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Danowhetaksa gen. nov. with two species from the early Eocene Ølst Formation from Denmark, the first Palearctic Whetwhetaksidae (Odonata: Cephalozygoptera)

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Abstract

We propose *Danowhetaksa* **n. gen.** (Odonata: Whetwhetaksidae) with two new species: *D. birgitteae* **n. gen. et sp**. and *D. rusti* **n. gen. et sp.** from the earliest Ypresian Stolleklint clay of the Ølst Formation in northwestern Denmark. Whetwhetaksidae has previously been known only from the Ypresian Okanagan Highlands of far-western North America, the new records are, therefore, the first from the Palearctic Region.

Key words: Odonata, Cephalozygoptera

Introduction

The earliest Ypresian Stolleklint clay of the Ølst Formation and the Fur Formation of northwest Denmark is famous for its numerous and often exceptionally well preserved fossils of marine and terrestrial life (*e.g.*, Pedersen *et al*. 2012; Rasmussen *et al*. 2016, Madsen & Rasmussen 2021). Fossil insects are particularly numerous in both formations and have been described for about a century (*e.g.*, Henriksen 1922; Larsson 1975; Heie 1993; Rust & Ansorge 1996; Rust 1998; 1999, and references therein; Archibald & Makarkin 2006). Odonata from the mo-clay (Fur Formation) have been studied since Henriksen (1922) described *Phenacolestes jutlandica* (Henriksen, now in the genus *Furagrion* Petrulevicius *et al*.), increasing in the last 25 years (Madsen & Nel 1997; Petrulevicius *et al*. 2007; 2008; Rust *et al*. 2008; Zessin 2011; Bechly & Rasmussen 2019).

Recently, Archibald *et al*. (2021) erected the extinct odonatan family Whetwhetaksidae for *Whetwhetaksa millerae* Archibald & Cannings of the Ypresian Okanagan Highlands of far-western North America, only a few million years younger than the Stolleklint clay. It is only known from wings, which are most like those of the extinct suborder Cephalozygoptera; however, the Cephalozygoptera is primarily diagnosed by head morphology (Archibald *et al*. 2021) and so they assigned Whetwhetaksidae to it tentatively.

Here, we describe a new genus with two species of Whetwhetaksidae from the Stolleklint clay, establishing the family in the Palearctic region.

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Material and methods

We examined two wings from the Stolleklint clay of the Ølst Formation in northwest Denmark using a Wild Heerbrugg M5A stereomicroscope and photographed them with a Canon EOS 5DII camera and a Canon EF 100 mm Macro lens. We use the wing venation nomenclature of Reik & Kukalová-Peck (1984) and Garrison *et al*. (2010). Abbreviations used are: 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. Compared contrary character states are provided in brackets.

Geological setting. The laminated Stolleklint clay constitutes the lowermost unit of the Ypresian (early Eocene) Ølst Formation (Heilmann-Clausen 1995) of Denmark. It has been estimated to reach 15 (Heilmann-Clausen 1995) or even *ca*. 24 meters thick (Jones *et al*. 2019). On the islands of Fur and Mors in the western Limfjord area of northwestern Denmark, the Stolleklint clay is succeeded by the 60 m thick diatomitic Fur Formation, but is overlain by more diatom-poor clays of the middle and upper Ølst Formation further towards the east and south. The Stolleklint clay was deposited during the Paleocene-Eocene Thermal Maximum (PETM), an interval of sharply increased temperature beginning at the Paleocene-Eocene boundary 56.0 million years ago (McInerney & Wing 2011; Westerhold *et al*. 2020), and lasting approximately 100,000 years. During the PETM, bottom water temperature increased by 5–8 °C in the North Atlantic area (Dunkley Jones *et al*. 2013) and sea surface temperature in the western Limfjord area of Denmark, was estimated to reach a minimum of 7–10 °C increase, while the sea surface palaeotemperature estimate for the upper part of the Stolleklint clay rose to close to 30 °C (Stokke *et al*. 2020).

