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

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Abstract

Danomantispa frandseni **gen. et sp. nov.** (Neuroptera: Mantispidae: Drepanicinae) is described from the earliest Eocene Fur Formation, Denmark. This is the first record of Mantispidae from this formation, and the northernmost finding of Drepanicinae. The new genus is easily distinguished from other drepanicine genera by mantispine-like pterostigma: the distal crossvein between Sc and RA is located in the distal part of the pterostigma, and the section of Sc distad it is nearly straight and rather short. Both Cenozoic genera (this genus and *Vectispa* Lambkin, 1986) are to some degree intermediate between Drepanicinae and Mantispinae: *Danomantispa* **gen. nov**. is a drepanicine with a mantispine-like pterostigma, and *Vectispa* is most probably a mantispine with a drepanicine-like pterostigma. Data on the climatic conditions of the existence of the subfamily in the past and today are summarized. We assume that the Fur Formation climate at the time of *D. frandseni* **sp. nov.** was highest microthermal/low mesothermal.

Key words: fossil insects, mantidflies, taxonomy, new genus and species, paleoclimate

Introduction

The Mantispidae, remarkable for their raptorial forelegs, today comprise nearly 400 extant species (Ohl & Oswald 2004; Oswald & Machado 2018). The family is widely distributed, but absent in northern regions of the Northern Hemisphere and southernmost regions of the Southern Hemisphere. Six subfamilies of Mantispidae are currently recognized: two are Mesozoic (Mesomantispinae and Doratomantispinae), and four are extant with fossil taxa (Drepanicinae, Symphrasinae, Mantispinae, and Calomantispinae) (Jepson 2015; Oswald & Machado 2018; Makarkin 2019; Lu *et al*. 2020).

Extant Drepanicinae comprise five genera: two from South America (*Drepanicus* Blanchard, 1851 and *Gerstaeckerella* Enderlein, 1910), two from Australia (*Theristria* Gerstaecker, 1885 and *Ditaxis* McLachlan, 1867) and one from southeast Asia (southeastern Tibet, northern Myanmar, southern Yunnan: *Allomantispa* Liu, Wu, Winterton et Ohl in Liu *et al*., 2015) (Lambkin 1986a; Ohl & Oswald 2004; Liu *et al*. 2015; Li *et al*. 2020). Seven extinct genera with nine species have been described from the Mesozoic: *Liassochrysa stigmatica* Ansorge & Schlüter, 1990 from the Early Jurassic (early Toarcian) of Dobbertin (Germany); *Promantispa similis* Panfilov, 1980 from the Late Jurassic of Karatau (Kazakhstan); *Sinuijumantispa ryonsangiensis* So & Won, 2022 from the Early Cretaceous (Barremian–Aptian) of Korea; *Aragomantispa lacerata* Pérez-de la Fuente & Peñalver, 2019 from the Early Cretaceous (Albian) Spanish amber; *Acanthomantispa grandis* Lu *et al*., 2020, *A. immaculata* Lu *et al*., 2020, *A. maculata* Lu *et al*., 2020, *Dicranomantispa zhouae* Lu *et al*., 2020, and *Psilomantispa abnormis* Lu *et al*., 2020 from mid-Cretaceous Myanmar amber (Liu *et al*. 2015; Pérez-de la Fuente & Peñalver 2019; Lu *et al*. 2020; So & Won 2022). One fossil species from the Late Cretaceous (Turonian) of Kyzylzhar (Kazakhstan), *i.e.*,

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Gerstaeckerella asiatica Makarkin, 1990, was assigned to an extant genus (Makarkin 1990; Makarkin & Khramov 2015).

Only one Cenozoic species, *i.e.*, *Vectispa relicta* (Cockerell, 1921) from the latest Eocene of the Bembridge Marls (England: see Jarzembowski 1980) was assigned to Drepanicinae by Lambkin (1986a), but was later transferred to the Mantispinae (Makarkin 2019; Perkovsky & Makarkin 2020). In particular, its forewing crossvein 2m-cu connects the stem of M and CuA as is characteristic of Mantispinae, whereas this crossvein connects MP and CuA in all Drepanicinae.

