



Redescription of the Upper Jurassic *Aeshna antiqua* Vander Linden, 1827 in the Anisopteran family Protolindeniidae (Odonata)

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Abstract

The holotype of the Upper Jurassic species ‘*Aeshna antiqua*’ Vander Linden, 1827, from the lithographic limestone of Bavaria (Solnhofen Konservat-Lagerstätte), is redescribed. It turns out that it is conspecific with *Protolindenia wittei* (Giebel, 1860), the type species of the genus *Protolindenia* Deichmüller, 1886. We therefore transfer ‘*Aeshna antiqua*’ to the genus *Protolindenia* under the name *Protolindenia antiqua* (Vander Linden, 1827) **comb. nov.**, and *Protolindenia wittei* is considered as a junior synonym of *P. antiqua* (Vander Linden, 1827).

Keywords: Insecta, Anisoptera, Petalurida, Mesozoic, Solnhofen, Germany

Introduction

The Lower Tithonian lithographic limestone of the area of Solnhofen-Eichstätt in Bavaria (Germany) is world-famous for its insect assemblage. Although not very abundant, the Odonata are especially diverse with, among the Anisoptera, representatives of the stem groups of the modern groups Aeshnoidea, Gomphida, Petaluroidea, and Epiproctophora (‘libelluloids’), plus some taxa in the Mesozoic family Aeschniidae (e.g., Nel *et al.*, 1998; Bechly, 2000, 2001, 2003, 2012a, 2012b; Bechly *et al.*, 1998, 2001; Fleck & Nel, 2003).

Dragonflies have long since been known from these layers (e.g., Vander Linden, 1827; Germar, 1839; Hagen, 1848, 1850, 1862; Giebel, 1856, 1860), but in many cases the original 19th century descriptions and illustrations are poor, and the locations of the type material of some taxa are still unknown. It is certainly the case of the enigmatic ‘*Aeshna antiqua*’ Vander Linden, 1827, which

is the oldest insect species to have been described from the Solnhofen Konservat-Lagerstätte (Bechly, 2012b). Handlirsch (1906: 591) doubtfully ascribed this species to the genus *Protolindenia* Deichmüller, 1886 and considered it as probably identical with either *P. wittei* or with the type species of his new genus *Mesuropetala*, i.e., *M. koehleri*. Bechly *et al.* (2001: 21) indicated that what is known about ‘*Aeshna antiqua*’ is ‘the wing length of 46 mm, the mere citations of the name by Hagen (in de Selys-Longchamps 1850: 362) and Giebel (1856: 279), and the statement of Hagen (1862) that it could be identical with *Protolindenia wittei*, which is irrelevant regarding the fact that this author synonymized ‘*Aeshna wittei* Giebel’ with ‘*P. münsteri* Germar’, but regarded ‘*Gomphus koehleri* Hagen’ as a distinct species. Since ‘*Aeshna antiqua*’ Vander Linden, 1827 and ‘*Aeshna*’ [sic] *schmiedeli* Giebel, 1856 could either be synonyms with *Mesuropetala muensteri*, or *Protolindenia wittei*, we regard the two former taxa as *nomina dubia* in Anisoptera *incertae sedis*. Bechly (2012a) listed ‘*Aeshna antiqua*’ as ‘*Protolindenia? antiqua* (Vander Linden, 1827) *nomen dubium* (‘vielleicht ein Synonym von *P. wittei* oder *M. muensteri*)’.

Pierre Léonard Vander Linden (1797–1831), a graduate of medicine from Bologna and Leuven universities, had a very short scientific career, but published several papers mostly dedicated to Recent Odonata, Hymenoptera, and Coleoptera of Western Europe and Indonesia (see references in Marchal, 1832; Morren, 1833; Wasscher *et al.*, 2016). He can be considered as the first professor of zoology in Belgium as he was appointed as such at the *Musée des sciences et des lettres* at Brussels in 1826 (e.g., Marchal, 1832; Morren, 1833; Wasscher *et al.*, 2016), that is, four years before Belgian independence. According to Wasscher *et al.* (2016), Vander Linden’s

