (very homoplastic character); hindwing base with distinct membranule, derived from the articular membrane and axillary cord (more probably a symplesiomorphy, since a distinct membranule is at least known from some Isophlebioptera, too); male second abdominal segment with a pair of lateral swellings of the antecostal suture (auricles) (reduced in all those Anisoptera that have also reduced the anal angle and anal triangle, e.g. Anacina and Libellulidae; thus maybe a symplesiomorphy, since auricles could well be secondary absent in Aeschnidiidae due to the same reason).

Aeschnidiidae belong to those odonate taxa with the most numerous autapomorphies, especially in the wing venation. Putative autapomorphies of Aeschnidiidae include: Discoidal triangles strongly transverse in both pairs of wings, and widely separated from arculus; hypertriangles very long and narrow; PsA and subdiscoidal triangles hypertrophied in both wings; both pairs of wings with a characteristic row of several (!) very distinct pseudo-anal loops beneath the anal vein that are limited by forward slanting secondary branches of AA (one such loop is also present in the forewing of some Stenophlebiidae and in Liassogomphidae, and might therefore represent a symplesiomorphy); basal accessory antenodals present between Ax0 and Ax1; arculus very close to Ax1 or even aligned with it; Ax2 basal of discoidal triangle; arculus weakly defined (reduction); nodal furrow strongly reduced (convergent to Epiophlebiidae and Stenophlebiidae); pseudo-ScP developed in the postnodal area; primary IR1 suppressed; areas between RP2 and IR2, and between RP3/4 and MA, distally widened, but again narrowed near wing margin; hindwing CuAa with max. three distal posterior branches; CuAb is reduced to an "oblique crossvein" between CuA and Aspl (NEL & MARTÍNEZ-DELCLÒS 1993); most of the original cubito-anal area is occupied by a concave secondary vein Aspl1 with numerous parallel posterior branches, alternating with convex intercalary veins (area of CuA strongly reduced); well-defined Rspl and Mspl present in both pairs of wings (convergent to Aeshnoptera and some Eurypalpida); hindwing AA with more than four parallel posterior branches, alternating with concave intercalary veins (anal supplements Aspl), thus anal area distinctly fan-like; anal margin of male hindwing of same shape as in female hindwing, without any anal angle or anal triangle (reversal); pterostigmata shifted basally (convergent to Isophlebiidae and Anacina) and more or less reduced (shortened and traversed by crossveins); very dense wing venation with numerous cells (convergent to Aktassiidae), and all wing spaces (e.g. median space, submedian space, discoidal triangle, and hypertriangle, etc.) traversed by numerous crossveins; wings totally or partly dark coloured; hindwings hardly shorter, or even slightly longer than forewings; abdomen distinctly shorter than wing length; female ovipositor hypertrophied; larval paraprocts (not the cerci!) strongly hypertrophied and forcep-like (BECHLY 1998, BECHLY et al. 1998, FLECK et al. in prep.).

The abdomen of *Urogomphus* and the other Aeschnidiidae is very short and stout, and especially the female abdomen is very broad. This structure of the abdomen seems to be a mixture of "primitive" (plesiomorphic) and derived (apomorphic) character states. Since nearly all other odonates have an abdomen that is much longer, compared to the wing length, this shortening must be regarded as an autapomorphy of Aeschnidiidae. On the other hand, the very broad female abdomen is also present in Isophlebiidae (basal stemgroup representatives of Anisoptera) and Petalurida (most basal representative of crowngroup of Anisoptera) and therefore rather seems to be a symplesiomorphy of these taxa.

5. The ovipositor of Aeschnidiidae

A very long ovipositor is meanwhile known from the basal genus *Urogomphus* (= *Lithoaeschnidium*), as well as the more derived genera *Aeschnidium*, *Malmaeschnidium*, *Bergeriaeschnidia*, and *Wightonia* (Nel & Martínez-Delclòs 1993; Bechly 1998), and therefore has to be regarded as a derived groundplan character (autapomorphy) of Aeschnidiidae. Nel & Martínez-Delclòs (1993: 83–84) regarded this ovipositor as a pseudo-ovipositor, similar but convergent to that of Cordulegastridae, i.e. mainly formed by the hypertrophied valvulae 1 (= gonapophyses VIII), while the valvulae 2 (= gonapophyses IX) are much shorter, and valvulae 3 (gonocoxa IX with gonostylus) are even completely reduced. I regard the referring specimens as too poorly preserved to be really certain about the detailed structure of the ovipositor, even though it is reasonable to assume that the left and right valvula 3, which together serve as a kind of ovipositor-sheath in Anisoptera, would not be useful for an ovipositor with extremely elongated gonapophyses. It can only be stated that Aeschnidiidae had an ovipositor with one or two pairs of very long gonapophyses, and that valvula 3 (if still present at all) did not extend the abdomen. Contrary to Fraser (1957), I suggest to restrict the term "pseudo-ovipositor" to an ovipositor-like structure that is not formed by the gonapophyses (valvulae 1 and 2), but by a secondary outgrowth of the female vulvar scale, as in the extant libellulid genus *Uracis* for example.