Here, a new genus and species is described from the earliest Eocene Fur Formation in Denmark, the first confident record of fossil Drepanicinae from the Cenozoic. Overviews of this Danish Lagerstätte have been provided by *e.g.*, Larsson (1975); Pedersen & Surlyk (1983), Archibald & Makarkin (2006), Pedersen *et al*. (2012), and Rasmussen *et al*. (2016). The Neuroptera are represented in the formation by Hemerobiidae, Chrysopidae, Osmylidae, Polystoechotidae, Berothidae, and now Mantispidae (Henriksen 1922; Schlüter 1982; Willmann & Brooks 1991; Willmann 1993; Andersen 2001; Archibald & Makarkin 2006; Makarkin & Perkovsky 2023, 2024; Makarkin *et al*. 2024). Previously, all of these species have been described from upper horizons of the formation (when specific layer data are available), which experienced a cooler climate than the lower sediments (Stokke *et al*. 2020). The mantispid described here is the first known neuropteran from the basal horizons (ash layers -24 to -29). The precise age of these ash layers is unknown, but the age of upper ash layer -17 is 55.6 Ma by ^{40}Ar/^{39}Ar (Storey *et al*. 2007; Stokke *et al*. 2020).

Materials and methods

The specimen is preserved in a stone washed out in a large landslide from a cliff near Gammelgård Strand, Fur Island, northern Jutland, Denmark. It was photographed with a Dino-Lite Edge AM7915MZTL camera and is deposited in the Natural History Museum of Denmark (NHMD). 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.

We use the mean annual temperature climate categories of Wolfe (1975): microthermal, ≤ 13°C; mesothermal, > 13°C, < 20°C; megathermal, ≥ 20°C.

Order Neuroptera Linnaeus, 1758

Family Mantispidae Leach, 1815

Subfamily Drepanicinae Enderlein, 1910

Genus *Danomantispa* gen. nov.

Type and only species. *Danomantispa frandseni* **sp. nov.**

Diagnosis. This new genus may be easily distinguished from other genera of Drepanicinae by pterostigma structure: distal crossvein/-s between Sc and RA located in its distal part; section of Sc distad it nearly straight, rather short (‘mantispine-like’) [this crossvein (or crossveins) located nearly in middle of pterostigma and section of Sc distad it curved and long in other genera].

Etymology. From Denmark and *Mantispa*, a genus-group name. Gender feminine.

Danomantispa frandseni **sp. nov.**

Fig. 1

Type material. Holotype: MGUH 34839 (accession number GM 2024.15), a nearly complete forewing collected on 13 August 2024 by John Frandsen (Erslev, Denmark) and deposited in the collection of the Natural History Museum of Denmark.

Type locality and horizon. Denmark: northern Jutland: north cost of Fur Island near Gammelgård Strand (56.841262N, 8.992038E); Fur Formation, lower part of Knudeklint Member (ash layers -24 to -29); earliest Eocene.

Etymology. From the surname of John Frandsen (Erslev, Denmark), collector of the holotype.

Description. Forewing *ca*. 16.2 mm long as preserved (estimated complete length *ca*. 16.7), 4.5 mm wide. Costal space dilated proximally, heavy constricted before pterostigma. Subcostal veinlets simple, widely spaced. Part of Sc closing pterostigma distally (distad distal crossvein between Sc, RA) nearly straight. Pterostigma dark, elongated, veinlets within it indiscernible; distal crossvein between Sc, RA located in distal part of pterostigma. Subcostal space relatively narrow, dilated before pterostigma; with three crossveins detected: basal one indiscernible or absent; two closely spaced intermediate ones distad origin of RP; one distal one very short. RA distally with two preserved simple veinlets (at least three in live). RA space narrowed toward apex, with three crossveins. RP originates rather far from wing base (at *ca*. 0.26% complete length), with 12 branches; all preserved branches forked once (some distal branches possibly simple). M basally appears to be fused with R, but might only be very close; forked far distad origin of RP. MA, MP each forked once. Fork of Cu not preserved. CuA pectinately forked, with two short simple branches. CuP, A1 deeply forked with all branches simple. First (basal) gradate series of crossveins not preserved. Second series represented by three crossveins: 2r-m connects stem of RP and MA; 2m-cu connects MP and CuA slightly proximad 2icu; 2icu connects 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 14 crossveins from distal branch of RP to CuA. Wing maculation probably absent.

