Zootaxa 5696 (3): 444–450
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5696.3.9
http://zoobank.org/urn:lsid:zoobank.org:pub:0A15AF79-597D-454B-AC66-F407C98287BC

A further new genus of Drepanicinae (Neuroptera: Mantispidae) from the earliest Eocene Fur Formation, Denmark

VLADIMIR N. MAKARKIN[1*], CHRISTIAN NIELSEN[2] & EVGENY E. PERKOVSKY[3]
[1]*Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch of the Russian Academy of Sciences, Vladivostok, 960022, Russia*
[2]*Frederiksvej 25, Frederiksberg 2000, Denmark*
chrnie2468@gmail.com; https://orcid.org/0009-0003-0427-3858
[3]*Natural History Museum of Denmark, Universitetsparken 15, Copenhagen, Denmark*
perkovsk@gmail.com; https://orcid.org/0000-0002-7959-4379
**Corresponding author: vnmakarkin@mail.ru; https://orcid.org/0000-0002-1304-0461*

Abstract

Protheristria roldae **gen. et sp. nov.** (Neuroptera: Mantispidae: Drepanicinae) is described from the earliest Eocene Fur Formation, Denmark. This is the second genus of Mantispidae and Drepanicinae from this formation. The new genus is distinguished from other drepanicine genera by a combination of fore- and hind wing venation character states: one gradate series of crossveins is present in the radial to intramedial spaces; pterostigma is short and pale; Sc distally (bordering the pterostigma) is very pale; all branches of RP are forked once. The two genera known from the Fur Formation, *Danomantispa* Makarkin *et al*., 2025 and *Protheristria* **gen. nov.**, are not closely related and certainly belong to different genus groups.

Key words: Neuroptera, Mantispidae, Drepanicinae, earliest Eocene, Fur Formation

Introduction

The Mantispidae constitute a relatively small family comprising nearly 400 extant and 50 extinct species in six subfamilies: †Mesomantispinae, †Doratomantispinae, Drepanicinae, Symphrasinae, Calomantispinae and Mantispinae (Jepson 2015; Oswald & Machado 2018; Lu *et al*. 2020; Li *et al*. 2023).

The small subfamily Drepanicinae includes eight genera: the Early Jurassic *Liassochrysa* Ansorge & Schlüter, 1990; the Late Jurassic *Promantispa* Panfilov, 1980; the early Eocene *Danomantispa* Makarkin *et al*., 2025; and five extant distributed in South America (*Drepanicus* Blanchard, 1851 and *Gerstaeckerella* Enderlein, 1910), Australia (*Theristria* Gerstaecker, 1885 and *Ditaxis* McLachlan, 1867) and southeast Asia (*Allomantispa* Liu, Wu, Winterton et Ohl in Liu *et al*., 2015) (Lambkin 1986; Ohl & Oswald 2004; Liu *et al*. 2015; Li *et al*. 2020). A fossil species from the Turonian of Kyzylzhar (Kazakhstan) was assigned to an extant genus, *i.e*., *Gerstaeckerella asiatica* Makarkin 1990 (Makarkin 1990; Makarkin & Khramov 2015). Other fossil genera previously assigned to the Drepanicinae either confidently or very probably do not belong to the subfamily (Li *et al*. 2025; Makarkin *et al*. 2025).

We recently described the first drepanicine species from the earliest Eocene Fur Formation of Denmark, *Danomantispa frandseni* Makarkin *et al*., 2025 (Makarkin *et al.* 2025). Here, we describe a further new genus and species of Drepanicinae from this formation.

Materials and methods

The specimen was collected in the Vangsgaard pit on Mors Island in northern Jutland, Denmark. Overviews of this earliest Eocene Danish Lagerstätte have been provided by *e.g.*, Larsson (1975); Pedersen & Surlyk (1983), Archibald & Makarkin (2006), Pedersen *et al*. (2012), and Madsen & Rasmussen (2021). Previously, the majority

 Accepted by X.-Y. Liu: 26 Aug. 2025; published: 25 Sept. 2025

of the Neuroptera species have been described from upper ('positive') horizons of the formation, *i.e*., the Silstrup Member (when specific stratigraphic data are available), and only one specimen (the holotype of *D. frandseni*) is from basal ('negative') horizons, *i.e*., the Knudeklint Member. The mantispid described here is also from a 'negative' horizon. It was found in a calcareous concretion in the Vangsgaard pit quarry, but its structure is most similar to that of the concretion located 0.5 m above ash layer -17 (see Madsen 2011). The age of ash layer -17 is approximately 55.6 Ma (Stokke *et al*. 2020).

