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# A new genus and species of Aeschnidiidae (Insecta: Odonata: Anisoptera) from the Solnhofen Limestone, Upper Jurassic, Germany

With 2 Text-figures

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## Abstract

*Bergeriaeschnidia inexpectata* n. g., n. sp. is described from the Upper Jurassic of S.W. Germany and compared with the known fossil Aeschnidiidae. The diversity of this family was a very important feature of insect evolution during the Upper Jurassic and Lower Cretaceous.

Key words: Insecta, Aeschnidiidae, taxonomy, Upper Jurassic, Solnhofen Limestone, Germany.

## Kurzfassung

[Eine neue Gattung und Art der Aeschnidiidae (Insecta, Odonata, Anisoptera) aus dem lithographischen Plattenkalk des deutschen Oberjura.] – *Bergeriaeschnidia inexpectata* n. g., n. sp. wird beschrieben und mit anderen bekannten fossilen Aeschnidiidae-Arten verglichen. Eine hohe Diversität ist sehr bezeichnend für die Familie Aeschnidiidae während des Oberjuras und der Unteren Kreide.

## Résumé

[Un nouveau genre et espèce d'Aeschnidiidae (Insecta: Odonata: Anisoptera) du calcaire lithographique du Jurassique supérieur d'Allemagne.] – *Bergeriaeschnidia inexpectata* n. g., n. sp. est décrit du Jurassique supérieur de la Bavière et comparé avec les Aeschnidiidae connus. La diversité de cette famille a été très importante durant le Jurassique supérieur et le Crétacé inférieur.

## Introduction

The fossil family Aeschnidiidae was very diverse during the Upper Jurassic and Lower Cretaceous. This family is known from Germany, England, Spain and also China, Siberia, Brazil and Australia. With no less than eighteen described genera and more than twenty-two described species, and numerous undescribed taxa from the Mesozoic of England, it appears to be one of the more diverse odonatan groups of this period (Nel & Martínez-Delclòs 1993 Martill & Nel, in press; Jarzembowski, Martínez-Delclòs & Nel, in prep.; Pritykina 1993).

At present, no less than four genera and four to six species have been described from the Upper Jurassic lithographic limestones (Solnhofen Limestone) of Bavaria. Thus, the discovery of a new, undescribed genus and species in the collec-

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tion of the Berger Museum (Eichstätt) from the same outcrops of Solnhofen–Eichstätt is rather unexpected.

We follow the wing venational interpretation and terminology of RIEK & KUKALOVÁ-PECK (1984), with slight modifications by NEL et al. (1993) and NEL & MARTÍNEZ-DELCLÒS (1993).

**Acknowledgements**

We are very grateful to Mr. GEORG BERGER, Director of the Berger Museum, Eichstätt, for the loan of the type specimen of *Bergeriaeschnidia inexpectata* n. g., n. sp.

## Systematic Palaeontology

Class Insecta LINNÉ 1758
Order Odonata FABRICIUS 1792
Suborder Anisoptera SELYS 1840
Family Aeschnidiidae HANDLIRSCH 1906

### *Bergeriaeschnidia* n. g.

Type species: *Bergeriaeschnidia inexpectata* n. sp.

Etymology: Named after Mr. BERGER, Director of the Berger Museum, Eichstätt.

Diagnose: This genus is characterized by the following features: (1) the wings are wide and distally rounded; (2) the hindwing discoidal triangle is distinctly narrower than that of the forewing; (3) there is a distinct oblique pterostigmal brace; (4) there is a distinct pterostigma; (5) the forewing primary antenodal crossveins are very approximate; (6) the area between RA and RP1 is very wide near the wing apex; (7) there is no secondary longitudinal vein between C and ScP in the antenodal area of the hindwing.

### *Bergeriaeschnidia inexpectata* n. sp.

Text-figs. 1-2

Etymology: *inexpectata* because the discovery of a new genus of Aeschnidiidae in the well-known Upper Jurassic fauna of Solnhofen was unexpected.