collections of extant insects have never been traced and these authors suggested that they were probably destroyed by carpet beetles and/or similar species. Until its recent rediscovery in the collections of the Liège University, the location of the holotype (by monotypy) of ‘*Aeshna*’ *antiqua* was unknown, precluding the reassessment of this species, but it was obvious that it was not part of Vander Linden’s collections. Indeed, according to Vander Linden (1827: 248), the specimen was collected by Jean-François Vander Maelen (recte: Vandermaelen, 1797–1872) and entrusted to him for description. Jean-François Vander Maelen was the brother of cartographer and geographer Philippe Vandermaelen (1765–1869), who founded the *Établissement géographique de Bruxelles* (1830–1880) that notably included a gallery of natural history. It is likely that the holotype of ‘*Aeshna*’ *antiqua* was collected in 1825, as suggested by Vander Linden (1827: 248), who mentioned J.-F. Vandermaelen’s recent travel in Germany, probably linked to the purchase of numerous lithographic stones in Solnhofen for his brother reported at that date by Anonymous (1880: 80).

This paper aims at redescribing ‘*Aeshna*’ *antiqua*, almost 200 years after its first description by Vander Linden (1827), and precisising its affinities.

Material and methods

The material is part of the palaeontological collections of the Liège University, Liège, Belgium (prefixed PAULg). It was photographed using a Nikon D850 digital camera, equipped with a 70mm f/2.8 Sigma macro lens.

The higher classification of fossil and extant Odonatoptera, as well as familial and generic characters follow the phylogenetic system proposed by Bechly (1996). Wing venation terminology follows Riek & Kukalová-Peck (1984), as amended by Nel *et al.* (1993) and Bechly (1996).

Abbreviation of venation: Ax1 and Ax2 primary antenodal crossveins; C costa; CuA cubitus anterior; CuP cubitus posterior; IRxx supplementary longitudinal veins between branches of RP; MAa anterior branch of media anterior; MAb posterior branch of media anterior; MP media posterior; Mspl supplementary vein in postdiscoidal area; RA radius anterior; RP radius posterior, Rspl supplementary vein in area between IR2 and RP3/4; PsA anterior branch of AA; ScP subcostal posterior.

All taxonomic acts established in the present work have been registered in ZooBank LSID (see below), together with the electronic publication under urn:lsid:zoobank.org:pub:BAB8D0A7-2C3B-4E1C-8D97-1A5603BD42C7

Systematic palaeontology

Order Odonata Fabricius, 1793

Suborder Anisoptera Selys-Longchamps (in Selys-Longchamps & Hagen, 1854)

Clade Petalurida Bechly, 1996

Family Protolindeniiidae Handlirsch, 1906

Genus *Protolindenia* Deichmüller, 1886

Type species. *Protolindenia antiqua* (Vander Linden, 1827) **comb. nov.** *Protolindenia wittei* (Geibel, 1860) is a junior synonym of *P. antiqua* (Vander Linden, 1827).

Other species. *Protolindenia viohli* Nel, Bechly & Martínez-Delclòs, 2001.

Protolindenia antiqua (Vander Linden, 1827) **comb. nov.**

(*Aeshna antiqua* Vander Linden, 1827)

(Figs 1, 2)

1827 *Aeshna antiqua* Vander Linden, p. 250, unnumbered fig.

1850 *Aeshna* [sic] *antiqua*; Hagen in de Selys-Longchamps, p. 362.

1856 *Ae.* [*Aeshna*] *antiqua*; Giebel, p. 279.

1862 *Aeshna* [sic] *antiqua*; Hagen, p. 107, 109, 112, 113, 136–137.

1890 *Uropetala antiqua*; Kirby, p. 172.

1906 (? *Protolindenia*) *antiqua*; Handlirsch, p. 591.

1939 ? *Protolindenia antiqua*; Handlirsch, p. 152.

2001 *Aeshna* [sic] *antiqua*; Bechly *et al.*, p. 20.

2012a *Protolindenia?* *antiqua*, *nomen dubium*; Bechly, unnumbered page.

2012b *Protolindenia?* *antiqua* *nomen dubium*; Bechly, unnumbered page.