Digital images of specimens wetted with deionized water was done with flash lighting and a P-51Camlift Driver ver. 2.6.1 controlling a Canon EOS K2-SC camera.

Venational terminology follows Breitkreuz *et al*. (2017). Crossveins are designated by the longitudinal veins to which they connect and are numbered in sequence from the wing base, *e.g.*, 2r-m, crossvein in the second gradate series between RP and M/MA.

Character states of compared taxa are provided in brackets.

Abbreviations: A1–A3, first to third anal veins; CuA, anterior cubitus; CuP, posterior cubitus; MA, anterior media; MP, posterior media; pt, pterostigma; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; Sc, subcosta.

Order Neuroptera Linnaeus, 1758

Family Mantispidae Leach, 1815

Subfamily Drepanicinae Enderlein, 1910

Genus *Protheristria* gen. nov.

Type and only species. *Protheristria roldae* **sp. nov.**

Diagnosis. May be easily distinguished from other genera of Drepanicinae by a combination of following venation character states: Both fore- hind wings: one gradate series of crossveins in the radial to intramedial spaces [two series in *Liassochrysa*, *Promantispa*, *Ditaxis*, *Allomantispa*]; pterostigma pale [dark in *Theristria*]; Sc distally (bordering the pterostigma) very pale, poorly discernible [well discernible in other genera]; all branches of RP forked once [at least some branches dichotomously forked in other genera except for a few species of *Theristria*].

Etymology. From the Greek *pro*, before, and *Theristria*, a genus-group name. Gender feminine.

Protheristria roldae sp. nov.

Figs 1–3

Type material. Holotype: MGUH 35093 (accession number GM 2025.1), an incomplete, poorly preserved specimen with all wings overlapping, collected on February 15, 2025 by Dorthe Rold and John Frandsen (Erslev, Denmark) and deposited in the collections of the Natural History Museum of Denmark.

Type locality and horizon. Denmark: northern Jutland: Mors Island: Vangsgaard pit (56.94130°N, 8.89170°E); Fur Formation, middle part of the Knudeklint Member (0.5 m above ash layer -17); earliest Eocene.

Etymology. From the surname of Dorthe Rold, one of collectors of the holotype.

Description. Body fragmentarily preserved. Head, abdomen missing; thorax crumpled, brownish (probably prothorax missing). Middle and hind legs fragmentarily preserved, pale. Middle leg femur elongate, rather stout; mid-tibia long, narrow. Hind femur elongate, rather narrow. Abdomen very poorly and fragmentarily preserved, details not discernable; setae short.

Forewing *ca*. 13.6 mm long, 3.9 mm wide. Costal space relatively narrow, dilated most at proximal 1/6 length, narrowed basad and distad. Subcostal veinlets fragmentarily preserved, simple, widely spaced. Pterostigma very pale, slightly brownish, relatively short, veinlets within it indiscernible but setae numerous; distal crossvein between Sc, RA probably located in central part of pterostigma. Subcostal space relatively narrow, slightly dilated before pterostigma; no crossveins detected. RA distally with three widely spaced veinlets: two proximal long (of these,

one shallowly forked); distal-most short. RA space with three crossveins. RP originates far from wing base (at *ca*. 0.29% complete length); with six branches, all forked once. M basally not fused with R; forked at level of origin of RP. MA, MP each once forked. Fork of Cu not preserved. CuA, CuP, forked once with all branches simple. A1 fragmentarily preserved. First (basal) gradate series of crossveins not preserved. Second series with three crossveins: 2r-m short, connecting stem of RP and MA; 2m-cu long, connecting MP at its origin and CuA opposite 2icu; 2icu long, connecting CuA, and anterior branch of CuP (proximal crossvein between RA, RP may belong to this series). Third series absent (intermediate proximal crossvein between RA, RP may belong to this series). Fourth (outer) series complete, nearly parallel to posterior margin, with seven crossveins from distal branch of RP to MP. Wing maculation probably absent. Setae on vein short, scarce; on costal margin denser.

