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Danolestes moelleri gen. et sp. nov., the first lestoid (Zygoptera: Odonata) from the early Ypresian Fur Formation of Denmark shows faunistic affinity to South America

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Abstract

We describe *Danolestes moelleri* **gen. et sp. nov.**, the first spreadwing damselfly (Odonata, Zygoptera, Lestoidea) known from the Danish earliest Eocene Fur Formation. The new taxon is placed in Lestoidea, and tentatively affiliated with *Priscalestes* and *Promegalestes*, two extinct genera known from Western Palearctic and South America respectively, highlighting the complex biogeographical affiliations of the Fur Formation biota. *D. moelleri* **gen. et sp. nov.** was preserved in a 'striated concretion' block from the Paleocene-Eocene Thermal Maximum (PETM) recovery phase. It is the second odonate and first zygopteran described from the PETM recovery phase of the Fur Formation.

Key words: Ypresian, Fur Formation, Odonata, Lestoidea

Introduction

The Lestoidea (Odonata, Zygoptera) is today a small superfamily of damselflies with less than 200 species in four families distributed across the globe except Antarctica and the Arctic (*e.g.*, Garrison *et al.*, 2010; Dijkstra *et al.*, 2013; Boudot & Kalkman, 2015; Simonsen *et al.*, 2022b). They inhabit most freshwater habitats, and some species have striking ecological specialization such as overwintering as adults (*e.g.*, Kalkman & Willigalla, 2015) or oviposition in soft-bark trees and bushes (*e.g.*, Boudot & Willigalla, 2015).

Our knowledge of fossil Lestoidea has especially increased over the past 30 years. Nel & Paicheler (1994) published a critical review of the then known fossils of the superfamily, listing 74 fossils, of which *ca*. 33% were of "uncertain systematic position". The family Sieblosiidae and a number of fossil taxa assigned to the Megapodagrionidae and Pseudolestidae have since been removed from the superfamily (Dijkstra *et al.*, 2014; Greenwalt & Bechly, 2014; Archibald *et al.*, 2021; Bybee *et al.*, 2021; Ware *et al.*, 2025). All Lestoidea *s. str.* assessed by Nel & Paicheler (1994) are from the Cenozoic Holarctic.

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Since Nel & Paicheler's (1994) seminal contribution, a number of lestoid fossils have been described from the Cretaceous (Jarzembowski *et al*., 1998; Vasilenko, 2005; Zheng *et al*., 2016; Huang *et al*., 2022), and Paleogene/Neogene (Nel *et al*., 1997; Nel & Jarzembowski, 1999; Petrulevičius & Nel, 2004; Wappler & Petrulevičius, 2007; Greenwalt & Bechly, 2014; Petrulevičius, 2018), including from South America (Petrulevičius & Nel 2004; Petrulevičius, 2018) and Southeast Asia (Zheng *et al*., 2016). In addition, the new extinct lestoid families Priscalestidae Wappler & Petrulevičius and Eolestidae Greenwalt & Bechly were named (Wappler & Petrulevičius, 2007; Greenwalt & Bechly, 2014), thus broadening their geographical and temporal distribution as well as the taxon concept. Perhaps surprisingly, there are no fossil lestoids known from the earliest Eocene Fur Formation of northern Denmark, which has from it a considerable number of odonates described (*e.g*., Rust *et al*., 2008; Bechly & Rasmussen, 2019; Simonsen *et al*.. 2022a, 2024a; Archibald *et al*., 2023).

Here we describe the first species of Lestoidea from the Fur Formation and discuss its relationship to other members of the superfamily, including its close affinity to *Promegalestes singularis* Petrulevičius & Nel from South America.

Material and methods

We examined a single, nearly complete wing (part and counterpart) preserved in a striated concretion block from the Paleocene-Eocene Thermal Maximum (PETM) recovery phase sediments of the earliest Ypresian Fur Formation in northwest Denmark. This (*ca*. 55 Myr) formation is world famous for the numerous, often very well -preserved, fossil insects, which number more than 20,000 (*e.g*., Rust, 1999; Pedersen *et al*., 2012; Madsen & Rasmussen, 2021). The fossil was photographed at the Fur Museum (FUM) with a Canon EOS 90D and a Canon EFs 60 mm f2.8 Macro lens.