Like in the superjacent Fur Formation, the laminated Stolleklint clay contains tephra layers, although much more scattered. Because of this, both the Fur and Ølst formations have been commonly included in the "ash-series" of previous literature. This tephra was imported by ash clouds generated by explosive volcanic activity in the North Atlantic Igneous Province related to the break-up of the continental crust between Greenland, UK and Norway, a major phase of the Atlantic Ocean history (Larsen *et al*. 2003). Seven numbered ash layers (nos. -39 to -33; Bøggild 1918) are known from the Stolleklint clay. The 14 cm thick ash layer -33 is usually regarded as its boundary with the Fur Formation in the Limfjord area. One or a few thin and hardened fossil-rich clay beds occur in the uppermost part of the Stolleklint clay close to the ash layers -33 and -34. These were described as so-called "shale layers" by some earlier workers, but strictly speaking they do not represent shales. The *Danowhetaksa rusti* **n. gen et. sp.** specimen was collected from one of these hardened layers within the uppermost 1.5 m of the Stolleklint clay, and the *Danowhetaksa birgitteae* **n. gen. et. sp.** specimen was collected at an unknown level below this.

Systematic paleontology

Order Odonata Fabricius

Suborder Cephalozygoptera Archibald, Cannings & Erickson

Family Whetwhetaksidae Archibald & Cannings

Remarks. We emend the diagnosis of Whetwhetaksidae of Archibald *et al*. (2021) based on the fossils described here by the following: character state 1, pterostigma at least seven times as long as it is wide (this was ten times width in Archibald *et al.* 2021), and remove character state 10, base to nodus percent wing length, as a synapomorphy for this group as this region is shorter in *Danowhetaksa* and does not now distinguish Whetwhetaksidae from Dysagrionidae or Sieblosiidae.

Danowhetaksa Simonsen, Ware & Archibald, new genus

Diagnosis. Most easily distinguished from *Whetwhetaksa* by: 1, pterostigma length *ca*. 7 times width [*ca*. 10 times]; 2, dark fascia mid-wing, basal wing hyaline [colouration extends to wing base where known]; 3, origin of IR2 closer

to nodus than to origin of R3-4 [closer to origin of R3-4], at least three crossveins between them [one]; 4, MP, CuA more widely separated distally [maximum *ca*. 10 cells at margin], not subparallel [maximum two cells, subparallel].

Type and included species. Type species, *Danowhetaksa birgitteae* **n. sp.** here designated; other included species, *Danowhetaksa rusti* **n. sp.**

Etymology. The genus name is formed from the prefix 'Dano-' referring to Denmark, and the suffix '-whetaksa' referring to the Whetwhetaksidae. Gender: feminine.

Danowhetaksa birgitteae Simonsen, Ware & Archibald, new species

Figure 1

Material. Holotype [FUM-M-17515]: an isolated wing preserved in a concretion block; the part is missing the basalmost and apical-posterior portions, and the counterpart is missing the apical-most portion including the pterostigma; collected by Birgitte Munk, 1996, Fur Stolleklint; deposited in the Fur Museum.