FIGURE 1. *Protheristria roldae* **sp. nov.**, holotype MGUH 35093 (GM 2025.1). A, part; B, counterpart. Scale bars = 2 mm.

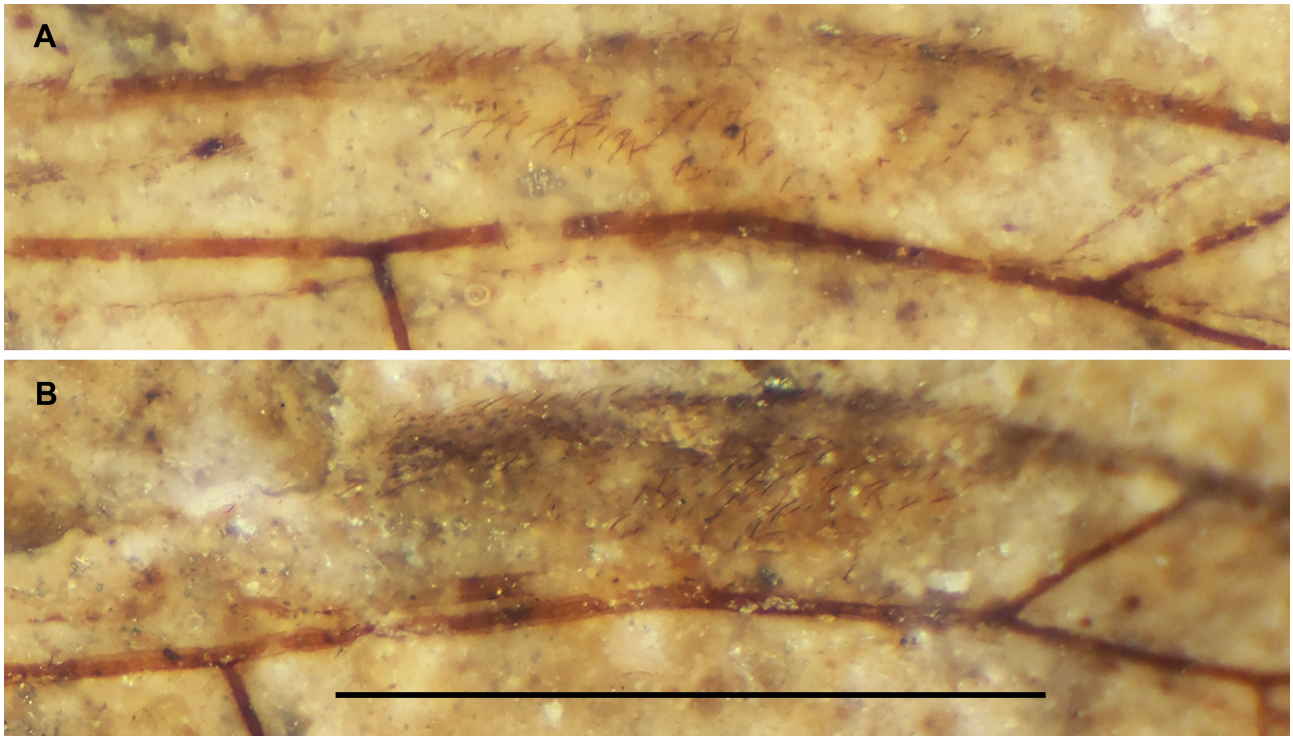

FIGURE 2. Pterostigmata of *Protheristria roldae* **sp. nov.**, holotype MGUH 35093 (GM 2025.1). A, forewing; B, hind wing. Scale bar = 2 mm (both to same scale).