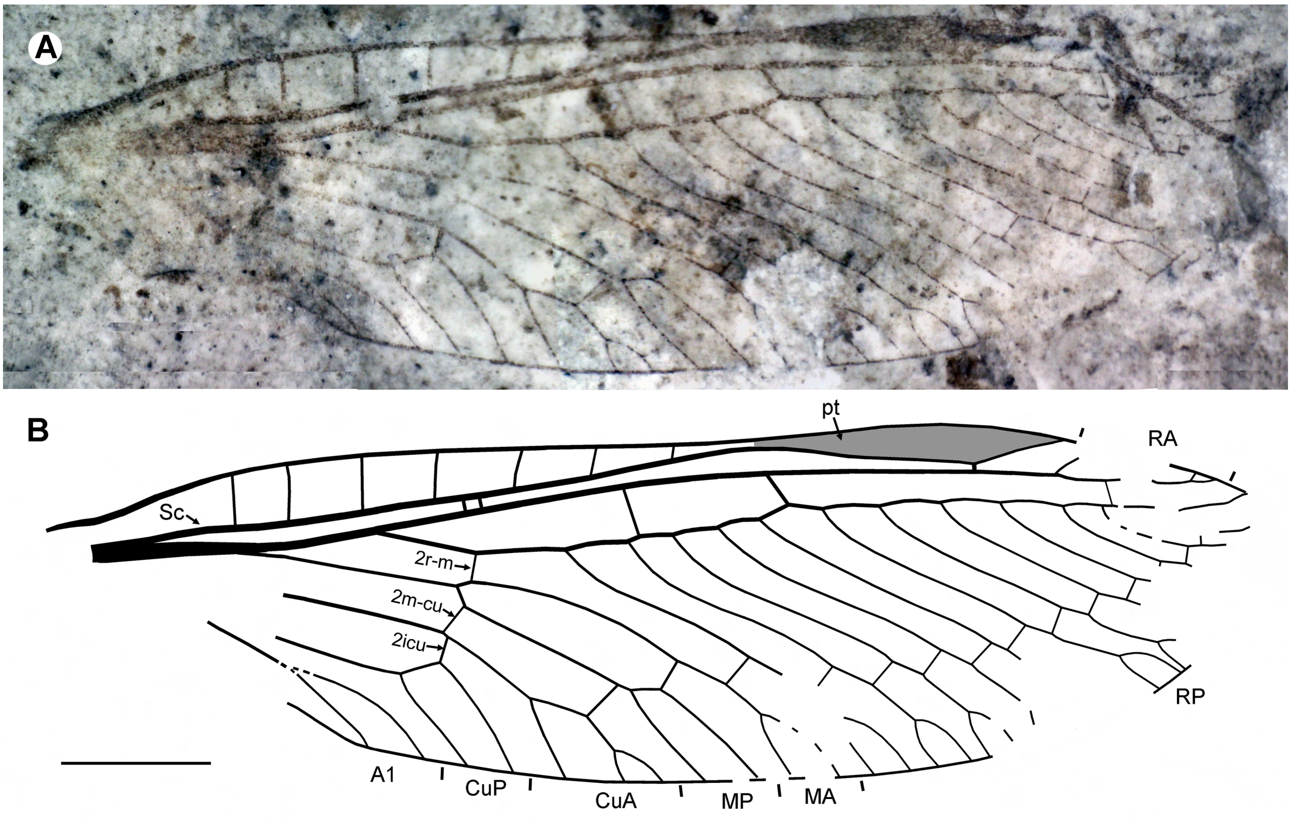

FIGURE 1. *Danomantispa frandseni* **gen. et sp. nov.**, holotype MGUH 34839, specimen as preserved. B, forewing venation. Scale bar 2 mm (both to same scale).