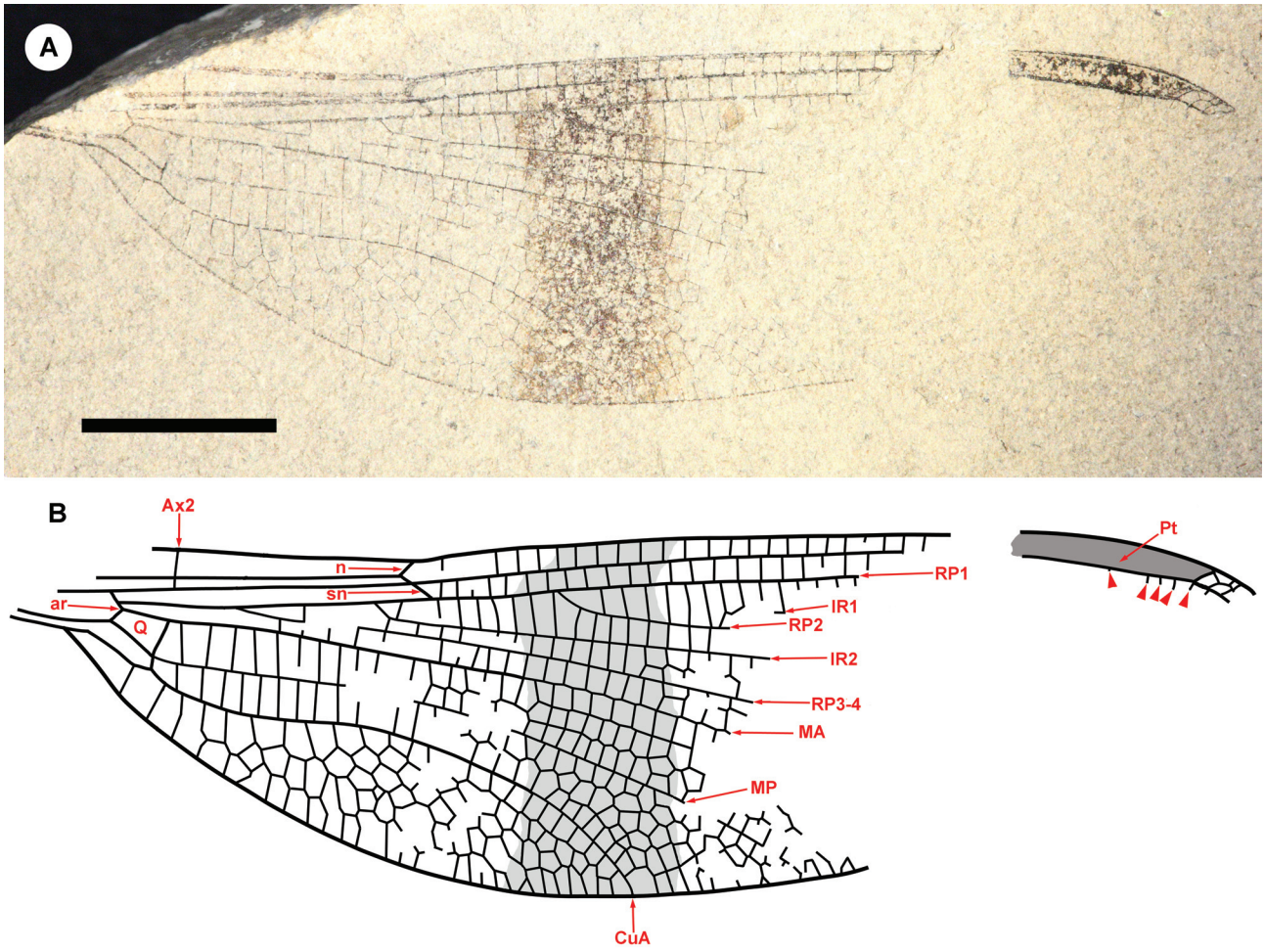

FIGURE 1. *Danowhetaksa birgitteae* **n. sp.**, holotype wing [FUM-N-17515]. A, photograph of part; B, drawing from part and counterpart. Short arrows indicate crossveins below pterostigma (see text). Scale bar is 5 mm.

Description. Holotype wing. Length, arculus to distal end of pterostigma: 28.0 mm; nodus to distal end of pterostigma: 20.3 mm; arculus to base of pterostigma: max 23.4 mm; nodus to base of pterostigma: max 16.2 mm; width: 9.3 mm. Pterostigma dark (damaged basally), preserved part approximately 5 mm in length, highly elongate, at least seven times longer than wide, subtends numerous cells, five crossveins detected by preservation, surely many more. Membrane with a transverse, sub-central dark fascia, slightly narrower than length of pterostigma, otherwise hyaline. Twenty-three crossveins preserved in postnodal space, 22 in postsubnodal space, only pair aligned.

