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A new genus of hawker dragonfly (Odonata: Anisoptera: Aeshnidae) from the Early Eocene Fur Formation of Denmark

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Abstract

A new genus and species of fossil hawker dragonfly, *Parabaissaeshna ejerslevense* **gen. et sp. nov.** (Aeshninae: Allopetaliini), is described from the Early Eocene Fur Formation (Mo-clay) of the island of Mors, northern Denmark. Its position among traditional "gomphaeschnine" dragonflies is discussed, and it is attributed to the tribe Allopetaliini as close relative to the Cretaceous genus *Baissaeshna*, documenting the survival of this lineage through the K-Pg mass extinction. The Recent genus *Boyeria* and the Eocene genus *Anglogomphaeschna* are also transferred to Allopetaliini.

Key words: fossil insect, Paleogene, Fur Formation, Gomphaeschninae, Allopetaliini

Introduction

Together with the insect fauna from the Late Paleocene Maíz Gordo Formation in Argentina (Petrulevicius *et al.* 1999), the fossil insects from the Early Eocene Ølst Formation and Fur Formation (Mo-clay) from the Limfjord area in Denmark belong to the oldest known fossil insects from the Paleogene (together with the even older fossil insects from Menat in France). Very well-preserved fossils of more than 200 species from 15 insect orders (Willmann 1990) have been found in these marine diatomitic sediments (Bonde 1979; Willumsen 2004; Rasmussen *et al.* 2016), including a lot of fossil damselflies (esp. Calopterygoidea) and dragonflies (esp. Gomphaeschnidae). Larsson (1975) reported 39 specimens and Rust (1999) studied 70 specimens of fossil odonates from the western Limfjord area. However, the fossil Anisoptera are much rarer than the Zygoptera (of which Petrulevičius *et al.* 2007 described three further specimens). Accordingly, Rust (1999) did only report 5 specimens of Anisoptera, of which Madsen & Nel (1997) described two species of the genus *Gomphaeschna*, revised by Bechly *et al.* (2001). Bechly (2005) described another specimen as new corduliid genus *Molercordulia*. Here we describe a new aeshnid genus and species from the Fur Formation, based on a perfectly preserved isolated forewing.

Methods

The macro photograph was made with a Nikon D7000 and a macro lens. With this photo as template the drawing was digitally made with Adobe Photoshop CC2018® imaging software on a MacBook Pro.

The used classification of odonates is mainly based on Bechly (1996, 2002) and Dijkstra *et al*. (2013). The terminology of odonate wing venation is based on Riek & Kukalová-Peck (1984), as modified by Nel *et al.* (1993) and Bechly (1996).

Abbreviations

C = Costal vein
ScP = Subcostal vein (Subcosta posterior)
RA = Radius anterior vein

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RP = Radius posterior vein
IR = Interradius vein
MA = Media anterior vein
MP = Media posterior vein
CuA = Cubitus anterior vein
CuP = cubital crossing (= anal crossing)
Ax = primary antenodal crossveins

Systematic Paleontology

Class Insecta Linné, 1758

Order Odonata Fabricius, 1793

Suborder Anisoptera Selys, 1854

Family Aeshnidae Leach, 1815

Subfamily Aeshninae Leach, 1815

Tribe Allopetaliini Cockerell, 1913

Parabaissaeshna gen. nov.

Type species. *P. ejerslevense* sp. nov. by monotypy.

Etymology. Named after its similarity and relationship to the Cretaceous aeshnid genus *Baissaeshna*.