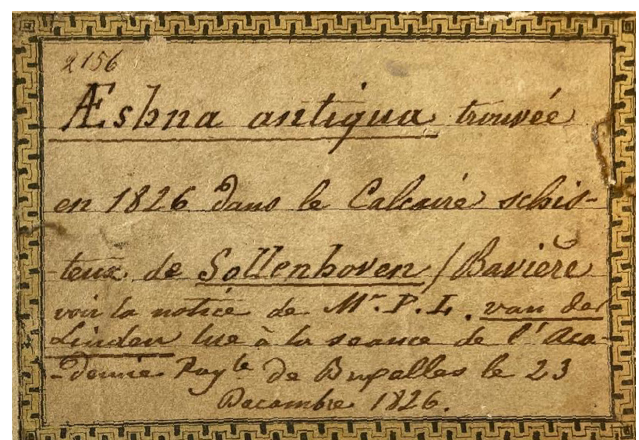


FIGURE 1. Original label associated with the type specimen of *Protolindenia antiqua* (Vander Linden, 1827) **comb. nov.**

Type material. Holotype (by monotypy) PAULg 2156 (a nearly complete adult, with right forewing broken and

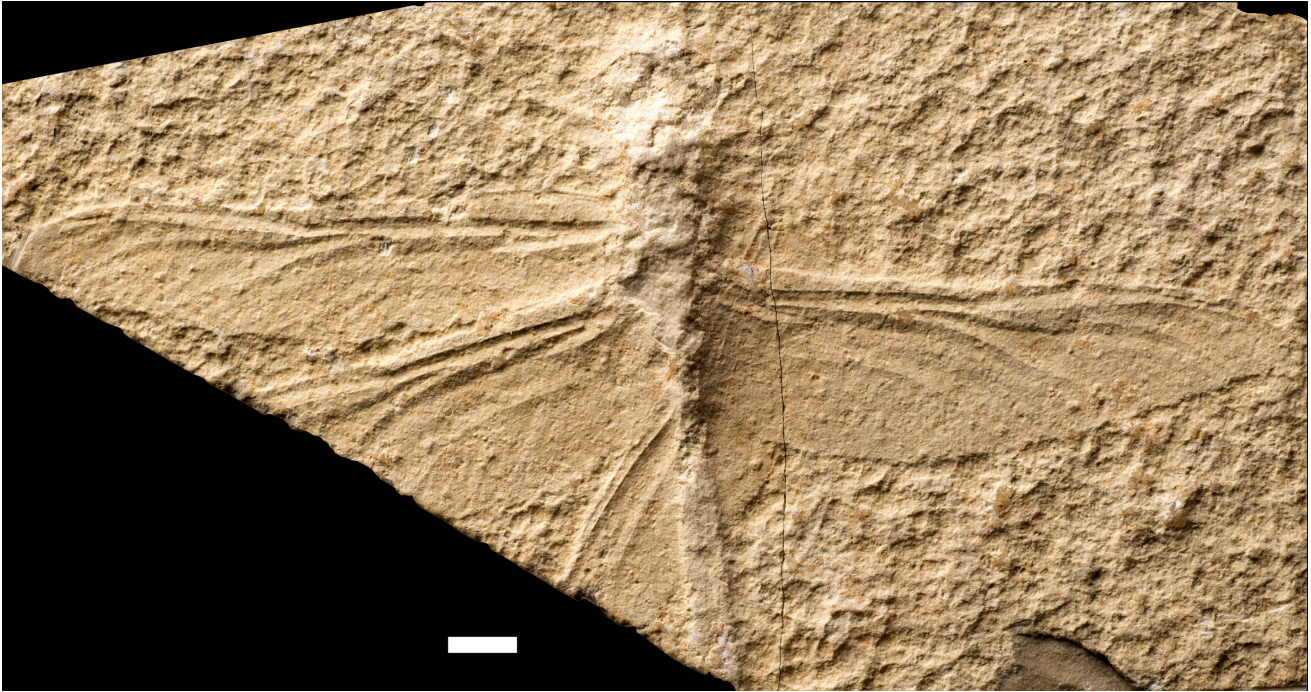


FIGURE 2. *Protolindenia antiqua* (Vander Linden, 1827) **comb. nov.**, holotype PAULg 2156. Photograph of hind wing base. Scale bar = 2 mm.

overlapping right hind wing, apex of abdomen missing), collected by Jean-François Vander Maelen, probably in 1825 (see above).

Type locality and horizon. Solnhofen, southern Franconian Alb, Bavaria, Germany, Late Jurassic, Malm ζ 2b ('oberer Weißjura'), early Tithonian, *Hybonotum* Zone, Solnhofen Lithographic Limestone (Altmühltal Formation; see Niebuhr & Pürner, 2014).