The very long ovipositor of Aeschnidiidae was certainly not suited for endophytic oviposition in plant tissues. On the other hand, all extant dragonflies with an exophytic oviposition in open water (gomphids and libelluloids) do have a strongly reduced ovipositor. Only Cordulegastridae have a similar ovipositor which is adapted to endosubstratic oviposition. Therefore, I presume that Aeschnidiidae, as well as Tarsophlebiidae and Steleopteridae, did have a similar mode of oviposition in soft substrates, like mud.

It is remarkable, that among the fossil insects known from Solnhofen Limestone there are three unrelated subgroups of Odonata with such a very long ovipositor: Tarsophlebiidae (according to Bechly 1996 the sistergroup of crowngroup Odonata), Steleopteridae (either a basal calopterygoid Zygoptera, or an epiophlebioid "Anisozygoptera"), and Aeschnidiidae ("advanced" stemgroup representative of Anisoptera). A recent re-preparation of the holotype of the Carboniferous dragonfly *Erasipteroides valentini* revealed a very long ovipositor, too (Bechly, Brauckmann & Zessin, in prep.). These facts seem to indicate that the elongated ovipositor belongs to the groundplan of Odonata and therefore represents a symplesiomorphy of the mentioned taxa. However, the ovipositor of extant Zygoptera, Epiophlebiidae, and basal Anisoptera is very similar, and completely corresponds to the type of ovipositor in the groundplan of Pterygota (thus not prolonged). Kukalová-Peck (1991) also reported this normal type of ovipositor for undescribed specimens of Meganisoptera ("protodonates"). Therefore, I preliminarily regard the elongated ovipositor of Tarsophlebiidae (Nel et al. 1993), Steleopteridae (Nel, Bechly & Martínez-Delclòs in prep.), and Aeschnidiidae as a triple convergence, due to adaptation to a particular (though unknown) palaeo-habitat.

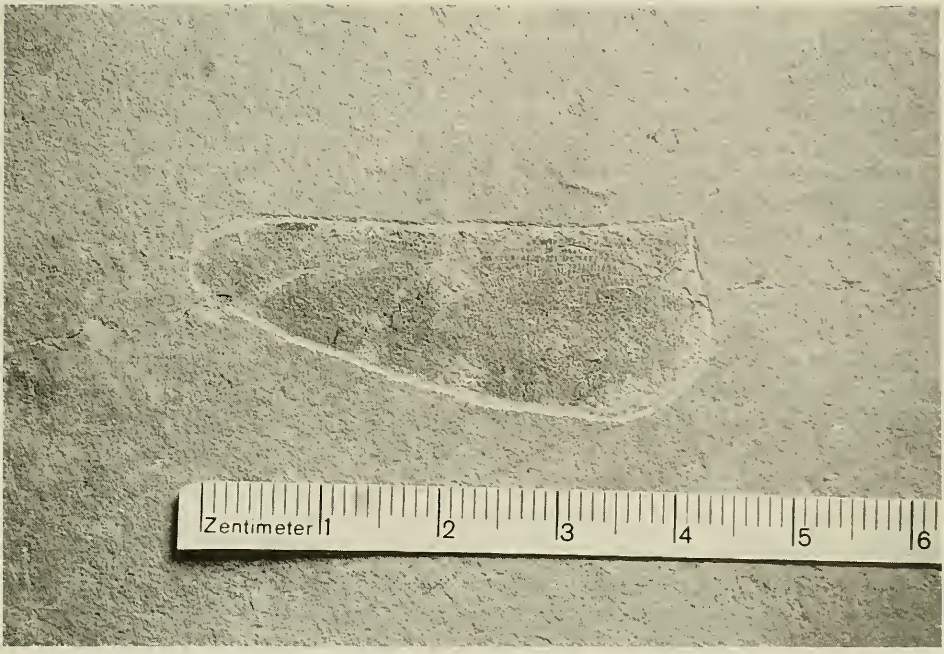

Fig. 34. *Aeschnidium densum*, SMNS 62661, plate. Scale as indicated by rule.