IR1 very poorly preserved, origin probably slightly zigzagged, seven cells distal to origin of RP2. RP2 originates seven cells distal to subnodus. IR2 originates approximately 8.5/10 distance arculus to nodus, preserved part of IR2 close to linear. RP3-4 originates approximately 4/10 distance arculus to nodus, preserved part of RP3-4 close to linear. MA linear in basal 1/3, starts zigzagging slightly about basal margin of darkened wing band, poorly preserved beyond band. MP linear from origin to terminus at wing margin, slightly curved. CuA linear from origin to terminus on wing margin, basal 2/3 subparallel to MA, then curving sharper to wing margin, terminates basal to mid-wing. MA-CuA space two cells wide where CuA starts curving away, widening to at least six cells at wing margin. CuA-A space well preserved, very broad, at least five cells wide. Quadrangle sub-trapezoid, broadest distally, approximately 1.3 times longer than wide. Anterior wing margin not preserved basal to arculus, so Ax1 not preserved. Ax2 approximately 2/10 distance arculus to nodus, just distal to anterodistal corner of quadrangle.

Diagnosis. Distinguished from *D. rusti* by any of: 1, RP1-2–IR2 space one cell wide, RP2–IR2 space to origin of IR1 (not preserved beyond this) [RP1-2–IR2 space becomes two cells wide *ca*. two cells basal origin of RP2]; 2, IR2–RP3-4 space becomes two cells wide *ca.* mid-way between origins of RP2, IR1 [ca. origin of IR2]; 3, seven crossveins in R1+2–IR2 space between nodus and origin of RP2 [*ca*. 9]. Further separated by colouration (sex unknown): narrow, dark fascia mid-wing [almost twice as wide], basally starting *ca*. five cells distal to nodus, includes origin of RP2, ends slightly distal to termination of CuA [anterior to R1+2 starts at nodus, posterior R1+2 just basal origin of IR2, ends on posterior margin just basal to termination of CuA, on anterior margin slightly more distal].

Deposit and age. Stolleklint clay, Ølst Formation, Stolleklint, Fur, Denmark; earliest Ypresian.

Etymology. An eponym formed from the given name of Birgitte Munk, who found and donated the holotype, recognising her contribution.

Remarks. Colouration is provided as supplementary in the diagnosis, as it is unknown if there are differences in colouration due to sexual dimorphism, variation between forewings and hind wings, or polymorphism in Whetwhetaksidae.

Although the wing base is not preserved, we estimate CuA to terminate on the margin just over half wing length.

Danowhetaksa rusti Simonsen, Ware, & Archibald, new species

Figure 2

Material. Holotype [MM-13418]: an isolated wing preserved in a concretion block, deposited in Museum Mors (Mo-clay Museum), collected by Henrik Madsen, October 31, 1993, Fur Stolleklint. The specimen was collected from a hardened bed within the upper 1.5 m of the Stolleklint clay near ash-layers -33 and -34.