Holotypus: Specimen n° 6, Berger Museum, Eichstätt, Bavaria, Germany. A cast is in the collection of the Paleontology Laboratory, National Museum of Natural History, Paris, France. – Stratum typicum: Upper Jurassic, Tithonian, Solnhofen Limestone. – Locus typicus: Eichstätt, Bavaria, Germany.

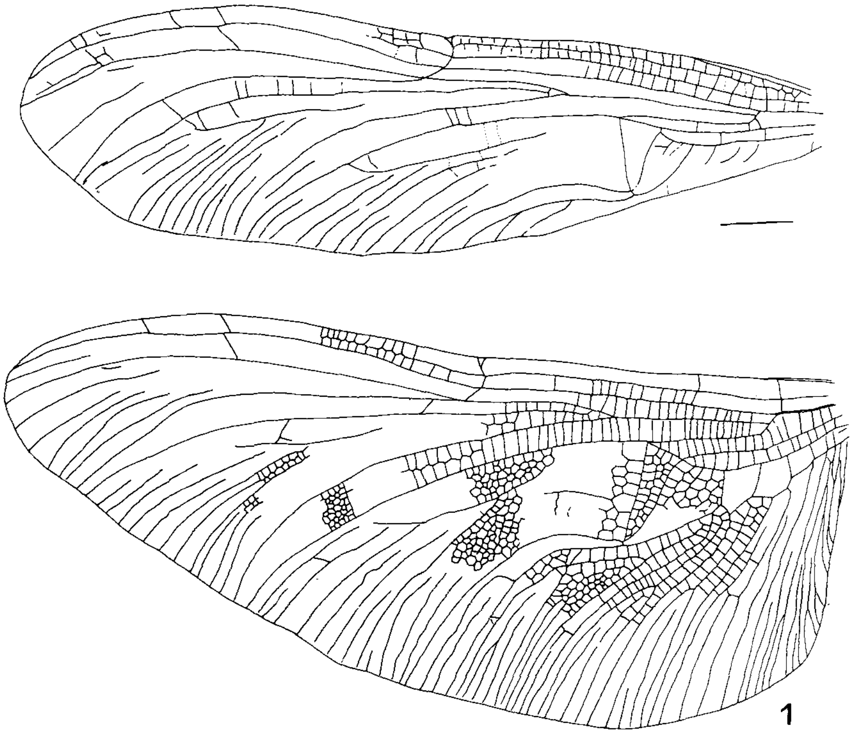
Another specimen, clearly belonging to the same species, is figured in FRICKHINGER (1994: 135, fig. 245), labelled "*Aeschnidium* spec., Eichstätt, 6 cm, coll. LEICH, Bochum".

Description:
The four wings are connected with the body. The head is very fragmentary and the body is poorly preserved. The right wings are not complete but the left wings are better preserved. There is no visible trace of coloration.

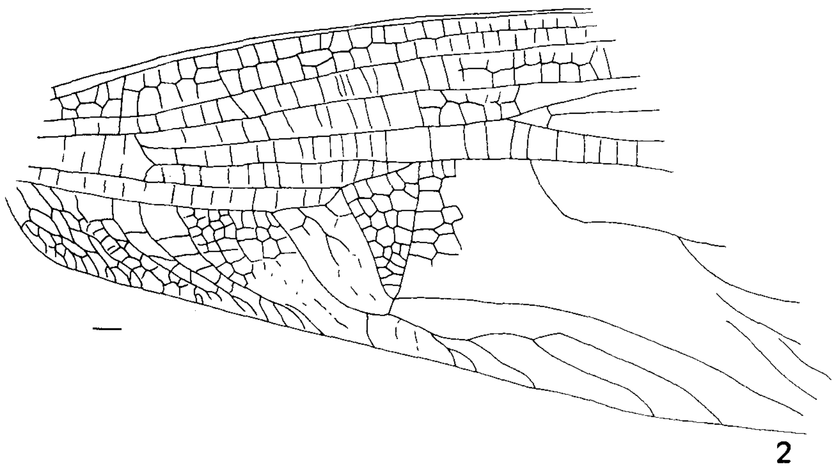
Length of the abdomen, 47.0 mm; width, 3.0 mm; length of the ovipositor, 7 mm; width, 0.2 mm. The abdomen is cylindrical without any constriction. The ovipositor shows that it is a female specimen. Length of the thorax, 16.0 mm; width, 7.0 mm; length of the head, 5.0 mm; width, 7.8 mm.