Diagnosis. This new genus is distinguished from all other fossil and recent genera within Aeshnidae by the following combination of forewing characters: basal space free; no 'cordulegastrid gap'; only one lestine oblique vein a single cell distal of subnodus; pterostigma long, covering six cells; two rows of cells between RA and RP1 basal of pterostigma; very distinct pseudo-IR1 originating beneath middle of pterostigma, with three rows of cells between it and RP1 and RP2 respectively; IR2 unforked; midfork and triangle separated by six antefurcal cells; Rspl parallel to IR2 and Mspl parallel to MA with two rows of cells between these vein pairs respectively; two rows of cells in posttrigonal space close to triangle; no aeshnid bulla of MA developed; hypertriangle divided into five cells, triangle divided into seven cells, and subtriangle divided into two cells (this pattern probably is an autapomorphy of this new genus).

Parabaissaeshna ejerslevense sp. nov.

Figures 1–2

Holotype. Isolated complete forewing of a dragonfly with collection no. MGUH 33076, deposited in the type collection of the Natural History Museum of Denmark, University of Copenhagen in Copenhagen (Denmark). The specimen was discovered by the amateur fossil collectors Frank Pedersen and Viggo Pedersen, Mors, and declared as Danekræ fossil trove DK 792.

Type locality and horizon. Mo-clay quarry near the village Ejerslev (56.93° N, 8.91° E), northern island of Mors, western Limfjord area, N. Jutland, Denmark. Calcareous concretion approximately 2 m above Ash layer -11 in the diatomites of the upper part of the Knudeklint Member, Fur Formation.

Stratigraphy. Dinoflagellate Zone 7 (corresponding to the acme of *Deflandrea oesbisfeldensis*) of Heilmann-Clausen (1985), earliest Ypresian, Early Eocene, Paleogene, ca. 56.0-54.5 million years. The Early Eocene age of the Fur Formation was recently established due to the presence of the Paleocene-Eocene Thermal Maximum (PETM) in the Stolleklint clay of the Ølst Formation, which is placed stratigraphically immediately below the Fur Formation (Heilmann-Clausen & Schmitz 2000; Schoon *et al.* 2013).

Etymology. A noun in the genitive case, named after the place of origin.

Diagnosis. Same as genus since monotypic.

Description of holotype (Figures 1–2). Well-preserved and complete isolated forewing of a hawker dragonfly of unknown sex. Total length 45.0 mm, max. width 10.4 mm. 4 secondary antenodal crossveins between the primary antenodal crossveins Ax1 and Ax2; 22 and 18 non-aligned secondary antenodal crossveins present distal of Ax2 in both rows respectively. Space between RA and RP basal of subnodus regularly crossed by 18 antesubnodal crossveins (no cordulegastrid gap of antesubnodals near subnodus). Nodus at 48.6% of wing length; nodal veinlet short and perpendicular; subnodal veinlet oblique. About 14 postnodal crossveins non-aligned with the 19 postsubnodal crossveins beneath them; no 'libellulid gap' of postsubnodal crossveins near subnodus. Pterostigma elongate, elongate (covering 6 cells), with oblique sides and broadened margins; oblique and strong stigmal brace vein aligned with anterior margin of pterostigma; about six crossveins between C and RA distal of pterostigma. Primary IR1 not developed; secondary IR1 originating beneath middle of pterostigma with 3 rows of cells between it and RP1, and three rows of cells between it and RP2; RP1 and RP2 basally parallel (2 rows of cells between them) and distally divergent with 3-9 rows of cells between them; RP2 originates at subnodus; RP2 undulating; only one lestine oblique vein between RP2 and IR2, a single cell distal of subnodus. IR2 originating on RP1/2, and not forked; space between RP2 and IR2 distally widened with 2-7 (mostly four) rows of cells between them. Rspl well defined, parallel to IR2 with two rows of cells between them; about 5 intercalary veins originating from Rspl. Midfork six cells distal of triangle; 13 antefurcal crossveins between RP and MA. RP3/4 and MA weakly undulate and parallel, with two rows of cells between them distally; no bulged 'aeshnid bulla' between MA and RP3/4. Posttrigonal area between MA and MP with two rows of cells near the triangle; trigonal planate well defined, originating at a slight kink on the distal side (MAb) of triangle; Mspl well defined, parallel to MA, with two rows of cells between them. Space between MP and CuA narrow; MP and CuA reaching far beyond level of nodus. CuA with 7-8 posterior branches; cubital field max. 5 cells in width. Anal field with two rows of cells. Arculus complete (closed) and broken (kinked), situated midway between Ax1 and Ax2. Hypertriangle long and narrow, divided by 4 crossveins. Discoidal triangle elongate and divided into seven cells. Subtriangle divided into 2 cells. Between CuP-crossing (= 'anal crossing') and basal subdiscoidal vein there are two crossveins. Basal space free. Wing hyaline without trace of color pattern, except for the dark pterostigma.

