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Stolleagrion foghnielseni (Odonata, Cephalozygoptera, Dysagrionidae) gen. et sp. nov.: a new odonatan from the PETM recovery phase of the earliest Ypresian Fur Formation, Denmark

THOMAS J. SIMONSEN[1,*], S. BRUCE ARCHIBALD[2,3,*], JAN A. RASMUSSEN[4,5], RENÉ L. SYLVESTERSEN[6], KENT OLSEN[7] & JESSICA L. WARE[8]

[1]*Department of Research and Collections, Natural History Museum Aarhus, Wilhelm Meyers Allé 10, Aarhus, DK-8000 Aarhus C, Denmark.*
[*]*corresponding author, t.simonsen@nathist.dk; https://orcid.org/0000-0001-9857-9564*
[2]*Beaty Biodiversity Museum, University of British Columbia, Vancouver, British Columbia, Canada.*
https://orcid.org/0000-0002-4397-2497
[3]*Museum of Comparative Zoology, 26 Oxford Street, Cambridge, Massachusetts, 02138, United States of America.*
**corresponding author, sba48@sfu.ca*
[4]*Museum Mors, Skarrehagevej 8, DK-7950 Nykøbing Mors, Denmark.*
https://orcid.org/0000-0003-0520-9148
[5]*Natural History Museum of Denmark, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark.*
jan.rasmussen@museummors.dk
[6]*Fur Museum, Nederby 28, DK-7884 Fur, Denmark.*
RLSY@museumsalling.dk; https://orcid.org/0000-0002-1946-4716
[7]*Department of Research and Collections, Natural History Museum Aarhus, Wilhelm Meyers Allé 10, Aarhus, DK-8000 Aarhus C, Denmark.*
kent@molslab.dk; https://orcid.org/0000-0002-5624-128X
[8]*Division of Invertebrate Zoology, American Museum of Natural History, NY, NY, 10024USA.*
jware@amnh.org; https://orcid.org/0000-0002-4066-7681

Abstract

We describe the new genus and species *Stolleagrion foghnielseni* **n. gen. et sp.** from the Fur Formation in northwestern Denmark based on a single fossil wing. This is the first odonatan described from the earliest part of the PETM recovery phase of the early Eocene. A combination of nine wing character states are considered to be diagnostic of the Dysagrionidae Cockrell only together with the cephalozygopteran head; however, the combination of these nine plus the presence of Ax0 is also diagnostic without the head. By this, we assign *Stolleagrion foghnielseni* to the Dysagrionidae and reassess the position of other odonates previously treated as *cf*. Dysagrionidae.

Key words: Odonata, Cephalozygoptera, Dysagrionidae, Fur Formation, PETM recovery phase, Ax0

Introduction

In the western part of the Limfjord area northwestern Denmark, the lowermost part of the Ypresian succession consists of the Fur Formation and the underlying Stolleklint clay of the Ølst Formation. Both formations are well known for their rich record of insect fossils (*e.g*., Henriksen 1922, Rust 1999, Petrulevičius *et al*. 2008, Madsen & Rasmussen 2021). Its Odonata fauna has especially received attention in recent years (*e.g*., Petrulevičius *et al*. 2008, Rust *et al*. 2008, Zessin 2011, Simonsen *et al*. 2022, Archibald *et al*. 2023 and references therein).

The Stolleklint clay and the Fur Formation not only represent slightly different times, but also very different paleoclimatic conditions (Pedersen *et al*. 2012, Madsen & Rasmussen 2021). Therefore, it seems reasonable to assume that these units preserved different communities. Within Odonata, the two fossils of *Danowhetaksa* Simonsen *et al*. (two species: Simonsen *et al*. 2022) were found below ash layer -33 in the Stolleklint clay, while *Furagrion* Petrulevičius *et al*. is known from about twenty fossils (two species: Archibald *et al*. 2023) restricted to the middle Fur Formation between ash layers -15 and +30.

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Here, we describe a new genus and species of Odonata from the PETM recovery phase in the lowermost part of the Fur Formation (Stokke *et al*. 2020) between ash layers -29 and -24 and treat it at the family and suborder level based on a reassessment of the diagnostic usefulness of the wing character states that it possesses.

Material and methods

We examine a single, nearly complete wing, part and counterpart, from a striated concretion block from the Fur Formation in northwest Denmark using a Wild Heerbrugg M5A stereomicroscope. The fossil was photographed with a Canon 5DII camera and a Canon EF 100 mm Macro lens.