Description. No trace of coloration on body or wings, wings probably originally hyaline; head very poorly preserved; thorax *ca.* 10.7 mm long, 4.6 mm wide; abdomen 3.2 mm wide.

Forewing 44.6 mm long, 10.0 mm wide; distance from nodus to arculus 18.2 mm, to pterostigma *ca.* 12.5 mm; Ax1 and secondary antenodal crossveins not discernable; Ax2 just basally of level of distal angle of discoidal cell; sectors of arculus distinctly separated; hypertriangle free, rather short; discoidal triangle nearly equilateral, three-celled; postdiscoidal area not especially widened distad; no Mspl; no pseudo-ScP distally of nodus; base of RP2 aligned with subnodus; RP2 and IR2 slightly diverging and weakly curved; one row of cells between RP2 and IR2 in basal part but two to three rows in distal half; area between RP1 and RP2 basally of pterostigma narrow but with two rows of cells in its distal part; IR1 present; no Rspl; RP3/4 and MA with a weak curve and with space between them widened in distal part, pterostigma elongate; oblique pterostigmal brace probably one cell

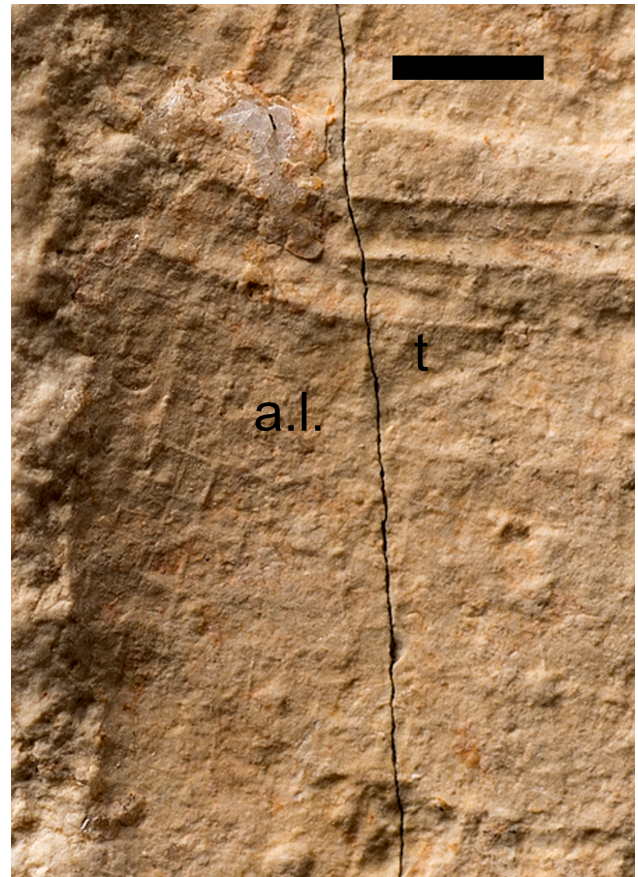


FIGURE 3. *Protolindenia antiqua* (Vander Linden, 1827) **comb. nov.**, holotype PAULg 2156. Photograph of habitus. Scale bar = 5 mm.

basally of basal side of pterostigma; postnodal crossveins not well preserved; space between C and RA distally of pterostigma rather short; one row of cells between MP and CuAa, with a narrowing of area between these veins before widening distally; cubito-anal area broad, with four rows of cells between CuAa and posterior wing margin; CuAa with five posterior veins below IR2; distinct pseudo-anal PsA present.

Hind wing venation similar to that of forewing, except in anal and cubito-anal areas, wing 42.1 mm long, 12.8 mm wide; distance from nodus to arculus 15.3 mm, to pterostigma *ca.* 13.2 mm; pterostigmal brace oblique, basal to pterostigma; discoidal triangle elongate; postdiscoidal area with three rows of cells distal of discoidal triangle; anal loop well-defined, posteriorly close, with four cells; anal area broad with five rows of cells below anal loop; cubito-anal area broad.