FIGURE 1. Photograph of holotype no. MGUH 33076 of *Parabaissaeshna ejerslevense* gen. et sp. nov. Scale bar = 10 mm.

Discussion

The following combination of derived forewing characters proves that this anisopteran fossil belongs within the family Aeshnidae (*sensu* Djikstra *et al.* 2013): RP1 and RP2 parallel till pterostigma; RP2 strongly undulate and not parallel to IR2; Rspl and Mspl present; triangle elongate; trigonal planate present. It can be attributed to the crown group because of the absence of the second (distal) lestine oblique vein, and the well-defined (non-zigzagged) Mspl.

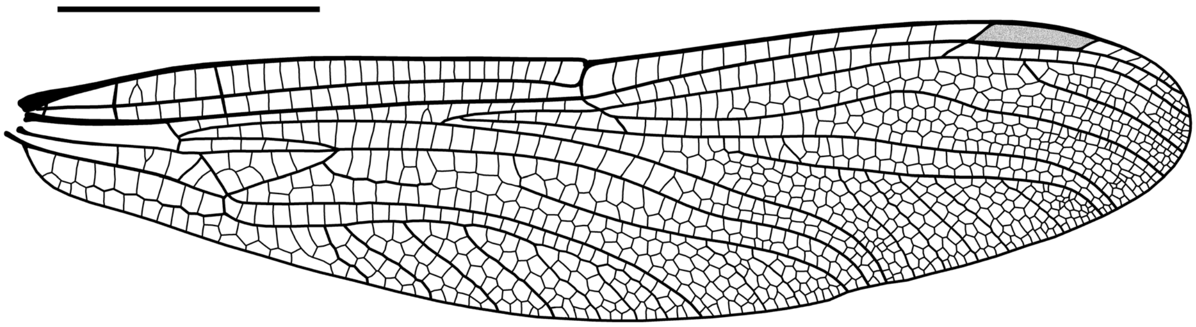

FIGURE 2. Drawing of holotype no. MGUH 33076 of *Parabaissaeshna ejerslevense* gen. et sp. nov. Scale bar = 10 mm.

The new fossil taxon has a relatively rare combination of relatively plesiomorphic characters that precludes an attribution to the more derived subgroups within Aeshninae, such as Rspl and Mspl parallel to IR2 and MA respectively (not strongly curved, but with two rows of cells between Rspl and IR2 and between Mspl and MA), IR2 unforked, and no aeshnid bulla of MA developed (Bechly *et al.* 2001).