Wing venation terminology follows Garrison *et al.* (2010). We use the following abbreviations: A, anal vein; ar, arculus; Ax0, antenodal crossvein 0; Ax1, antenodal crossvein 1; Ax2, antenodal crossvein 2; CuA, cubitus anterior; IR1, intercalary vein 1; IR2, intercalary vein 2; MA, media anterior; MP, media posterior; n, nodus; pt, pterostigma; Q, quadrangle; RP1, radius posterior 1; RP2, radius posterior 2; RP3-4, radius posterior 3+4; sn, subnodus. By linear we mean that a vein is not zigzagged.

Geological setting

The fossil was found at the Stolleklint outcrop situated on the north coast of Fur Island in the western Limfjord area of Denmark. This locality is dominated by the early Eocene (Ypresian) Stolleklint clay, an informal unit comprised of the lowermost Ølst Formation and the overlying clayey marine diatomite of the Fur Formation together spanning approximately 1.0–1.4 million years (Jones *et al*. 2023). Both units crop out in the western Limfjord area of Denmark and are especially common in beautifully exposed coastal cliffs on the islands of Fur and Mors (Pedersen & Surlyk 1983, Heilmann-Clausen 1995). The 60 m thick Fur Formation contains more than 200 distinct ash layers up to 18 cm thick, divided into a ‘negative’ (layers -39 to -1) and ‘positive’ ash series (layers +1 to +140) by Bøggild (1918). They are interpreted as derived from explosive North Atlantic Igneous Province (NAIP) volcanism (Larsen *et al*. 2003). The distinct *c.* 14 cm thick ash layer -33 is usually regarded as situated close to the boundary between the Fur and Ølst Formations in the Limfjord area (Heilmann-Clausen *et al.* 1985, Heilmann-Clausen 1995) although Pedersen & Surlyk (1983) also included the diatom-poor sedimentary succession between the ash layers -39 and -33 in the Fur Formation.

The vast majority of the Stolleklint clay was deposited during the Paleocene-Eocene Thermal Maximum (PETM) and reaches an estimated thickness of 24 m at Fur (Stokke *et al*. 2020, Jones *et al*. 2023). The PETM was initiated by a rapid global warming where the temperature increased by 5–8 °C in less than 10 kyr (Zachos *et al*. 2001) and is estimated to have lasted 170 kyr (Röhl *et al*. 2007). Stokke *et al*. (2020) estimated that during the PETM the sea surface temperature (SST) in the western Limfjord area of Denmark reached close to 30 °C for the upper part of the Stolleklint clay after an increase in temperature of minimum 7–10 °C. At the end of the PETM main phase, the North Sea was isolated from the North Atlantic in less than 12 kyr by NAIP thermal uplift closing the English Channel (Jones *et al*. 2023).

Based on dinoflagellate cyst assemblages (Heilmann-Clausen 1994), delta ^{13}C values (Jones *et al*. 2019) and TEX_{86} data (Stokke *et al*. 2020), it has been suggested that the earliest part of the succeeding clayey diatomites of the Fur Formation represent the succeeding PETM recovery phase, when SST decreased by more than 10 °C (Stokke *et al*. 2020) over an estimated 160 kyr (Jones *et al*. 2023). Thus, the recovery phase largely covers the slightly more than 5 m thick succession from ash layer -33 to a level between ash layer -21a and -19 and includes the level where the odonatan described here was found.

Systematic paleontology

Order Odonata

Suborder Chephalozygoptera Archibald, Cannings & Erickson

Family Dysagrionidae Cockrell

Genus *Stolleagrion* Simonsen, Archibald & Ware, new genus
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Diagnosis. *Stolleagrion* is most easily distinguished from other Dysagrionidae by the combination of: pterostigma long, narrow (> 5.5x longer than wide) and RP1 strongly curved distad pterostigma.

Type and included species. The type species *Stolleagrion foghnielseni* sp. nov., here designated, is the only known species.

Etymology. The genus name is formed from the prefix 'Stolle-' referring to the type locality Stolleklint, and the suffix '-agrion', commonly used in Zygoptera and Cephalozygoptera genus names. Gender: neutral.

***Stolleagrion foghnielseni* Simonsen, Archibald & Ware, new species**
Figures 1–2
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Material. Holotype wing FUM-M 14257a, b, part and counterpart: the part is almost complete, with few sections missing; collected by René L. Sylvestersen, January 2017, Fur Stolleklint; deposited in the Fur Museum.