Hind wing 10 mm long as preserved (estimated complete length *ca*. 11.0–11.5 mm), *ca*. 3.0 mm wide. Costal space not preserved except pterostigmal region. One subcostal veinlet partly preserved. Pterostigma very similar to that of forewing in shape and color; veinlets within it indiscernible but setae numerous; distal crossvein stout, between Sc, RA located in central part of pterostigma. Subcostal space relatively broad, almost not dilated before pterostigma; with one distal crossvein detected, short and stout. Stem of RA very shallowly forked distally, with two long simple veinlets. RA space slightly narrowed toward apex, with three crossveins. RP originates rather far from wing base; with six branches, all forked once (distal-most branch very shallowly forked). M forked far distad origin of RP. MA, MP each forked once. Two crossveins preserved between MP, CuA: 2m-cu long, 3m-cu shorter than 2m-cu. CuA fragmentarily preserved, probably pectinately forked, with one preserved simple branch. CuP, anal veins not preserved. First (basal) gradate series of crossveins not preserved. Second series represented by two crossveins: 2r-m moderately long, connecting stem of RP and MA; 2m-cu long, connecting MP and CuA. Third series absent (intermediate proximal crossvein between RA, RP may belong to this series). Fourth (outer) series complete, nearly parallel to posterior margin, with seven crossveins from distal branch of RP to CuA. Wing maculation probably absent. Setae on veins short, scarce; on costal margin denser.

Remarks. A few veins in basal parts of wings seen in the photograph (Fig. 1) are not depicted in drawings (Fig. 3) as it is impossible to determine which wings they belong to.

