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A new remarkable genus and species of Mantispidae (Neuroptera) from the earliest Eocene of Denmark

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Abstract

Heiemantispa storozhenkoi **gen. et sp. nov.** (Neuroptera: Mantispidae) is described from the earliest Eocene Fur Formation, Denmark. The genus is distinguished from others of the family by a combination of forewing character states: a simple CuP (unique in Drepanicinae, if it belongs to that subfamily) and a basally unfused M and R. The venation of *Heiemantispa* **gen. nov.** is most similar to that of *Protheristria* Makarkin *et al*., 2025, also from the Fur Formation. Both genera are known only from incomplete wings of their type species, the venation of which does not allow them to be confidently assigned to either the subfamily Drepanicinae or Calomantispinae.

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

Introduction

The Mantispidae comprise nearly 400 extant and 54 extinct species in six subfamilies: †Mesomantispinae, †Doratomantispinae, Drepanicinae, Symphrasinae, Calomantispinae and Mantispinae (several fossil genera have not been assigned to a subfamily) (Jepson 2015; Oswald & Machado 2018; Lu *et al*. 2020; Li *et al*. 2023; Makarkin & Staniczek 2026).

Today, the subfamily Drepanicinae is unevenly distributed and includes forty species in five genera: *Drepanicus* Blanchard, 1851 and *Gerstaeckerella* Enderlein, 1910 from South America; *Theristria* Gerstaecker, 1885 and *Ditaxis* McLachlan, 1867 from Australia; and *Allomantispa* Liu, Wu, Winterton et Ohl in Liu *et al*., 2015 from southeast Asia (Lambkin 1986; Ohl & Oswald 2004; Liu *et al*. 2015; Li *et al*. 2020). Calomantispinae comprise two genera: *Calomantispa* Banks, 1913 from Australia and *Nolima* Navás, 1914 from southwestern USA south to Costa Rica (Lambkin 1986b; Reynoso-Velasco & Contreras-Ramos 2019).

Fossils of these two subfamilies are extremely scarce. The Turonian *Gerstaeckerella asiatica* Makarkin, 1990 from Kyzylzhar (Kazakhstan) was the only fossil species confidently considered to belong to Drepanicinae (Li *et al*. 2024). Other Mesozoic genera previously assigned to it (Liu *et al*. 2015; Pérez-de la Fuente & Peñalver 2019; Lu *et al.* 2020; So & Won 2022) are now considered to not belong to the subfamily, however, the subfamily assignments of these need detailed revision. Recently, *Danomantispa frandseni* Makarkin *et al*., 2025b and *Protheristria roldae* Makarkin *et al*., 2025a were described from the earliest Eocene Fur Formation of Denmark (but see below on the drepanicine affinity of the latter). The only fossil genus which likely belong to Calomantispinae is the monotypic *Protonolima* Makarkin, 2019 from the early Eocene Green River Formation in the USA (Makarkin 2019).

The earliest Eocene Fur Formation in Denmark is the only Cenozoic deposit in the Old World where reliable remains of Drepanicinae and/or Calomantispinae have been found. Here, we describe a new genus and species from this formation with venation consistent with both subfamilies. Further, we re-evaluated the subfamily assignment of *Protheristria* Makarkin *et al*., 2025a. Its venation also allows to assign the genus to be assigned to either.

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The Fur Formation represents one of the best-known Eocene Lagerstätte. Overviews of the formation have been provided by *e.g.*, Larsson (1975); Pedersen & Surlyk (1983), Archibald & Makarkin (2006), Pedersen *et al*. (2012), and Madsen & Rasmussen (2021).

Materials and methods

Two specimens were collected at Vangsgaard pit on Mors Island in northern Jutland (Denmark) in the same concretion with the holotype of *Protheristria roldae* Makarkin *et al*., 2025a (Mantispidae), the holotype of *Mesypochrysa frandseni* Makarkin *et al*, 2026 (Chrysopidae), and the holotype of the first Eocene Roproniidae (Hymenoptera) (Perkovsky & Rasnitsyn 2026). This calcareous concretion was found in the Vangsgaard pit quarry, but its structure is most like that of concretions located 0.5 m above ash layer -17 (see Madsen 2011). It is approximately 120 cm long, 60 cm wide, and 40 cm thick, and contains about 240 insect fossils (Ch. Nielsen, pers. comm.). Ash layer -17 is approximately 55.6 Ma (Stokke *et al*. 2020).

Digital images of specimens wetted with deionized water were done with flash lighting and a P-51 Camlift 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 uncertain

Genus *Heiemantispa* gen. nov.