Forewing: length, 56.0 mm; width, 16.8 mm; distance from base to nodus, 25.5 mm; to arculus, 23.5 mm; distance from nodus to pterostigma, 15.8 mm; to the apex, 30.5 mm; distance from the pterostigma to the apex, 12.0 mm. RP separates from MA very near (0.4 mm) to the base of RP + MA. MA is strongly angulate in the arculus. The posterior part of the arculus is a strong crossvein between MA and MP + Cu. The arculus is approximately opposite to the first primary antenodal crossvein. The nodal structures are not very well preserved but ScP clearly crosses through the nodus. ScP fades distally in the postnodal area between C and RA, 7.5 mm distally of the nodus. The two primary antenodal crossveins are distinctly stronger than the secondaries. Distance between Ax1 and the base, 4.2 mm; between Ax1 and Ax2, 3.8 mm; between Ax2 and the nodus, 18.3 mm. The secondary antenodal crossveins are numerous (more than twenty). There is a secondary zigzagged longitudinal vein between C and ScP from the base of Ax1 to the nodus; no such secondary vein occurs between ScP and RA. The postnodal area is not very well preserved. The area between RA and RP1 is greatly widened distally, especially distal of the pterostigma. The pterostigma is not very sclerotized. Its basal side is a strong, rather oblique crossvein but the distal side is weaker. The pterostigmal brace is a long, strong and oblique crossvein below the basal side of the pterostigma. The hypertrigonal space is 9.0 mm long, 0.75 mm wide and crossed by numerous simple crossveins. The discoidal triangle is transverse, 5.3 mm long and 3.1 mm wide, divided into many cells, disposed in two or three rows, but their exact number is unknown. The distal side (MAb sensu NEL & MARTÍNEZ-DELCLÒS 1993) of the discoidal triangle is straight, 5.3 mm long. The costal side is 3.1 mm long and the proximal side is curved and 5.2 mm long. The median area is crossed by many simple crossveins. The submedian area is crossed by numerous simple crossveins, with vein CuP being identical to other crossveins. The subdiscoidal area is very well-defined, irregularly triangular in shape and divided into many small cells. The free part of CuA, between the posterior angle of the discoidal triangle and its fusion with AA, is short (0.3 mm). Vein PsA (AA0 sensu NEL et al. 1993) reaches in the proximal angle of the discoidal triangle and is more or less divided into smaller distal branches which fade away in the subdiscoidal area. The anal area is very wide and divided into several groups of small cells defined by parallel, posteriorly-directed branches of AA. The more basal posterior branches of AA are very long and extend obliquely to reach the posterior margin of the wing. Vein CuA is very short, 13.0 mm long, and reaches the posterior wing margin distinctly basal of the nodus. The cubito-anal area is smaller than the anal area and the area between CuA and MP. Vein MP is distinctly longer than CuA and reaches the posterior wing margin opposite the nodus. The postdiscoidal area is very wide, with about ten rows of cells distal of the discoidal triangle. It is distinctly wider near the posterior wing margin. Vein Mspl is well-defined, with three to five rows of cells between Mspl and MA; it reaches MA distally. Vein MA is a slightly curved vein. RP3/4 is also a slightly curved vein, more or less parallel with MA in its proximal part but these veins come closer together near the posterior wing margin. In the area between RP3/4 and MA, there are four to seven rows distal of the nodus and two or three rows of cells near the posterior wing margin. Vein IR2 begins one cell distal of the base of RP3/4. The area between RP3/4 and IR2 is very broad with many secondary veins reaching the posterior wing margin and a well-defined vein Rspl. There are three or four rows of cells between Rspl and IR2. RP2 begins opposite the subnodus. There are numerous (about fifteen) Bq crossveins between IR2, RP and RP2. The oblique crossvein "O" is not preserved. There are four or five rows of cells in the area between IR2 and RP2 but these veins strongly come closer together near the posterior wing margin. The area between RP2 and RP1 is very broad, with many secondary concave veins but no well-defined vein IR1.