Wing venation terminology follows Riek & Kukalová-Peck (1984) and Garrison *et al*. (2010). We use the following abbreviations: A, anal vein; ar, arculus; 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.

To test the systematic position of the fossil we describe here, we included it in the wing character dataset of Ware *et al*. (2025) and analysed its phylogenetic affinities as described therein using maximum likelihood as described in Ware *et al*. (2025) (the dataset is provided in Supplementary Material S1). We also added the lestoid genus *Priscalestes* Wappler & Petrulevičius, 2007 (Priscalestidae), while *Promegalestes* Petrulevičius & Nel, 2004 (family indet.), known only from the holotype, is too poorly preserved to score a meaningful number of characters. We further added the megapodagrionid genera *Allopodagrion* Förster, 1910 and *Sciotropis* Rácenis, 1959 (De Marmels, 2001) to test whether *Danolestes* **gen. nov.** could be associated with that group. We refer to Ware *et al*. (2025) for a full character list and methodological details. The distal angle of the quadrangle (see below) was measured in GIMP 2.10 based on the drawing in figure 2 by Petrulevičius & Nel (2004) for *P*. *singularis*, and the drawing in Figure 1 here for *D*. *moelleri* **gen. et sp. nov.**

Systematic palaeontology

Order Odonata Fabricius, 1793

Suborder Zygoptera Selys, 1854

Superfamily Lestoidea Calvert, 1901

Family uncertain

Genus *Danolestes* Simonsen, Archibald & Ware gen. nov.

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Type species. *Danolestes moelleri* Simonsen, Archibald & Ware **sp. nov**., here designated.

Etymology. The name is formed from the prefix 'Dano-' referring to Denmark, and the suffix '-*lestes*' referring to Lestoidea.

Diagnosis. Within the Lestoidea *Danolestes* **gen. nov.** is most similar to *Promegalestes* and *Priscalestes* with which it shares a very acute distal angle of the quadrangle; MP distinctly curved after its origin; vein 'O' slightly oblique; RP3-4 originates between arculus and subnodus, closer to subnodus; IR2 likely (see below) originates close to origin of RP3-4; most subnodal and postsubnodal crossveins aligned (few preserved in *Promegalestes*). *Danolestes* **gen. nov.** can be distinguished from these taxa by: MA weakly zigzagged in distal half (*Promegalestes* and *Priscalestes* not zigzagged); origin of RP2 eight cells from subnodus (*Promegalestes* four, poorly preserved in *Priscalestes*, but probably five); distance between subnodus and origin of RP2 >2 times distance between subnodus and origin of MA (<1.5 times in *Promegalestes* and *Priscalestes*). It can further be distinguished from *Promegalestes* by: distal angle of quadrangle more acute, *ca*. 22° (*Promegalestes* distinctly less acute, *ca*. 37°); and lacks intercalary vein between MA and RP3-4 (origin of which is preserved in *Promegalestes*). It can further be distinguished from *Priscalestes* by: intercalary vein between IR1 and RP2 present (missing in *Priscalestes*).

Danolestes moelleri Simonsen, Archibald & Ware sp. nov.

urn:lsid:zoobank.org:act:23290065-26C2-49B4-9A56-A55D669E4396
(Fig. 1)

Material. Holotype wing FUM-N 19441a, b, part and counterpart, part almost complete with few sections missing; collected by Claus Møller, July 2024, Fur Stolleklint; deposited in the Fur Museum (FUM), Fur Nederby, Denmark.

Etymology. An eponym formed from the surname of Claus Møller, who found the holotype.

Diagnosis. As for the genus.