Type and only species. *Heiemantispa storozhenkoi* **sp. nov.**

Diagnosis. May be easily distinguished from other genera of the family by forewing CuP simple [forked in all other genera except three species (see Discussion)] and M not fused basally with R [fused for long distance in *Nolima* and Mantispinae].

Etymology. From the surname of Ole Engel Heie (10 May 1926 – 4 January 2019), a Danish entomologist and paleoentomologist, and *Mantispa*, a genus-group name. Gender feminine.

Heiemantispa storozhenkoi sp. nov.

Figs 1–4

Type material. Holotype: NHMD 2042530 (accession number GM 2025.6a), collected by Dorthe Rold and John Frandsen on February 15, 2025, deposited in the collections of the Natural History Museum of Denmark; incomplete right wings and fragmentary left forewing. Next to the holotype specimen are syncompressions of nearly complete Ectobiidae (Dictyoptera), and incomplete Trichoptera and Cylindrotomidae (Diptera).

Paratype: NHMD 2043537 (accession number GM 2025.7); a nearly complete forewing. Other data are the same as for the holotype.

Type locality and horizon. Denmark: northern Jutland: Mors Island: Vangsgaard pit (56.941308°N, 8.891708°E); Fur Formation, middle part of the Knudeklint Member (0.5 m above ash layer -17); earliest Eocene.

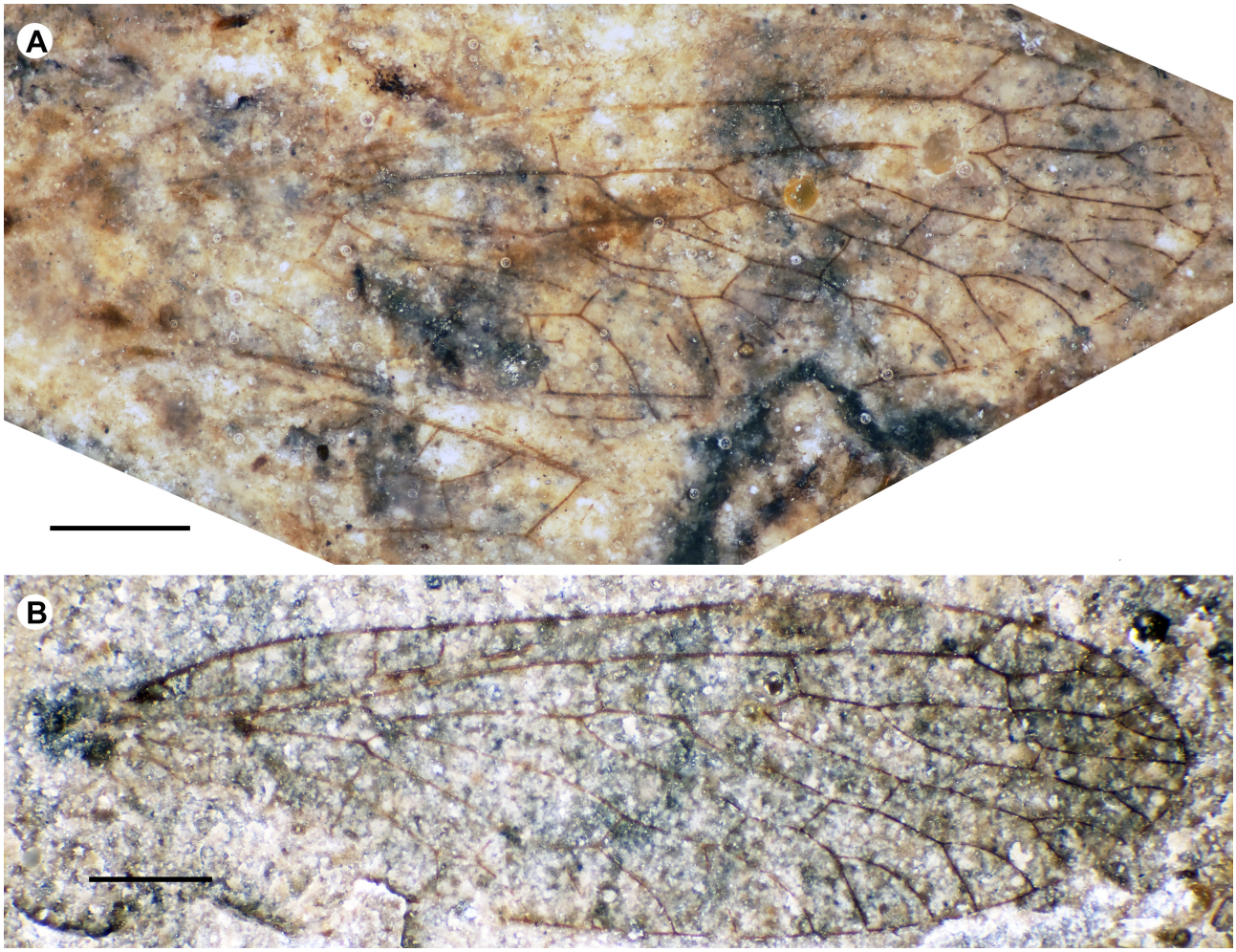

FIGURE 1. *Heiemantispa storozhenkoi* **sp. nov.**, A, holotype NHMD 2042530 (GM 2025.6a); B, paratype NHMD 2043537 (GM 2025.7). Scale bars = 1 mm.