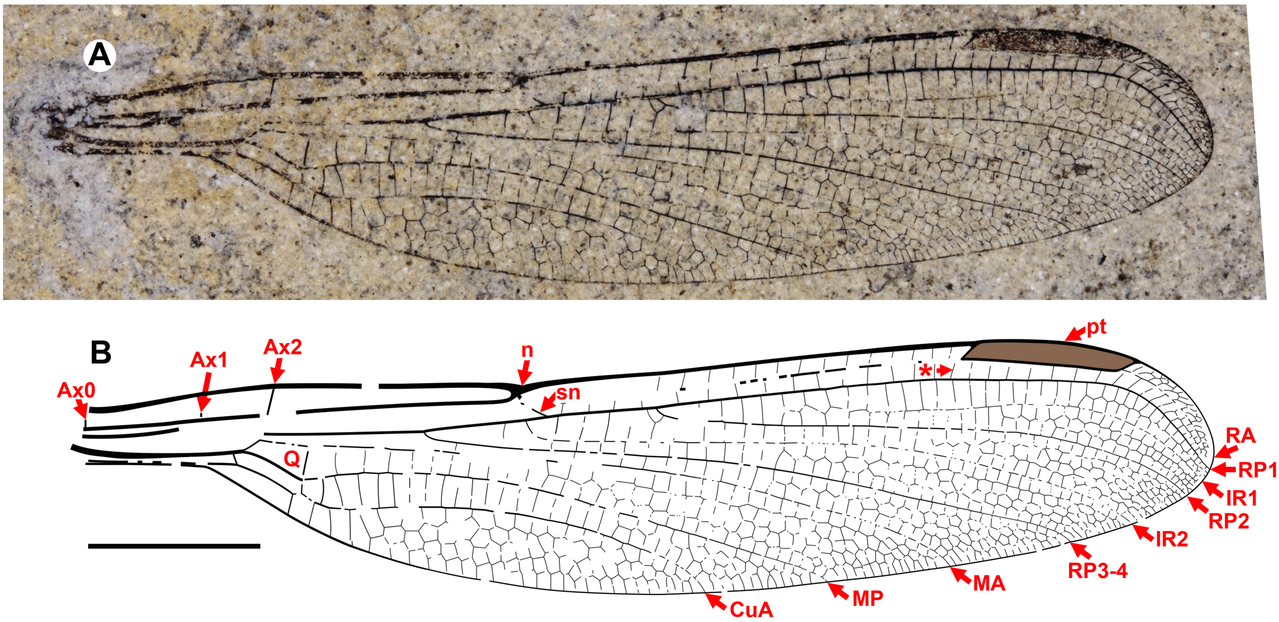

FIGURE 1. *Stolleagrion foghnielseni* n. sp. holotype wing (FUM-N-14257). A, photograph of the part; B, drawing from the part. See text for abbreviations. Scalebar is 5 mm.

Description. Holotype wing (Figs 1–2). Length, 32.8 mm; arculus to distal end of pterostigma, 24.9 mm; nodus to distal end of pterostigma, 17.6 mm; arculus to base of pterostigma, 20.3 mm; nodus to base of pterostigma, 13.0 mm; maximum width, 6.6 mm. Pterostigma dark, elongate: 4.7 mm long, *ca*. 5.6 times longer than wide, subtends 7.5 cells. Membrane hyaline. Ax0, Ax1 poorly preserved but confidently present (Fig. 2), Ax2 distinct, Ax0 appears not synsclerotised with wing base. Ax1 *ca*. 2/3 distance wing base to arculus; arculus aligned with Ax2. Quadrangle dysagrionoid in shape, *i.e.*, not more rectangular as in Eodysagrioninae Rust, Petrulevičius & Nel (*e.g.* Rust *et al.* 2008, fig. 1). Fourteen crossveins preserved in postnodal space (basal quarter not well preserved), 16 in postsubnodal space to pterostigma, at least three pairs aligned. Brace vein present, very weakly angled. RA only well-preserved distad pterostigma, strongly curved there, C-RA space two cells wide. RP1 well preserved, strongly curved distad pterostigma, RA–RP1 space two cells wide near apex. IR1 well preserved, zigzagged origin six cells distad origin of RP2, RP1–IR1 space three cells wide at margin. RP2 origin five cells distad nodus, abnormally small first cell basad RP2 origin formed by Y-branch of RP2–IR2 crossvein, IR1–RP2 space three cells wide at margin. IR2 origin half cell basad subnodus, linear, slightly curving distally, RP2–IR2 space at least 10 cells wide at margin. RP3-4 origin *ca*. 2/3 the distance from arculus to subnodus, linear, slightly curving distally, IR2–RP3-4 space at least 10 cells wide at margin. MA linear, slightly curving distally, RP3-4–MA space 16 cells wide at margin. MP linear, slightly curving distally, basal 1/3 subparallel to MA, then curving away gently, terminating beyond mid-wing, MA–MP space basally one cell wide, 15 cells wide at margin. CuA linear, basal 4/5 subparallel to MP, then curving away to wing margin, terminates *ca*. mid-wing, 3rd MP-CuA cross vein slightly oblique, MP-CuA space two cells wide from *ca*. 2/3 its length, widening to 12 cells at wing margin. CuA-A space well preserved, broad, 4–5 cells wide.