Hindwing: length, 58.0 mm; width, 25.0 mm; width opposite to the nodus, 24.0 mm; distance from base to nodus, 25.5 mm; to arculus, 5.3 mm; distance from the nodus to the pterostigma, 17.5 mm; to the apex, 32.5 mm; distance from the pterostigma to the apex, 10.1 mm. RP separates from MA very near (0.8 mm) to the base of RP + MA. MA is strongly angular in the arculus. The posterior part of the arculus is a strong crossvein between MA and MP + Cu. The arculus is exactly opposite to the first primary antenodal crossvein Ax1. The nodal structures are not very well preserved but ScP clearly crosses the nodus. The nodus is approximately midway between the base and the apex of the wing. ScP fades away in the postnodal area between C and RA, 11.7 mm distal of the nodus. The two primary antenodal crossveins are distinctly stronger than the secondaries. Distance between Ax1 and the wing base, 4.7 mm; between Ax1 and Ax2, 5.8 mm; between Ax2 and the nodus, 15.0 mm. The secondary antenodal crossveins are numerous (more than twenty). There is no secondary zigzagged longitudinal vein between C and ScP and between ScP and RA. The postnodal area is not very well preserved. The area between RA and RP1 is greatly widened distally, especially distal of the pterostigma. The pterostigma is not very sclerotized. Its basal side is a strong and rather oblique crossvein but its distal side is weaker. The pterostigmal brace is a long strong and oblique crossvein opposite to the basal side of the pterostigma. The hypertrigonal space is 7.7 mm long and 1.3 mm wide and crossed by numerous simple crossveins. The discoidal triangle is transverse, 7.2 mm long and 2.5 mm wide, divided into two rows of many cells (about thirty). The distal side (MAb sensu NEL & MARTÍNEZ-DELCLÒS 1993) of the discoidal triangle is straight, 7.2 mm long. The costal side is 2.5 mm long and the proximal side is curved and 7.0 mm long. The median area is crossed by many simple crossveins. The submedian area is crossed by numerous simple crossveins, vein CuP being identical to the other crossveins. The subdiscoidal area is very well-defined, irregular quadrangular in shape and divided into many small cells. The free part of CuA, between the posterior angle of the discoi-



Text-fig. 1. *Bergeriaeschnidia inexpectata* n. g., n. sp., holotype, left forewing and hindwing (scale: 5 mm).



Text-fig. 2. *Bergeriaeschnidia inexpectata* n. g., n. sp., holotype, base of the right forewing (scale: 1 mm).

dal triangle and its fusion with AA, is short (0.1 mm long). Vein PsA (AA0 sensu Nel et al. 1993) reaches the proximal angle of the discoidal triangle and is more or less divided into smaller distal branches which fade away in the subdiscoidal area. The anal area is very wide. Distance between AA and the posterior wing margin, 18.3 mm. AA has five branches directed towards the posterior wing margin, which delimit six groups of small cells, posteriorly closed by a distinct pseudovein somewhat parallel to AA. The secondary convex veins AAspli ($1 < i < 7$) (sensu Nel & Martínez-Delclòs 1993) between the veins AAj ($1 < j < 5$) are strong. There is no anal angle and no anal triangle. Vein AA is not fused with the sides of the discoidal triangle. Vein CuAb (CuA2 sensu Nel & Martínez-Delclòs 1993) is not preserved but the main branch CuAa of CuA is relatively short, divided only into two branches which reach the posterior margin. The cubital area between these branches is very narrow, distinctly narrower than the cubito-anal area. CuAa is very short, 16.8 mm long and reaches the posterior wing margin distinctly basal of the nodus. The cubito-anal area is smaller than the anal area and the area between CuA and MP. Vein MP is simple but distinctly longer than CuAa and reaches the posterior wing margin opposite to the nodus. The postdiscoidal area is very wide, with about eight rows of cells distal of the discoidal triangle. It is distinctly wider near the posterior wing margin. Vein Mspl is well defined, with four to five rows of cells between Mspl and MA. It reaches MA distally. Vein MA is slightly curved. Vein RP3/4 is also slightly curved, more or less parallel with MA in its proximal part but RP3/4 and MA come closer together near the posterior wing margin. In the area between RP3/4 and MA, there are four to seven rows of cells distal of the nodus and two or three row of cells near the posterior wing margin. Vein IR2 begins one cell distal of the base of RP3/4. The area between RP3/4 and IR2 is very broad with many secondary veins reaching the posterior wing margin and a well-defined vein Rspl. There are three or four rows of cells between Rspl and IR2. RP2 begins opposite to the subnodus. There are numerous (about fifteen) Bq crossveins between IR2, RP and RP2. One oblique crossvein "O" is preserved, 2.5 mm distal of the subnodus. There are four or five rows of cells in the area between IR2 and RP2 but these veins strongly come closer together near the posterior wing margin. The area between RP2 and RP1 is very broad, with many secondary concave veins but no well-defined vein IR1.