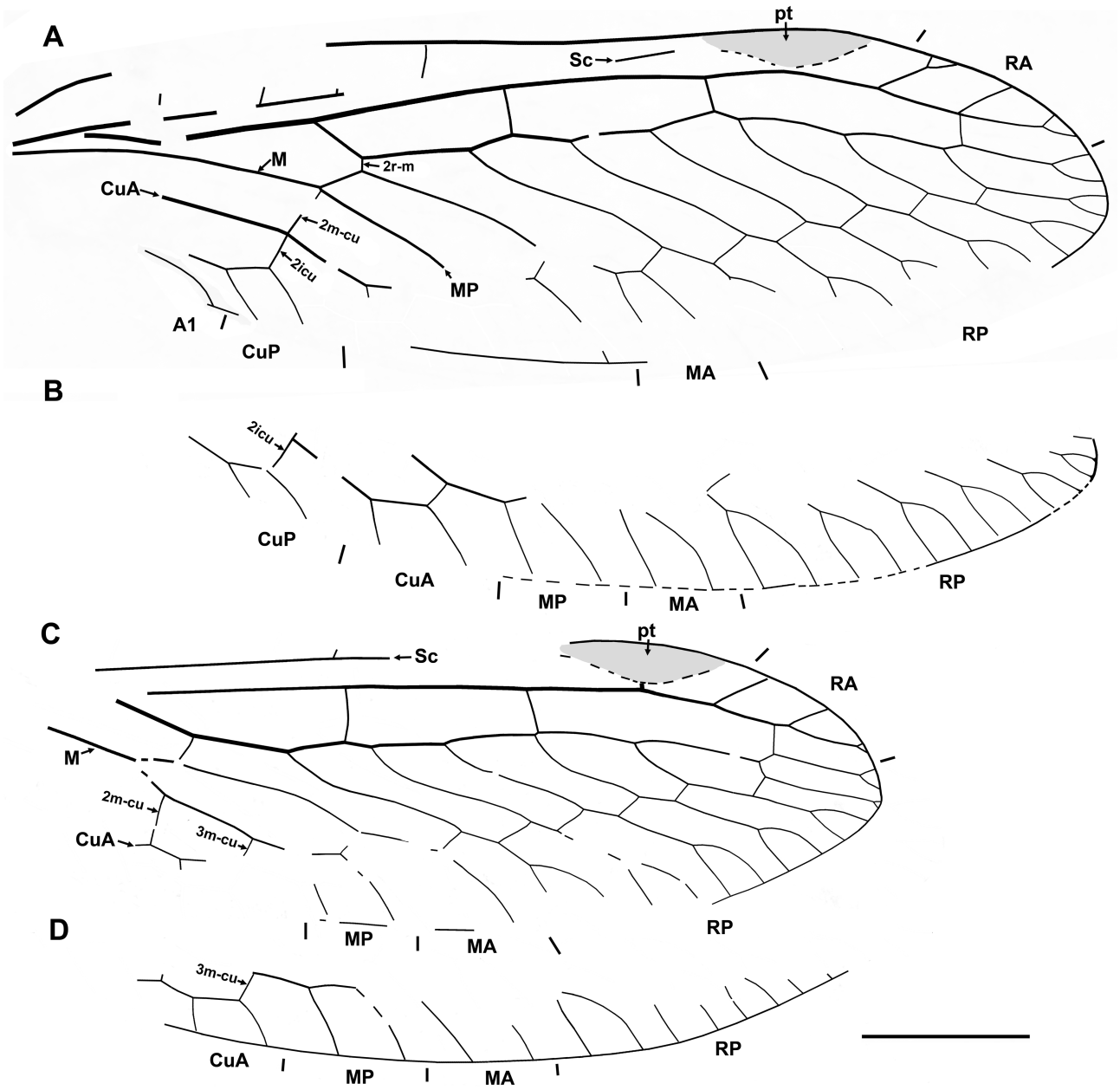

FIGURE 3. *Protheristria roldae* **sp. nov.**, holotype MGUH 35093 (GM 2025.1). A, right forewing; B, left forewing; C, right hind wing; D, left hind wing. Scale bar = 2 mm (all to same scale).

Discussion

The wing venation of the new genus is typical for Drepanicinae, *e.g.*, M is not fused basally with R; crossvein 2m-cu connects MP and CuA, and the structure of the pterostigma is characteristic of the subfamily. It possesses one gradate series of crossveins in the radial to intramedial spaces as in four other genera of Drepancinae: *i.e.*, the extant *Drepanicus*, *Gerstaeckerella* and *Theristria*, and the early Eocene *Danomantispa*. In other genera of the subfamily, there are two such gradate series. Superficially, the venation of *Protheristria* **gen. nov.** is most similar to small species of the South American *Gerstaeckerella* (*e.g.*, *G. chilensis* (Hagen, 1859)) and the Australian *Theristria*. Their wing shape and size are also similar. Unfortunately, drawings of the venation or photographs of wings with clearly preserved venation are provided for only a few of the twenty-four species of *Theristria* described (Esben-Petersen, 1929: Pl. 3, fig. 2; Handschin, 1935: Fig. 18; Lambkin, 1986: Figs 78, 126). It is probable that at least some branches of RP in most species of the genus are dichotomously forked (see Lambkin, 1986: Figs 78, 126). However,

all branches of RP at least in few species of *Theristria* are forked once like in the new genus, *i.e*., *T. stigma* (Esben-Petersen, 1929: Pl. 3, fig. 2), and probably *T. imperfecta* Lambkin, 1986. In all other species of Drepanicinae, at least some branches of RP are dichotomously forked.

The pterostigma of *Protheristria* **gen. nov.** is pale, the distal part of Sc bordering the pterostigma is very poorly visible and its incorporated veinlets are not discernible (Fig. 3). However, numerous setae within the pterostigma show the direction of Sc and the presence of several incorporated veinlets. The pterostigma of *Theristria* is always dark, but that of *Gerstaeckerella* may be short and pale with indistinct incorporated veinlets. The structure of the pterostigma of *Protheristria* **gen. nov.** is in general most similar to that of *Gerstaeckerella*, and other drepanicine genera (except the distal part of its Sc is almost indiscernible).

Two genera of Drepanicinae known from the Fur Formation strongly differ. *Danomantispa* is the only drepanicine genus possessing a mantispine-like pterostigma: long and dark with the distal crossvein between Sc and RA located in the distal part of the pterostigma, and the section of Sc distad it is nearly straight and rather short (Makarkin *et al*. 2025: Fig. 1). The pterostigma of *Protheristria* **gen. nov.** is completely different (see Fig. 2), more similar to that of other drepanicine genera. Obviously, these two genera belong to different genus groups. Unfortunately, both lack characters of the head, foreleg, pronotum, and genitalia, making it difficult to determine their relationships in greater detail.