There are only four subgroups of aeshnids that show this combination of characters, viz. Gomphaeschninae (especially the Recent genera *Linaeschna* Martin, 1908 and *Oligoaeschna* Selys, 1889 as well as the fossil genus *Anglogomphaeschna* Nel & Fleck, 2014), Allopetaliini (including the Recent genus *Allopetalia* Selys, 1873, and maybe the fossil genus *Baissaeshna* Pritykina, 1977), Oplonaeschnini (including the Recent genera *Oplonaeschna* Selys, 1883 and *Basiaeschna* Selys, 1883, as well as the fossil genera *Oligaeschna* Piton & Théobald, 1939, *Huncoaeshna* Petrulevičius et al., 2010, and *Kvacekia* Prokop & Nel, 2002, and the Recent genus *Boyeria* McLachlan, 1896 (especially the fossil species "*Boyeria*" *europeae* (Nel et al., 1996) that was originally referred to the genus *Allopetalia*). All these genera were originally classified in the same subfamily Gomphaeschninae (e.g., Tillyard & Fraser 1940; Wighton & Wilson 1986; Bridges 1994; Nel *et al.* 1994), but later shown to belong to different clades within Aeshnidae. However, the phylogenetic analysis of fossil evidence and wing venation (Bechly 1996, 2002; Bechly *et al.* 2001), comparative recent morphology of genitalia (von Ellenrieder 2002; Peters & Theischinger 2007), and genetic evidence (Carle *et al.* 2015) lead to incongruent results concerning the placement of the mentioned four subgroups or even their generic composition. Therefore, the internal phylogeny of Aeshnidae is still far from established.

Nevertheless, the presence of two rows of cells between RA and RP1 even far basal of the pterostigma is a 'primitive' character state that is only shared by the new fossil with the genera *Allopetalia*, *Baissaeshna* (especially *B. zherikhini* Bechly et al., 2001), *Anglogomphaeschna*, and *Boyeria*. Of these four genera only *Baissaeshna* shares with *Parabaissaeshna* gen. nov. a very distinct pseudo-IR1 that originates beneath the middle of the pterostigma, but it differs in the presence of three rows of cells in the basal posttrigonal area.

The new fossil is also very similar to the fossil genus *Anglogomphaeschna* from the Late Eocene of the Isle of Wight (Nel & Fleck 2014), which has the apex with pterostigma and IR1 not preserved, and from which the new fossil mainly differs by the presence of accessory cubito-anal crossveins and the absence of a 'cordulegastrid gap' (however, the latter is only weakly developed in *Anglogomphaeschna*). The presence of two rows of cells between RA and RP1 basal of the pterostigma makes an attribution of *Anglogomphaeschna* to Gomphaeschninae highly unlikely, so that this genus is here transferred to Allopetaliini.

Finally, the new fossil is very similar to the preserved part of the wing of *Boyeria europeae* from the Miocene of France, from which it only differs in the higher number of cells between midfork and triangle, the presence of more rows of cells between the distal parts of RP2 and IR2, and the slightly undulate RP3/4 and MAa. It is very unfortunate that the basal half of the wing of the type of *B. europeae* is not preserved, because it is in this area of the wing, where the generic differences between *Boyeria* and other *Allopetaliini* are found. Nevertheless, a second specimen was described by Nel *et al.* (1997) in which the wing base is preserved showing a crossed median area as in the extant *Boyeria*. It is the reason why Nel *et al.* (1997) transferred this taxon into *Boyeria*. It is not surprising that *B. europeae* was originally described in the genus *Allopetalia*, and the studies by De Marmels (2000) and von

Ellenrieder (2002) revealed similarities in larval and genital morphology between the two genera *Boyeria* and *Allopetalia*. For this reason the genus *Boyeria* is here also transferred to Allopetaliini, which are thus now comprising five known genera of hawker dragonflies with two rows of cells between RA and RP1 as diagnostic character, otherwise only present in some Telephlebiinae. The crossed median space of *Boyeria* clearly represents an autapomorphy of this genus, so that this difference cannot be considered as valid evidence against an allopetaliine relationship.

Conclusions

Because of the rarity of Paleocene and Early Eocene odonate fossils and the stratigraphic proximity to the important K-Pg boundary, this fossil represents an interesting contribution to our knowledge of the Paleogene odonate fauna of Europe, and emphasizes the diversity of basal hawker dragonflies in the Cretaceous and Paleogene, before the diversification of the "higher" aeshnines. The survival of a close relative or even descendent of the Cretaceous genus *Baissaeshna* to the Paleogene is a further example of Mesozoic taxa that made it through the major mass extinction at the K-Pg boundary.

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