Description. Holotype wing. Arculus to distal end of pterostigma: 26.7 mm. Nodus to distal end of pterostigma: 18.9 mm. Arculus to basal end of pterostigma: 22.6 mm. Nodus to basal end of pterostigma: 14.8 mm. Width: 8.8 mm. Pterostigma dark, 5.2 mm in length, *ca*. 8 times longer than wide, subtends numerous cells, eight crossveins detected by preservation, surely more. Wing hyaline with transverse dark fascia, as in diagnosis, *ca*. 1.5 times length of pterostigma. Postnodal and postsubnodal spaces poorly preserved, but only one pair of crossveins appears aligned. IR1 very poorly preserved, origin probably zigzagged. RP2 originates 8 cells distal to subnodus. IR2 originates *ca*. 8/10 distance arculus to nodus, preserved part of IR2 close to linear. RP3-4 originates *ca*. 4/10 distance arculus to nodus, preserved part of RP3-4 close to linear. Preserved part of MA linear through fascia. Preserved part of MP linear (terminus missing). CuA linear from origin to terminus on wing margin, basal 2/3 subparallel to MA, then curving sharper to wing margin, terminates just to mid-wing beyond fascia. MA-CuA space two cells wide where CuA starts curving away, widening to at least four cells well before estimated terminus at wing margin. CuA-A space moderately well preserved, very broad, at least 5 cells wide. Quadrangle sub-trapezoid broadest distally, approximately 1.3x longer than wide. Ax0 present, synsclerotised with wing base. Arculus close to, slightly distal of Ax1. Ax2 partly preserved, *ca*. fifth distance arculus to nodus, just distal to quadrangle.

Diagnosis. Distinguished from *D. birgitteae* as in its diagnosis, above.

Deposit and age. Stolleklint clay, Ølst Formation, Stolleklint, Fur, Denmark; earliest Ypresian.

Etymology. An eponym formed by the surname of the German paleoentomologist Jes Rust, whose extensive work has greatly increased our knowledge of mo-clay insects.

Remarks. Garrouste & Nel (2015) described the monobasic Pseudostenolestidae from the latest Ypresian at

Messel, Germany (*Pseudostenolestes bechlyi* Garrouste & Nel) and discussed ways in which it resembles the Dysagrionidae and Sieblosiidae (Cephalozygoptera). It shares a distinctive quadrangle shape with the Whetwhetaksidae, which the Dysagrionidae and Sieblosiidae also possess. Notably, the arculus of *P. bechlyi* is positioned near Ax1 as in the Whetwhetaksidae. In *P. bechlyi*, the arculus and Ax1 are opposite, while in Whetwhetaksidae Ax1 is just basal to the arculus—slightly closer to it in *Danowhetaksa* than in *Whetwhetaksa*. The pterostigma is also long in *P. bechlyi*, although not as long as in the Whetwhetaksidae. Unlike the Whetwhetaksidae, however, it possesses the oblique vein "O", shared with the Sieblosiidae, and unlike the Whetwhetaksidae, Sieblosiidae, and Dysagrionidae, it has a very short petiole. Pseudostenolestes differs from the Zygoptera, Cephalozygoptera, and Whetwhetaksidae by its distinctive, strong vein Cuab originating at the middle posterior of the subquadrangle and directed towards the wing base, by which they assign it to the Isophlebioptera, previously only known from the Mesozoic.

In most Zygoptera, Ax0 is absent or obscured by sclerotization at the wing base (Bechly 1996, and see Rehn, 2003). It is present without associated sclerotization in *Whetwhetaksa* and in Cephalozygoptera (Archibald *et al*. 2021). In *D. rusti* **n. sp.** it is present and associated with sclerotization basally, but not obscured by it.