Acknowledgements

We thank John Frandsen and Dorthe Rold (Erslev, Denmark) for donating the specimen to NHMD; Henrik Madsen (Museum Mors, Denmark) for discussion; Alisa A. Perkovsky (NHMD) for help in photography; and S. Bruce Archibald (University of British Columbia, Canada) for editing the English and useful comments. The research of VNM was carried out within the framework of the state assignment of Ministry of Science and Higher Education of the Russian Federation (theme No. 124012400285-7). EEP was supported by the Scholars at Risk Ukraine (SARU) program, jointly funded by the Villum Foundation, Carlsberg Foundation and Novo Nordisk Foundation.

References

Ansorge, J. & Schlüter, T. (1990) The earliest Chrysopid: *Liassochrysa stigmatica* n. g., n. sp. from the Lower Jurassic of Dobbertin, Germany. *Neuroptera International*, 6, 87–93.

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 Palaeontology*, 4 (2), 119–155. [Errata: 4 (3), 307]
https://doi.org/10.1017/S1477201906001817

Blanchard, C.É. (1851) Nevropteros. *In*: Gay, C. (Ed.), *Historia Física y Política de Chile. Zoologia. Vol. 6*. En casa del autor, Paris, pp. 85–142.

Breitkreuz, L.C.V., Winterton, S.L. & Engel, M.S. (2017) Wing tracheation in Chrysopidae and other Neuropterida (Insecta): A resolution of the confusion about vein fusion. *American Museum Novitates*, 3890, 1–44.
https://doi.org/10.1206/3890.1

Enderlein, G. (1910) Klassifikation der Mantispiden nach dem Material des Stettiner Zoologischen Museums. *Stettiner Entomologische Zeitung*, 71, 341–379.

Esben-Petersen, P. (1929) Australian Neuroptera. VI. *Queensland Naturalist*, 7, 31–35.

Gerstaecker, [C.E.]A. (1885) Vier decaden von Neuropteren aus der Familie Megaloptera Burm. *Mittheilungen aus dem Naturwissenschaftlichen Verein für Neu-Vorpommern und Rugen*, 16, 1–49.

Hagen, H.A. (1859) Beitrag zur Kenntniss der Neuropteren. *Stettiner Entomologische Zeitung*, 20, 405–412.

Handschin, E. (1935) Indo-australische Neuropteren und Mecopteren. *Revue Suisse de Zoologie*, 42, 683–714.
https://doi.org/10.5962/bhl.part.117937

Jepson, J.E. (2015) A review of the current state of knowledge of fossil Mantispidae (Insecta: Neuroptera). *Zootaxa*, 3964 (4), 419–432.
https://doi.org/10.11646/zootaxa.3964.4.2

Lambkin, K.J. (1986) A revision of the Australian Mantispidae (Insecta Neuroptera) with a contribution to the classification of the family I. General and Drepanicinae. *Australian Journal of Zoology*, Supplementary Series, 116, 1–142.
https://doi.org/10.1071/AJZS116