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

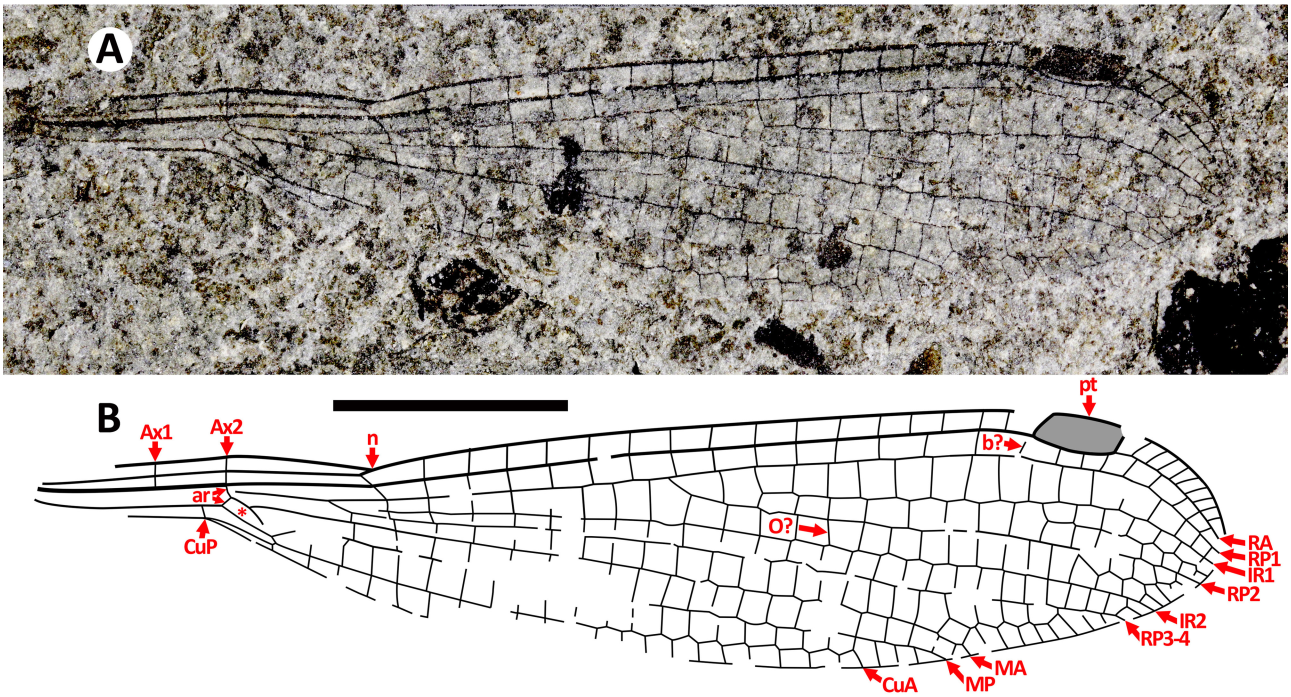

FIGURE 1. *Danolestes moelleri* **gen. et sp. nov.** holotype wing (FUM-N 19441). **A**, photograph of the part. **B**, drawing from the part and counterpart. See text for abbreviations. Scale bar = 5 mm.

Description. Holotype wing (Fig. 1). Length 25.1 mm; arculus to distal end of pterostigma, 19.6 mm; nodus to distal end of pterostigma, 16.7 mm; arculus to basal end of pterostigma, 17.6 mm; nodus to basal end of pterostigma, 14.7 mm; maximum width, 5.5 mm. Pterostigma dark, 3.0 mm long, 3.9 times longer than wide, subtends three cells. Membrane hyaline. Ax1 and Ax2 well preserved. Ax1 *ca*. 2/3 distance wing base to arculus, Ax2 aligned with arculus. Quadrangle lestoid type with distal vein of the discoidal cell MAb very oblique (Bechly, 1996) with the distal angle being *ca*. 22°. Subnodal space with 16 crossveins, postsubnodal space with 15, most aligned as pairs. Brace vein possibly present, very weakly angled. Costa weakly convex. RA well preserved, C-RA space one cell wide. RP1 well preserved, originating at arculus between RA and quadrangle, not adjacent to RA, RP1-IR1 space one cell wide. IR1 well preserved, zigzagged, origin two cells distad origin of RP2, IR1-RP2 space two cells wide at margin with a distinct intercalary vein present. RP2 origin 6.5 distad nodus, RP2-IR2 space probably 5 cells wide at margin. Slightly oblique crossvein 'O' present, 2.5 cells distad origin of RP2. A second oblique crossvein present, 4.5 cells distad origin of RP2. Origin of IR2 basad subnodus, either not preserved, probably originating close to origin of RP3-4 or as a stub not connected to RP3-4, directed toward origin of RP3-4. IR2 slightly zigzagged in *ca*. third quarter of wing, IR2-RP3-4 space two cells wide at margin. RP3-4 originates *ca*. 2/3 distance from arculus to subnodus, mostly linear, RP3-4-MA space nine cells wide at margin. MA mostly linear, but slightly zigzagged distally, slightly curved at margin, MA-MP space one cell wide at margin. MP strongly curved immediately after origin, probably linear basally, but poorly preserved, slightly zigzagged distally, MP-CuA space probably four cells wide at margin. CuA linear basally, zigzagged distally, CuA-A space one cell wide.