## Discussion

The fore- and hindwing transverse discoidal triangles and the specialized hindwing anal area clearly demonstrate that *Bergeriaeschnidia* n. g. belongs to the Aeschnidiidae. It differs from all the well-known species, and more especially from the taxa of the same outcrops, in the following characters: (1) its wings are very wide and rounded; (2) the area between RA and RP1 is very wide near the apex of the wings; (3) its forewing discoidal cell is distinctly wider than the one of the hindwing one. The known species of Aeschnidiidae from Solnhofen-Eichstätt are the following: *Aeschnidium densum* (Hagen 1862), *Lithoaeschnidium viohli* Nel & Martínez-Delclòs 1993, *Malmaeschnidium mayeri* Nel & Martínez-Delclòs 1993, *Urogomphus giganteus* (Germar 1839), possibly *Urogomphus eximius* (Hagen 1862) and *Urogomphus abscissus* (Hagen 1862). These two last species are very poorly known and considered by Nel & Martínez-Delclòs (1993) as incertae sedis. Nevertheless, *U. eximius* and *U. abscissus* have distinctly longer wings (wing length between 72 to 78 mm) than *Bergeriaeschnidia inexpectata* n. g., n. sp. These characters are also sufficient for distinguishing *Bergeriaeschnidia* n. g. from the following taxa: *Iberoaeschnidium conquensis* Nel & Martínez-Delclòs 1993, *Lleidoaeschnidium valloryi* Nel & Martínez-Delclòs 1993, *Gigantoaeschnidium ibericus* Nel & Martínez-Delclòs 1993, *Santanoptera gabbotti* Martill & Nel, in press, *Leptaeschnidium latum* Pritykina 1977 and *Wightonia araripina* Carle 1990.

Several species of Aeschnidiidae are poorly known because they are based on fragmentary material. Thus, their comparison with *Bergeriaeschnidia* is more difficult. *Nannoaeschnidium pumilio* Nel & Martínez-Delclòs 1993, known from the basal half of a hindwing, has distinctly smaller wings (hindwing width, 9.0 mm for *N. pumilio*) with narrower and more triangular subdiscoidal space than *Bergeriaeschnidia* n. g. *Aeschnidium bubas* Westwood 1854 (type species of the genus *Aeschnidium*) is known from a hindwing only, and differs from *Bergeriaeschnidia* in its very wide hindwing discoidal triangle. *Aeschnidium antiquum* (Brodie 1845) is known from a fragment of the basal half of a hindwing. After the revision of the holotype of *A. antiquum* (Jarzembowski, Martínez-Delclòs & Nel, in prep.), it is known that *Bergeriaeschnidia* n. g. has broader hindwings than *A. antiquum* (wing width, 17 mm). Also, *A. antiquum* has two rows of cells in the area between RP and MA, opposite to the discoidal cell, instead of one as in *Bergeriaeschnidia* n. g. *Aeschnidiella kabanovi* Zalesky 1953, known from two hindwing fragments, has smaller wings (wing width, 11 mm) and a narrower discoidal triangle than *Bergeriaeschnidia* n. g. *Hebeiaeschnidia fengningensis* Hong 1982 is based on an incomplete hindwing and is a very poorly defined genus and species, considered by Nel & Martínez-Delclòs (1993) as an incertae sedis. Nevertheless, from the interpretation of Hong (1982) its cubito-anal area is very different from that of *Bergeriaeschnidia*, without any pseudo-vein that would delimit groups of small cells. *Aeschnidiopsis flindersiensis* Tillyard 1917 is also a very poorly known species because the type specimen and a specimen studied by Riek (1954) have very different structures in the cubito-anal area, as noted by Nel & Martínez-Delclòs (1993). Nevertheless, the type specimen of *A. flindersiensis* has a very narrow and long discoidal triangle which is unlike *Bergeriaeschnidia* n. g. *Brunneaschnidia jiuquanensis* Hong 1982 is considered by Nel & Martínez-Delclòs (1993) as an incertae sedis. From Hong's (1982) reconstruction, *B. jiuquanensis* would also differ from *Bergeriaeschnidia* n. g. in the cubito-anal area, which is very similar to that of *Hebeiaeschnidia*, but also in its median space which is free of crossveins, the very wide discoidal triangles with few cells, and the lack of any longitudinal secondary vein between ScP and C, but these structures are very uncertain in *Brunneaschnidia*.