Discussion

The new genus is most similar to Drepanicinae, Mantispinae and Calomantispinae by the structure of the pterostigma, which is located in the distal part of the costal space, *i.e.*, between Sc and the costal margin (see Lambkin 1986a for details). The genus is assigned with certainty to Drepanicinae, based on a combination of the following forewing states: its A1 is forked [simple in Mantispinae]; M is probably not fused basally with R (although they closely approach) or they are fused for a short distance [fused for a long distance in Mantispinae and Calomantispinae]; and crossvein 2m-cu connects MP and CuA [connecting the stem of M and CuA in Mantispinae and Calomantispinae (except some *Calomantispa* Banks, 1913)]. The structure of the pterostigmal area of other mantispid subfamilies (Symphrasinae, Doramantispinae and Mesomantispinae) strongly differs from that of the new genus. The Sc of these three subfamilies is fused with RA distally, and the pterostigmal area is located distad this fusion between Sc+RA and the costal margin. Otherwise, the forewing venation of Doramantispinae is very similar to that of Drepanicinae (see *e.g*., Shi *et al*. 2019: Fig. 3). The forewing venation of Symphrasinae and Mesomantispinae further differs from *Danomantispa* **gen. nov.** by the presence of the recurrent and branched humeral veinlet (see *e.g*., Jepson *et al*. 2013: Fig. 1C; Ardila-Camacho *et al*. 2024: Fig. 2A).

The forewing venation of *Danomantispa* **gen. nov.** is most similar to that of the genus *Gerstaeckerella* in having one gradate series of crossveins in the radial to intramedial spaces [two in *Liassochrysa* Ansorge & Schlüter, 1990, *Promantispa* Panfilov, 1980, *Allomantispa*, *Ditaxis*]; the presence of a short distal crossvein between Sc and RA [two to nine extremely short in *Theristria*; long in *Acanthomantispa* Lu *et al*., 2020, *Dicranomantispa* Lu *et al*., 2020, *Psilomantispa* Lu *et al*., 2020]; one or two relatively short branches of CuA [at least three long branches in *Drepanicus*, *Acanthomantispa*, *Dicranomantispa*].

However, the pterostigma of the new genus is more similar to that of Mantispinae, especially to such genera with rich venation as *Euclimacia* Enderlein, 1910 and *Entanoneura* Enderlein, 1910 (see *e.g*., Enderlein 1910: Figs 2, 3; Lambkin 1986b: Fig. 655). In Mantispinae, the distal crossvein (or crossveins) between Sc and RA is located in the distal part of the pterostigma, and the section of Sc distad it is nearly straight and rather short, similar to that of *Danomantispa* **gen. nov**. In other Drepanicinae, this crossvein (or crossveins) is located nearly in the middle of the pterostigma, and the section of Sc distad it is often curved and long. By this, the structure of the pterostigma in *Vectispa relicta* is drepanicine-like (see Jarzembowski 1980: Fig. 30), although other preserved characters are characteristic of Mantispinae. We may state, therefore, that both Cenozoic genera are to some degree intermediate between Drepanicinae and advanced Mantispinae: *Danomantispa* **gen. nov**. is a drepanicine with the mantispine-like pterostigma, and *Vectispa* is probably a mantispine with a drepanicine-like pterostigma.

The subfamilies Drepanicinae, Mantispinae and Calomantispinae form a monophyletic clade, and their close relationship is undoubted (Lambkin 1986a; Liu *et al*. 2015; Li *et al*. 2024). The more ancient subfamily Drepanicinae is certainly ancestral to younger subfamily Mantispinae. Some morphological characters (such as the structure of the pterostigma) found in *Danomantispa* **gen. nov**. are seen later in Mantispinae.