Discussion

Phylogenetic analysis

Our analysis does not recover Lestoidea as a monophyletic clade since *Hemiphlebia* Selys is excluded from it and the thaumatoneurid *Thaumatoneura* MacLachlan, 1897 included as sister to *Synlestes* in a clade we call the 'lestoid clade', which also comprises *Phylolestes* Christiansen, *Perilestes* Hagen, *Perissolestes* Kennedy, *Synlestes* Selys, *Archilestes* Selys, and *Lestes* Leach (Fig. 2). However, the bootstrap support for this arrangement is poor. *Danolestes* **gen. nov.** is recovered as sister to *Priscalestes* with strong bootstrap support within the 'lestoid clade' indicating a close relationship between these two genera.

We place *Danolestes moelleri* **gen. et sp. nov.** in the superfamily Lestoidea based on the origin of RP3-4 and likely origin of IR2 between the arculus and subnodus, the very acute distal angle of the quadrangle, the strong basal curve on MP just after the origin, the likely presence of an oblique crossvein 'O', vein MA being at least weakly zigzagged distally, and most postnodal and aligned postsubnodal crossveins, which according to Bechly (1996), Petrulevičius & Nel (2004), Wappler & Petrulevičius (2007), and Greenwalt & Bechly (2014) strongly support placement in the superfamily. The origin of IR2 is confidently basad the subnodus, but its exact position is not clear by preservation: it is either close to the origin of RP3-4 or it is a stub directed toward the origin of RP3-4 but not connected to that vein.

Our phylogenetic analysis, suggests that it is sister to *Priscalestes* Lestoidea. Among extant Lestoidea, it differs from Hemiphlebiidae in possessing an intercalary vein in addition to IR1 and IR2 (between IR1 and RP2), having more than eight postnodal crossveins, and in having an oblique crossvein 'O' (*e.g*., Greenwalt & Bechly, 2014). While the crossvein that we identify as 'O' is only slightly oblique, we proceed with this assumption, as this is like the slight obliquity of 'O' in some extant lestoids, *e.g*., *Archilestes latialatus* Donnelly (see Garrison *et al*., 2010: fig. 480) and *Lestes spumarius* Hagen (Garrison *et al*., 2010 fig. 506).

It differs from Perilestidae in not having the posterior margin of the subquadrangle fused to the wing margin, IR2 not originating close to the origin of RP2, and lacking additional intercalary veins (*e.g*., see Greenwalt & Bechly, 2014). It differs from Synlestidae (excluding *Megalestes* Selys) in not having the posterior margin of the subquadrangle fused to the wing margin, and IR2 not originating at the subnodus (*e.g*., Greenwalt & Bechly, 2014). It differs from Lestidae in MA not being strongly zigzagged for most of its length, and IR2 and RP3-4 originating closer to the subnodus than to the arculus (*e.g*., Greenwalt & Bechly, 2014). It differs from *Megalestes* by its MA being only weakly zigzagged in the distal half and IR2 and RP3-4 originating closer to the subnodus than to the arculus (*e.g*., Wappler & Petrulevičius, 2007).