Discussion

The fossil fits quite well with the original figure of Vander Linden (1827), with the right forewing broken and overlapping the hind wing and distal part of abdomen missing. The wing venation of the holotype is relatively well-preserved showing essential structures to define the relationships of '*Aeshna*' *antiqua*. Due to the rather large size of this dragonfly, few genera are potential candidates for its placement, *viz.*, the aeshnopteran families Cymatophlebiidae and Mesuropetalidae, and the petalurodean family Protolindeniidae. A position in the Cymatophlebiidae is unlikely because of the absence of a well-defined vein Rspl. The Mesuropetalidae have the hind wing anal loop longitudinally elongate, vs as long as broad in '*Aeshna*' *antiqua* (Bechly *et al.*, 2001). Overall, the Aeshnoptera are characterized by the veins RP1 and RP2 closely parallel distal of the subnodus with one row of cells in-between, while the area between these veins is broadened in '*Aeshna*' *antiqua*.

Nel *et al.* (2001) proposed the following diagnosis for the Protolindeniidae, for which the type of '*Aeshna*' *antiqua* shows several: 'oblique pterostigmal brace present and basally recessed well-basal of pterostigma (visible); area between costal margin and RA, distal of pterostigma, elongate and crossed by many veins (visible); forewing discoidal triangle not transverse but nevertheless broad (visible) and three-celled (not visible); hind wing discoidal triangle longitudinal elongate and two- or three-celled (visible); well-defined subtriangles on all wings, those of forewings being three-celled but those of hind wings unicellular (visible); anal loop usually posteriorly open and small (3–4 cells) (in our fossil, the anal loop is 3–4 celled but posteriorly close); no distinct

veins Rspl and Mspl (visible); two oblique crossveins 'O' (not visible); two primary antenodals stronger than the secondaries, separated by two or three secondaries (not visible); arculus nearer Ax1 than Ax2 (not visible); Ax2 basal of distal angle of discoidal triangle (not visible); IR1 very long and straight and originating well basal of pterostigma [visible], below pterostigmal brace; MA and RP3/4 closely parallel and undulate near posterior margin (visible); IR2 and RP2 relatively straight and closely parallel, area between them being narrowed distally (visible); CuA divided into five to seven parallel posterior branches (visible); distinct pseudo-anal PsA present in forewing (visible). The preservation does not allow to see many of the crossveins, rendering uncertain the state of some characters. Nevertheless, this specimen fits well in the Protolindeniidae. This family comprises the two genera *Protolindenia* and *Austroprotolindenia* Beattie & Nel, 2012 (Australia). *Austroprotolindenia* has no IR1 and no pseudo-IR1, vs our fossil has a distinct IR1 (Beattie & Nel, 2012; Nel *et al.*, 2017). *Protolindenia* currently comprises two species from the Jurassic of Bavaria, *P. wittei* and *P. viohli*.

Protolindenia viohli is characterized as follows: hind wing pterostigmal brace completely reduced; forewing pterostigmal brace only one cell basal of pterostigma and not oblique; forewing subdiscoidal triangle unicellular, instead of being three-celled in *P. wittei*; the anal loop seems to be posteriorly better closed, even though this last character is rather variable in *P. wittei* (Nel *et al.*, 2001). Our fossil has a hind wing pterostigmal brace and its forewing subdiscoidal triangle is three-celled, excluding an attribution to *P. viohli*.

The wings' sizes are compatible with those of the two species of *Protolindenia* (hind wing 42.1 mm long). The hind wing discoidal cell is posteriorly well close, but this character is rather variable in *P. wittei*, and specimen 1965 IV of the Museum of Munich shows a similar anal loop (Nel *et al.*, 1998: fig. 24). Thus, we consider that the holotype of '*Aeshna*' *antiqua* belongs to the same species as *P. wittei*. It is necessary to put '*Aeshna*' *antiqua* in the genus *Protolindenia*, and, as it was described before *P. wittei*, it is necessary to synonymize *P. wittei* with *Protolindenia antiqua* (Vander Linden, 1827).

Conclusion

The rediscovery of the holotype (by monotypy) of '*Aeshna*' *antiqua* Vander Linden, 1827, long considered *nomen dubium* (*e.g.*, Bechly, 2012a, 2012b), sheds new light on the first insect species to be described from the famous Solnhofen Konservat-Lagerstätte. The reassessment of Vander Linden (1827)'s species clearly demonstrates that

Protolindenia wittei (Giebel, 1860) has to be considered a junior synonym of the former taxon. Therefore, '*Aeshna antiqua*' is the type species of the genus *Protolindenia* Deichmüller, 1886.

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