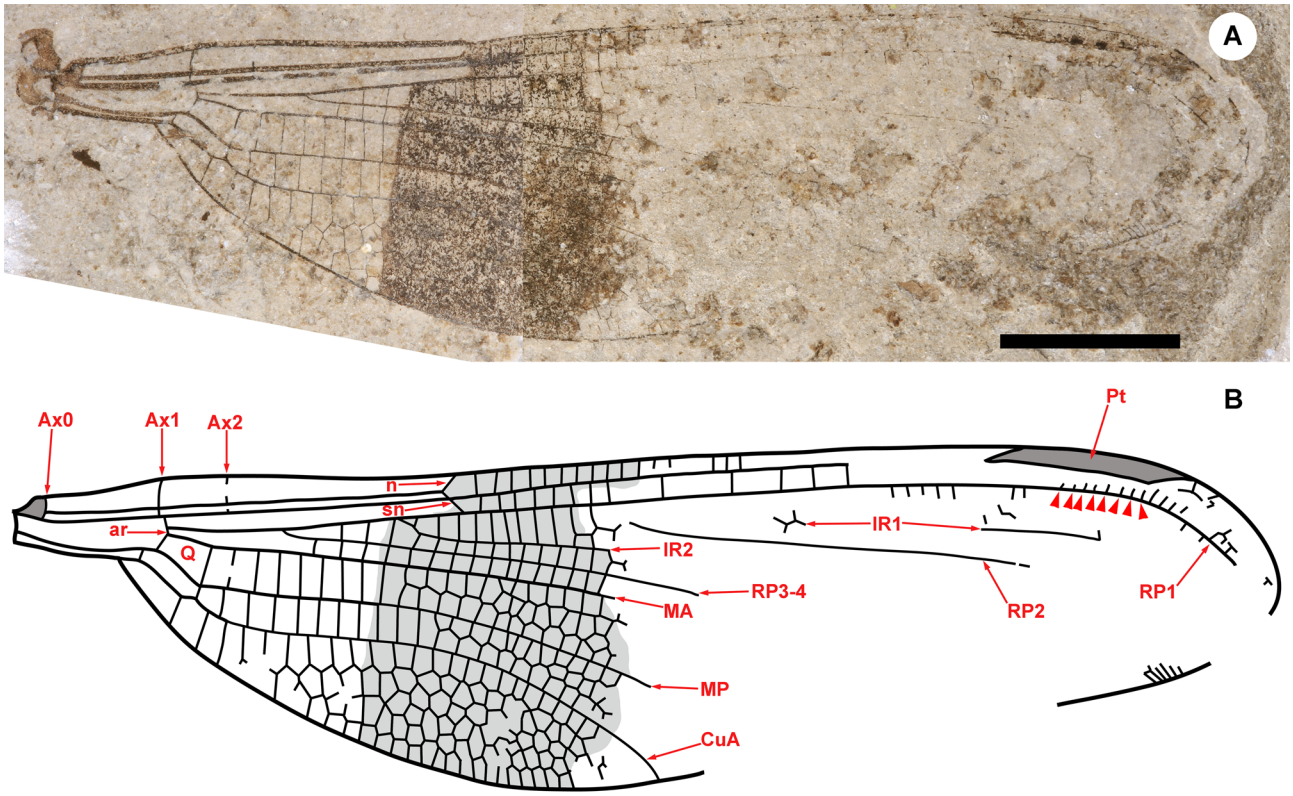

FIGURE 2. *Danowhetaksa rusti* **n. sp.**, holotype wing [MM-13418]. A, combined photograph of part and counterpart; B, drawing from part and counterpart. Short arrows indicate crossveins below pterostigma (see text). Scale bar is 5 mm.

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References

Archibald, S.B., Cannings, R.A., Erickson, R.J., Bybee, S.M. & Mathewes, R.W. (2021) The Cephalozygoptera, a new, extinct suborder of Odonata with new taxa from the early Eocene Okanagan Highlands, western North America. *Zootaxa*, 4934(1), 1–133.
https://doi.org/10.11646/zootaxa.4934.1.1

Archibald, S.B. & Makarkin, V.N. (2006) Tertiary Giant Lacewings (Neuroptera: Polystoechotidae) revision and description of new taxa from western North America and Denmark. *Journal of Systematic Paleontology*, 4, 119–155, 307 (errata).
https://doi.org/10.1017/S1477201906001817

Bechly, G. (1996) Morphologische Untersuchungen am Flügelge der der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata) unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. *Petalura, B blingen*, Special Volume, 2, 1–402.