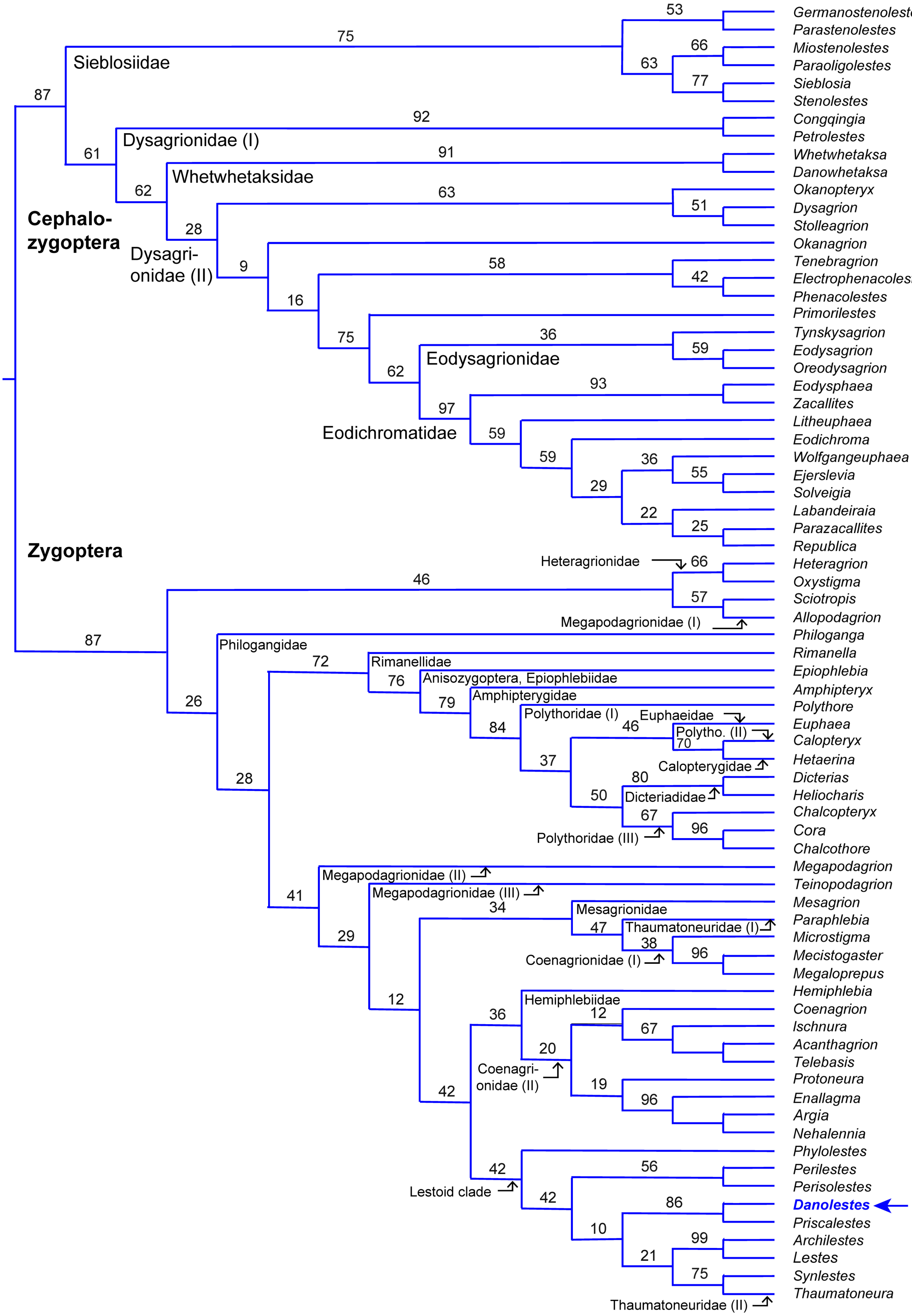

FIGURE 2. Phylogenetic tree from the maximum likelihood analysis of the phylogenetic position of *Danolestes moelleri* **gen. et sp. nov.** (blue) clearly indicating its placement within the lestoid clade (including *Thaumatoneura*). Numbers above the branches indicate Bootstrap support values.