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.
Leach, W.E. (1815) Entomology. *In*: Brewster, D. (Ed.), *Edinburgh Encyclopaedia. Vol. 9. Part 1.* William Blackwood, Edinburgh, pp. 57–172.
Li, H.Y., Wu, C., Ohl, M. & Liu, X.Y. (2020) A new sexually dimorphic mantidfly species of *Allomantispa* Liu et al., 2015 from China (Neuroptera: Mantispidae). *Journal of Asia-Pacific Entomology*, 23 (4), 988–1002. https://doi.org/10.1016/j.aspen.2020.08.009
Li, H.Y., Zhuo, D., Wang, B., Nakamine, H., Yamamoto, S., Zhang, W.W., Jepson, J.E., Ohl, M., Aspöck, U., Aspöck, H., Nyunt, T.T., Engel, M.S., Benton, M.J., Donoghue, P. & Liu, X.Y. (2025) A double-edged sword: Evolutionary novelty along deep-time diversity oscillation in an iconic group of predatory insects (Neuroptera: Mantispoidea). *Systematic Biology*, 74 (3), 395–420. https://doi.org/10.1093/sysbio/syae068
Li, H.Y., Zhuo, D., Wang, B., Nakamine, H., Yamamoto, S., Zhang, W.W., Ling, J.N., Ohl, M., Aspöck, U., Aspöck, H. & Liu, X.Y. (2023) New genera and species of Mantispoidea (Insecta, Neuroptera) from the mid-Cretaceous Kachin amber, northern Myanmar. *Palaeoentomology*, 6 (6), 549–611. https://doi.org/10.11646/palaeoentomology.6.6.1
Linnaeus, C. (1758) *Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1. 10th Edition.* Salvii, Holmiae, 824 pp. https://doi.org/10.5962/bhl.title.542
Liu, X.Y., Winterton, S.L., Wu, C., Piper, R. & Ohl, M. (2015) A new genus of mantidflies discovered in the Oriental region, with a higher-level phylogeny of Mantispidae (Neuroptera) using DNA sequences and morphology. *Systematic Entomology*, 40 (1), 183–206. https://doi.org/10.1111/syen.12096
Lu, X.M., Wang, B., Zhang, W.W., Ohl, M., Engel, M.S. & Liu, X.Y. (2020) Cretaceous diversity and disparity in a lacewing lineage of predators (Neuroptera: Mantispidae). *Proceedings of the Royal Society (B)*, 287, 20200629. https://doi.org/10.1098/rspb.2020.0629
Madsen, H. (2011) Cementsten og hærdede lag i askeserien. Available from: https://www.vestjyskstenklub.dk/galleri/Cementsten%202010/oversigt%20cementsten.html (accessed 5 May 2025)
Madsen, H. & Rasmussen, J.A. (2021) *Geologien fortæller: Moler og Fossiler/What geology tells: The mo-clay and its fossils*. Museum Mors, Nykøbing Mors, 103 pp.
Makarkin, V.N. (1990) New lacewings (Neuroptera) from the Upper Cretaceous of Asia. *In*: Akimov, I.A. (Chief Ed.), *News of faunistics and systematics*. Naukova Dumka, Kiev, pp. 63–68. [in Russian]
Makarkin, V.N. & Khramov, A.V. (2015) A new fossil species of snakeflies (Raphidioptera: Mesoraphidiidae) from the Late Cretaceous of Kazakhstan, with notes on Turonian Neuropterida. *Cretaceous Research*, 52, 407–415. https://doi.org/10.1016/j.cretres.2014.02.010
Makarkin, V.N., Perkovsky, E.E. & Nielsen, C. (2025) A new genus of Drepanicinae (Neuroptera: Mantispidae) from the early Eocene Fur Formation, Denmark. *Zootaxa*, 5570 (3), 583–590. https://doi.org/10.11646/zootaxa.5570.3.9
McLachlan, R. (1867) New genera and species, &c., of neuropterous insects; and a revision of Mr. F. Walker's British Museum Catalogue of Neuroptera, part ii. (1853), as far as the end of the genus Myrmeleon. *Journal of the Linnean Society of London*, *Zoology*, 9, 230–281.
Ohl, M. (with collaboration with John D. Oswald) (2004) Annotated catalog of the Mantispidae of the World (Neuroptera). *Contributions on Entomology, International*, 5, i–ii + 131–262.
Oswald, J.D. & Machado, R.J.P. (2018) Biodiversity of the Neuropterida (Insecta: Neuroptera, Megaloptera, and Raphidioptera). *In*: Foottit, R.G. & Adler, P.H. (Eds.), *Insect Biodiversity: Science and Society. Vol. 2*. John Willey & Sons Ltd, Oxford, pp. 627–671. https://doi.org/10.1002/9781118945582.ch21
Panfilov, D.V. (1980) [New representatives of lacewings (Neuroptera) from the Jurassic of Karatau]. *In*: Dolin, V.G., Panfilov, D.V., Ponomarenko, A.G. & Pritykina, L.N. (Eds.), *Fossil insects of the Mesozoic*. Naukova Dumka, Kiev, pp. 82–111. [in Russian]
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) Molerområdets geologi—sedimenter, fossiler, askelag og glacialtektonik. *Geologisk Tidsskrift*, 2011, 41–135.
Pedersen, G.K. & Surlyk, F. (1983) The Fur Formation, a late Paleocene ash-bearing diatomite from northern Denmark. *Bulletin of the Geological Society of Denmark*, 32, 43–65. https://doi.org/10.37570/bgsd-1983-32-03
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