Bechly, G. & Rasmussen, J.A. (2019) A new genus of hawker dragonfly (Odonata: Anisoptera: Aeshnidae) from the Early Eocene Fur Formation of Denmark. *Zootaxa*, 4550 (1), 123–128.
https://doi.org/10.11646/zootaxa.4550.1.6

Bøggild, O.B. (1918) Den vulkanske Aske i Moleret samt en Oversigt over Danmarks ældre Tertiærbjergarter. *Særtryk af Danmarks Geologiske Undersøgelse*, 2, 33.
https://doi.org/10.34194/raekke2.v33.6819

Dunkley Jones, T., Lunt, D.J., Schmidt, D.N., Ridgwell, A., Sluijs, A., Valdes, P.J. & Maslin, M. (2013) Climate model and proxy data constraints on ocean warming across the Paleocene–Eocene Thermal Maximum. *Earth-Science Review*, 125, 123–145.
https://doi.org/10.1016/j.earscirev.2013.07.004

Fabricius, J.C. (1793) *Entomologica systemica emendata et acuta, Secundum classes, ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus*. C.G. Proft, Hafniae, 519 pp.
https://doi.org/10.5962/bhl.title.125869

Garrison, R.W., von Ellenrieder, N. & Louton, J.A. (2010) *Damselfly genera of the New World: an illustrated and annotated key to the Zygoptera*. Johns Hopkins University Press, Baltimore, Maryland, 490 pp.

Garrouste, R. & Nel, A. (2015) New Eocene damselflies and the first Cenozoic damseldragonfly of the isophlebiopteran lineage (Insecta: Odonata). *Zootaxa*, 4028 (3), 354–366.
https://doi.org/10.11646/zootaxa.4028.3.2

Heie, O. (1993) Insects from the Fur Formation in Denmark (Mo-clay, Upper Paleocene—Lower Eocene?). 8. Aphidoidea (Homoptera). *Meyniana*, 45, 57–64.
https://doi.org/10.1127/njgpm/1993/1993/239

Heilmann-Clausen, C. (1995) Palæogene aflejringer over Danskekalken. *In*: Nielsen, O.B. (Ed.), *Danmarks geologi fra Kridt til i dag*. *Aarhus Geokompendier. 1*. Geologisk Institut, Aarhus Universitet, Aarhus, pp. 69–114.

Henriksen, K.L. (1922) Eocene insects of Denmark. *Danmarks Geologiske Undersøgelse*, 2 (37), 1–36.
https://doi.org/10.34194/raekke2.v37.6823

Jones, M.T., Percival, L.M.E., Stokke, E.W., Frieling, J., Mather, T.A., Riber, L., Schubert, B.A., Schultz, B., Tegner, C., Planke, S. & Svensen, H.H. (2019) Mercury anomalies across the Palaeocene-Eocene Thermal Maximum. *Climate of the Past*, 15, 217–236.
https://doi.org/10.5194/cp-15-217-2019

Larsen, L.M, Fitton, J.G. & Pedersen, A.K. (2003) Paleogene volcanic ash layers in the Danish Basin: composition and source areas in the North Atlantic Igneous Province. *Lithos,* 71, 47–80.
https://doi.org/10.1016/j.lithos.2003.07.001

Larsson, S.G. (1975) Palaeobiology and the mode of burial of the insects of the lower Mo-clay of Denmark. *Bulletin of the Geological Society of Denmark*, 24, 193–209.

Madsen, H.O.R. & Nel, A. (1997) Two new fossil species of *Gomphaeschna* Selys, 1871 in the Paleocene / Eocene of Denmark (Odonata: Aeshnoidea). *Annales de la Société Entomologique de France*, New Series, 33, 285–293.

Madsen, H. & Rasmussen, J.A. (2021) *Geologien fortæller: Moler og Fossiler / What geology tells: The mo-clay and its fossils*. Museum Mors, 103 pp. ISBN 87-87566-91-5.