Among fossil lestoids, it differs from *Priscalestes* in having a distinct intercalary vein between IR1 and RP2, and RP2 and IR2 being separated by at least five cells at the margin (Wappler & Petrulevičius, 2007). It differs from Eolestidae in having only one intercalary vein between IR1 and RP2, no supporting sectors in the MA-CuA field, and in IR2 and RP3-4 originating closer to the subnodus than to the arculus (*e.g.*, Greenwalt & Bechly, 2014). It differs from the unplaced fossil lestoid genus *Lutetialestes* Greenwalt & Bechly in having no supporting sectors in the MA-CuA field, and in IR2 and RP3-4 originating closer to subnodus than to the arculus (*e.g.*, Greenwalt & Bechly, 2014). It differs from the unplaced lestoid genus *Cretalestes* Jarzembowski *et al*. in MA being only weakly zigzagged in the distal half, and IR2 and RP3-4 originating closer to the subnodus than to the arculus (Jarzembowski *et al*., 1998).

Danolestes moelleri **gen. et sp. nov.** is similar in some ways to *Promegalestes singularis*, described from an incomplete fossil from the Maíz Gordo Formation of Argentina (Petrulevičius & Nel, 2004). They share the distinctive origin of RP3-4 and apparently IR2 (see above) between the arculus and subnodus, and the distinctly curved MP. *Danolestes* **gen. nov.** is also similar in several ways to *Priscalestes*, with which it shares this origin of IR2 and RP3-4, the acute angle distal angle of the quadrangle, and the distinctly curved MP, as well as the mostly aligned post nodal and post subnodal crossveins (Wappler & Petrulevičius, 2007). *Danolestes* **gen. nov.** differs from *Promegalestes* and *Priscalestes* in several ways: the MA is not zigzagged in *P. singularis* (Petrulevičius & Nel, 2004) or *Priscalestes* (Wappler & Petrulevičius, 2007), while it is weakly zigzagged in *Danolestes* **gen. nov.**; IR2 and RP3-4 originate closer to subnodus in *Danolestes* **gen. nov.** than they do in *Promegalestes* or *Priscalestes* (Wappler & Petrulevičius, 2007); the distal angle of the quadrangle is considerable more acute in *Danolestes* **gen. nov.** compared to *Promegalestes*; *Danolestes* **gen. nov.** has a distinct intercalary vein between IR1 and RP2, which is missing in *Priscalestes* (not preserved in *Promegalestes*). Finally, the distance between the origin of RP2 and subnodus is more than two times longer than the distance between the subnodus and the origin of MA in *Danolestes* **gen. nov.**, but only 1.1 to 1.3 times longer in *Promegalestes* and *Priscalestes*, respectively. We therefore place the fossil in the new genus *Danolestes* **gen. nov.** and tentatively suggest that it may be closely related to, yet distinct from *Promegalestes* and *Priscalestes*. We note that the venation of *Danolestes* **gen. nov.**, *Promegalestes*, and *Priscalestes* might be at least in part convergent and so they might form a grade within the higher Lestoidea where the origins of IR2 and RP3-4 have not become as far recessed as they are in Lestidae and *Megalestes*.

Although several Lestoidea are known from Paleogene and Neogene Western Palearctic (Nel & Paicheler, 1994; Nel & Jarzembowski, 1999), *Danolestes moelleri* **gen. et sp. nov.** is its first member from the Fur Formation. It is evidently not closely related to other Western Palearctic Lestoidea, other than probably *Priscalestes*. If our interpretation is correct, *Danolestes* **gen. nov.** and *Promegalestes* and *Priscalestes* comprise another example of Paleogene insects from the Fur Formation having close known relatives very far from current Denmark as previously demonstrated for *e.g*., Polystoechotidae (Neuroptera) (Archibald & Makarkin, 2006), Whetwhetaksidae (Odonata) (Simonsen *et al*., 2022a), Apachyidae (Dermaptera) (Simonsen *et al*., 2024b), and 'Nogodinidae' (Auchenorrhyncha) (Simonsen *et al*., 2025).

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

Supplementary Material S1