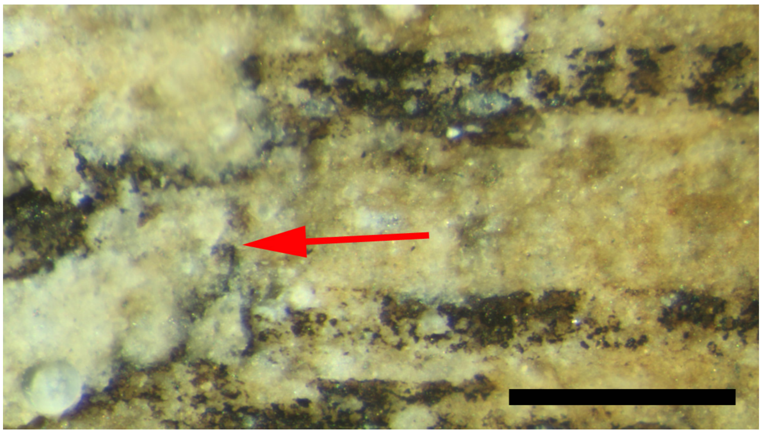

FIGURE 2. *Stolleagrion foghnielseni* n. sp. holotype wing (FUM-N-14257). Detail of wing base showing Ax0 (red arrow). Scalebar is 0.5 mm.

Diagnosis. As for the genus.

Deposit and age. Striated concretion between ash layers -29 and -24, Fur Formation, Stolleklint, Fur, Denmark; earliest Ypresian.

Etymology. The specific epithet is an eponym formed from the middle and surnames of Ole Fogh Nielsen, a Danish amateur entomologist and paleontologist, whose work (especially his books) have inspired Danish natural historians for decades.

The systematic position of *Stolleagrion*

"Cephalozygoptera bearing a normal nodus [Sieblosiidae: highly modified]" would be the most succinct diagnosis defining the Dysagrionidae concept. If the Whetwhetaksidae Archibald & Cannings are cephalozygopteran, then adding "and with an arculus positioned near Ax2 [Whetwhetaksidae: near Ax1]" would be all that is necessary to delimit the family. However, the great majority of fossil odonates are disarticulated wings, leaving assignment to Cephalozygoptera impossible without its defining head. This is further complicated by many or even all of the nine wing character states characteristic of the Dysagrionidae (Archibald *et al.* 2021) appearing convergently in Zygoptera and perhaps beyond (Archibald *et al*. 2023). Archibald *et al*. (2023) believed that this creates a problem that cannot be overcome, that these nine dysagrionoid character states can be only suggestive—even if at times strongly so—that a fossil wing belongs to the Dysagrionidae. They raised the possibility, however, that the presence of Ax0 as a tenth character state in combination with these might constitute a reliable wing diagnosis of the family.

We consider this to be the case, and, therefore, propose that the wings of Dysagrionidae may be confidently distinguished from those of other odonates by a combination of these ten wing character states: crossvein O is absent, the arculus is close to Ax2, it has a dysagrionoid quadrangle (see Archibald *et al*. 2021, 2023), the nodus is at more than a quarter wing length, CuP and AA are briefly free distad the petiole, RP3-4 originates *ca*. one to usually two thirds the length from arculus to subnodus, the antesubnodal space is without crossveins, the CuA–A space is expanded in the middle at least two cells wide, CuA ends on the posterior margin at or beyond mid-wing, and has an Ax0.

As the *S. foghnielseni* wing possesses all ten of these, we assign it to the Dysagrionidae, which then consists of *Congqingia* Zhang, *Dysagrion* Scudder, *Electrophenacolestes* Nel & Arillo, *Okanagrion* Archibald & Cannings, *Okanopteryx* Archibald & Cannings, *Primorilestes* Nel *et al*., *Phenacolestes* Cockerell, *Petrolestes* Cockerell, *Stolleagrion*, and *Tenebragrion* Bechly *et al*.

Challenges to the validity of Cephalozygoptera suggesting that its characteristic head shape is an artefact of preservation (Nel & Zheng 2021, Nel & Jouault 2022) have been addressed previously (Archibald & Cannings 2021, Archibald *et al*. 2023)—we refer to these publications for further discussion.

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