6. Possible explanation for the extinction of Aeschnidiidae

The Aeschnidiidae have been one of the most diverse subgroups of odonates in the Upper Jurassic and Lower Cretaceous, with about 25 known species (incl. a few yet unnamed species). Aeschnidiidae had a world-wide distribution, since they are recorded from all continents except North America. However, this group is extinct now, and there are no known records from the Upper Cretaceous or Tertiary either. NEL & MARTÍNEZ-DELCLÒS (1993: 97) regarded the reasons for the disappearance of Aeschnidiidae as particularly mysterious. What might have been the "mysterious" reasons for the decline of this, once flourishing group, in the late Mesozoic? I believe that their decline and extinction was directly caused by the evolution of modern (crowngroup) birds in the Upper Cretaceous. At least it is evident that the last known Aeschnidiidae existed in the Lower Cretaceous, while the first crowngroup representatives of birds appeared in the Upper Cretaceous. Of course this correlation alone would not be sufficient evidence.

Fortunately there is further evidence from the morphology of aeschnidiid wings. These wings show reductions of several structures that are directly related with a powerful flapping flight, such as the pterostigma, the nodus, and the arculus (BECHLY 1996). Furthermore, the wings show typical adaptations for gliding, such as the strongly expanded anal area and the very transverse discoidal triangles. The latter are known to support the generation of camber (WOOTTON 1991), which is a property that is more useful for gliding than for flapping flight. Thus, it seems well reasonable to assume that Aeschnidiidae were highly adapted for gliding, but have been relatively slow and clumsy in active flight. This over-specialization made these animals to an easy prey for larger aerial predators. They were obviously swift enough to escape the few insectivorous pterosaur species, but probably not swift enough to escape the numerous insectivorous modern birds. This hypothesis is even strengthened by the circumstance that most aeschnidiids have been rather large insects (wing span 60–200 mm, most species with a wing span of more than 100 mm). BECHLY (1995, 1996), furthermore, predicted that the wings of Aeschnidiidae have been coloured, because extant odonates with a comparably dense wing venation mostly have dark coloured wings (e.g. *Calopteryx* or *Neurothemis*). This speculation is now definitely confirmed, since the new *Urogomphus* species from Nusplingen has a distinct colour pattern preserved (see above), while the *Aeschnidium densum* specimen from Nusplingen (Fig. 34) proves that the wings of this species have been entirely coloured (an artifact is unlikely since the *Cymatophlebia* specimen from the same locality does not have dark wings, while the *Urogomphus* specimen shows a symmetrical colour pattern in both pairs of wings). Preserved colour pattern is also known from *Lleidoaeschnidium valloryi* (five brown bands) (very well visible in TISCHLINGER 1996: fig. 13), *Nannoaeschnidium pumilio* (partly coloured wings) and *Gigantoaeschnidium ibericum* (totally dark coloured wings), even though NEL & MARTÍNEZ-DELCLÒS (1993) still considered the possibility that in the latter species the coloration might also be secondary, due to the fossilization process.

To sum up: Aeschnidiidae were generally large insects, with conspicuously coloured wings, and highly adapted for gliding flight. Such insects have been the perfect candidates to become exterminated by swift insectivorous birds. The same might have happened to most "anisozygopteres" that only survived the Mesozoic with two extant relic species of the genus *Epiophlebia*. Only two lineages of Odonata could prosper after the evolution of modern birds: The Zygoptera that are adapted for slow manoeuvring flight between dense vegetation (hide-and-seek strategy), and crowngroup Anisoptera that are adapted to very fast flight, correlated with a much improved vision (watch-and-escape strategy). Extant Libellulidae are very good gliders, too, but did not reduce their flapping flight capabilities at all (no reductions of pterostigma, nodus, or arculus).

It is quite probable that predation by aerial vertebrates also exterminated the giant pterygote insects of the Palaeozoic. These large flying insects (Palaeodictyoptera, Odonatoptera – "Protodonata", and Ephemeroptera) are only known from the Carboniferous and Permian, when actively flying vertebrates were completely absent. Under these circumstances insects could grow to the maximum size that was physically possible (constraint), in a co-evolution of phytophagous prey insects (e.g. Palaeodictyoptera) and insectivorous predatorial insects ("protodonates"). With the rise of pterosaurs in the Triassic all those giant pterygotes disappeared and never reappeared.

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