McInerney, F.A. & Wing, S.L. (2011) The Paleocene-Eocene Thermal Maximum: A Perturbation of Carbon Cycle, Climate, and Biosphere with Implications for the Future. *Annual Review of Earth and Planetary Sciences*, 39, 489–516.
https://doi.org/10.1146/annurev-earth-040610-133431

Pedersen, G.K., Pedersen, S.A.S., Bonde, N., Heilmann-Clausen, C., Larsen, L.M., Lindow, B., Madsen, H., Pedersen, A.K., Rust, J., Schultz, P.B., Storey, M. & Willumsen, P. S. (2012) Moleområdets geologi—sedimenter, fossiler, askelag og glacialtektonik. *Geologisk Tidsskrift*, 2011, 41–135.

Petrulevičius, J.F., Nel, A., Rust, J., Bechly, G. & Kohls, D. (2007) New Paleogene Epallagidae (Insecta: Odonata) recorded in North America and Europe. Biogeographic implications. *Alavesia*, 1, 15–25.

Petrulevičius, J.F., Wappler, T., Wedmann, S., Rust, J. & Nel, A. (2008) New megapodagrionid damselflies (Odonata: Zygoptera) from the Paleogene of Europe. *Journal of Paleontology*, 82, 1173–1181.
https://doi.org/10.1666/07-091.1

Rasmussen, J.A., Madsen, H., Schultz, B.P., Sylvestersen, R.L. & Bonde, N. (2016) *The lowermost Eocene deposits and biota of the western Limfjord region, Denmark—Field Trip Guidebook. 2nd International Mo-clay Meeting, 2–4 November 2016*. Museum, Skive and the Fossil and Mo-clay Museum, Museum Mors, Nykøbing Mors, 38 pp.

Rehn, A.C. (2003) Phylogenetic analysis of higher-level relationships of Odonata. *Systematic Entomology*, 28, 181–239. https://doi.org/10.1046/j.1365-3113.2003.00210.x

Riek, E.F. & Kukalová-Peck, J. (1984) A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Canadian Journal of Zoology*, 62, 1150–1166. https://doi.org/10.1139/z84-166

Rust, J. (1999) *Biologie der Insekten aus dem ältesten Tertiär Nordeuropas*. Habilitationsschrift, Georg-August-Universität, Göttingen, 482 pp., 34 pls.

Rust, J. (1998) Fossil insects from the Fur and Ølst formations ("mo-clay") of Denmark (upper Palaeocene/lowest Eocene). *Proceedings of the first international Palaeoentomological Conference*, *Moscow*, 1998, 135–139.

Rust, J. & Ansorge, J. (1996) Bemerkentswerde Moler-Insekten. *Fossilen*, 6/96, 359–364.

Rust, J., Petrulevičius, J.F. & Nel, A. (2008) The first damselflies from the lowermost Eocene of Denmark, with a description of a new subfamily (Odonata, Zygoptera, Dysagrionidae). *Palaeontology*, 51, 709–713. https://doi.org/10.1111/j.1475-4983.2008.00780.x

Stokke, E.W., Jones, M.T., Tierney, J.E., Svensen, H.H. & Whiteside, J.H. (2020) Temperature changes across the Paleocene-Eocene Thermal Maximum—a new high-resolution TEX86 temperature record from the Eastern North Sea Basin. *Earth and Planetary Science Letters*, 544, 116388. https://doi.org/10.1016/j.epsl.2020.116388

Westerhold, T., Marwan, N., Drury, A.J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J.S.K., Bohaty, S.M., De Vleeschouwer, D., Florindo, F., Frederichs, T., Hodell, D.A., Holbourn, A.E., Kroon, D., Lauretano, V., Littler, K., Lourens, L.J., Lyle, M., Pälike, H., Röhl, U., Tian, J., Wilkens, R.H., Wilson, P.A. & Zachos, J.C. (2020) An astronomically dated record of Earth's climate and its predictability over the last 66 Million Years. *Science*, 369, 1383–1387. https://doi.org/10.1126/science.aba6853

Zessin, W. (2011) Neue Insecten aus dem Moler (Paläozän/Eozän) von Dänemark Teil 1 (Odonata: Epallagidae, Megapadagrioniidae). *Virgo*, 14, 64–73.