The family Mantispidae is a relatively thermophilic group compared with, *e.g*., such families as Hemerobiidae, Chrysopidae and Coniopterygidae. The oldest known Drepanicinae (*Liassochrysa stigmatica*) lived in the early Toarcian, the warmest ('super-greenhouse') interval of the Jurassic (*e.g*., Hermoso *et al*. 2013; Xu *et al*. 2018). The climate of the Oxfordian/Kimmeridgian Karabastau Formation, in which *Promantispa similis* was found, and the Turonian Kyzylzhar (both Kazakhstan), in which *Gerstaeckerella asiatica* was found, was arid subtropical (Vakhrameev 1988), *i.e*., probably high mesothermal. The diverse drepanicines preserved in mid-Cretaceous Myanmar amber (three genera, five species) lived in tropical conditions. The genera *Sinuijumantispa* So & Won, 2022 and *Aragomantispa* Pérez-de la Fuente & Peñalver, 2019 are not drepanicines. The former genus was recently assigned to Mesomantispinae (see Li *et al*. 2024), and the latter belongs to Doramantispinae judging from the preserved venation, especially by the structure of its pterostigmal area typical of other doramantispids.

Extant Drepanicinae have a disjunct distribution (see Introduction). Species of the subfamily are rare to very rare, except for some in Australia. The three known species of *Allomantispa* are restricted to mountainous regions of southeast Asia (see Introduction), which are covered by tropical or subtropical forests (Li *et al*. 2020). The twenty-two known species of the two Australian genera *Theristria* and *Ditaxis* occur in mainly low to mid altitudes of nearly across the entire continental of Australia. Those species are known mostly from megathermal and mesothermal localities, but a few localities in alpine regions of the Snowy Mountains may be high microthermal (Lambkin 1986a). It is noteworthy that the subfamily has not been collected in Tasmania.

The habitats of the eleven species in the genera *Drepanicus* and *Gerstaeckerella* are very poorly known with published data limited mainly to their systematics and collection localities (*e.g*., Erichson 1839; Blanchard 1851; Hagen 1859; Brauer 1867; Enderlein 1910; Navás 1910, 1912, 1925, 1926, 1930a, b, 1932; Rehn 1939; Williner & Kormilev 1958; Penny & da Costa 1983; Ardila-Camacho & Garcia 2015; Silva *et al*. 2016; Ardila-Camacho *et al*. 2018). These two South American genera are found as far south as 39°38'S in Chile and 38°56'39.66"S in Argentina at low altitudes from nearly sea level to approximately 1000 m above sea level. Most localities have megathermal or high mesothermal climates, but the southernmost localities have high microthermal to low mesothermal climates. Thus, the climatic conditions in which representatives of Drepanicinae lived and continue to live has been consistently about high mesothermal to megathermal throughout their existence to the present day, rarely high microthermal to low mesothermal.

The holotype of *Danomantispa frandseni* **sp. nov.** was found in the lowest part of the Fur Formation (ash layers -24 to -29); the lower boundary of the formation being at ash layer -33 (Rasmussen *et al*. 2016). The underlying Ølst Formation was deposited during the Paleocene-Eocene Thermal Maximum (PETM). However, the earliest Fur Formation was deposited during a period of relatively sharp cooling, returning to pre-PETM values (the so called "recovery phase"), from ash layer -33 to -21 when sea surface temperature decreased by >10^{o}C (Stokke *et al*. 2020). Aphids, a good indicator of strong post-PETM cooling (Perkovsky & Wegierek 2018), were quite rare in these layers, 4.1 times less common than in layers +25 to +30 (Rust 1999). However, glendonite (indicators of the cold bottom temperatures) is not known from these layers (Vickers *et al.* 2024), indicating that cooling in the time of *Danomantispa frandseni* **sp. nov.** could be not too strong relative to the upper layers (see Prokin *et al*. 2024). The majority of extant rove beetles of the subtribe Pinophilina (Staphylinidae), a representative of which has been recently described from the same layers, are subtropical and tropical, but some taxa are cold tolerant (Jenkins Shaw *et al*. 2024 and references therein). Therefore, based on all of these data, we may assume that the conditions during the recovery phase were highest microthermal to low mesothermal.

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