*Sinaeschnidia heishankowensis* HONG 1965 and *S. huzhouensis* ZHOU & WEI 1980 are better known than preceding taxa. They differ from *Bergeriaeschnidia* in the primary antenodal crossveins which are much more distant (distance between Ax1 and Ax2, 6 mm instead of 3.5 mm) and by their longer wings (60 to 70 mm long). The wings of *Aegyptidium aburasiensis* SCHLÜTER & HARTUNG 1982 have almost the same shape as *Bergeriaeschnidia*, even if they are distinctly smaller (37.5 mm long instead of 56 to 58 mm for *Bergeriaeschnidia*). *Aegyptidium* also differs in its narrower forewing discoidal triangle and the absence of the pterostigma and pterostigmal brace.

The phylogenetic affinities of *Bergeriaeschnidia* within the Aeschnidiidae are not very clear because the phylogenetic relationships between the different genera are almost unknown, as shown in NEL & MARTÍNEZ-DELCLÒS (1993) first attempt at a phylogenetic study. *Bergeriaeschnidia* is related to the taxa which have a pseudo-vein parallel with AA in the hindwing anal area (the great majority of the genera, except *Aeschnidiopsis*, possibly *Brunneaschnidia* and *Hebeiaeschnidia* and an undescribed Lower Cretaceous species from England). *Bergeriaeschnidia* shares with *Aeschnidium densum*, *Lithoaeschnidium viohli* and *Malmoaeschnidium mayeri* the presence of a strong pterostigmal brace but this structure is probably plesiomorphic. *Bergeriaeschnidia* shares with *Aegyptidium* the wide areas between C and RA and between RA and RP1 near the wing apex, if SCHLÜTER & HARTUNG's (1982) reconstruction is accurate. Thus, no definite conclusion can be reached concerning the phylogenetic affinities of *Bergeriaeschnidia*.

*Bergeriaeschnidia* n. g. is the fifth genus of Aeschnidiidae known from the Upper Jurassic of Solnhofen–Eichstätt. With this new taxon, the Aeschnidiidae is the most diverse odonatan family from these sediments. The same situation seems to occur in the Lower Cretaceous of Las Hoyas (Spain) and the British Lower Weald Clay and Upper Purbeck. The Lower Cretaceous faunas of China, Australia and Brazil are too imperfectly known to allow any definite, or even temporary, conclusion concerning their odonatan diversity. Nevertheless, the Aeschnidiidae is the most diverse odonatan family in the world during this period. Of course, this conclusion has to be considered in context because fossilisation artefacts could have occurred for the Mesozoic Zygoptera. These small delicate insects are rarely fossilised but they are frequent in some favorable layers, such as the British Weald Clay (BECHLY et al., in press). Nevertheless, the Aeschnidiidae remains the most diverse Mesozoic anisopteran family.

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