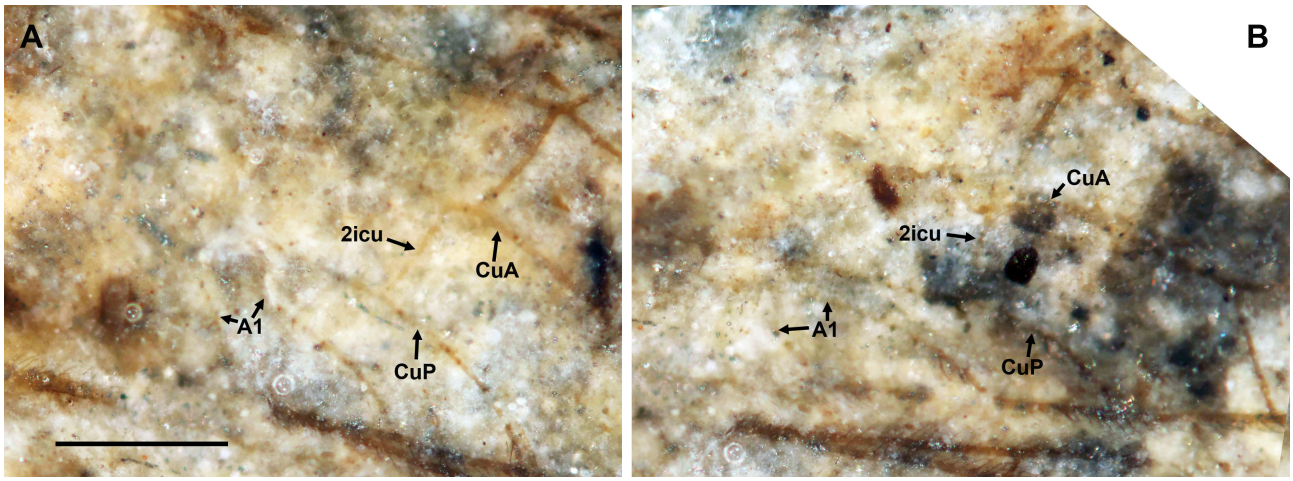

FIGURE 2. The forewing CuP area of *Heiemantispa storozhenkoi* **sp. nov.**, holotype NHMD 2042530 (GM 2025.6a). A, right wing; B, left wing (converted to standard right view). Scale bar = 0.5 mm (both to same scale).

Etymology. From the surname of Sergey Yu. Storozhenko, a Russian entomologist and paleoentomologist in honor of his 70th birthday.

Description. *Holotype* NHMD 2042530 (GM 2025.6a). Forewing approximately 8.6 mm long, 2.6 mm wide. Costal space incompletely preserved. Costal margin markedly concave before pterostigma. Basal subcostal

veinlets probably simple, widely spaced. Pterostigma pale, slightly brownish, short; three veinlets within it clearly discernible; distal crossvein between Sc, RA located in middle of pterostigma. Subcostal space incompletely preserved; no crossveins detected. RA distally with two widely spaced simple veinlets: proximal longer, distal shorter. RA space with three crossveins: 2ra-rp located distad origin of RP1 so that basal cell between RA, RP long, narrowed proximally; 3ra-rp located opposite pterostigma; 4ra-rp located distad proximal veinlet of RA. RP originates far from wing base at acute angle (at approximately 24% complete length), its anterior trace rather deeply forked; with four branches, all forked once. M forked distad origin of RP. MA, MP each once forked. CuA forked once with simple branches. CuP simple. A1 forked once. First (basal) gradate series of crossveins with one partially preserved crossveins (1m-cu). Second series with three crossveins: 2r-m short, connecting stem of RP and MA; 2m-cu long, connecting MP near its origin and CuA slightly distad 2icu; 2icu long (2ra-rp may belong to this series). Third series absent (3ra-rp may belong to this series). Fourth (outer) series complete, nearly parallel to posterior margin, with six crossveins from distal branch of RP to CuA (4ra-rp may belong to this series). Wing maculation probably absent. Setae on veins and margins rather short and sparse.

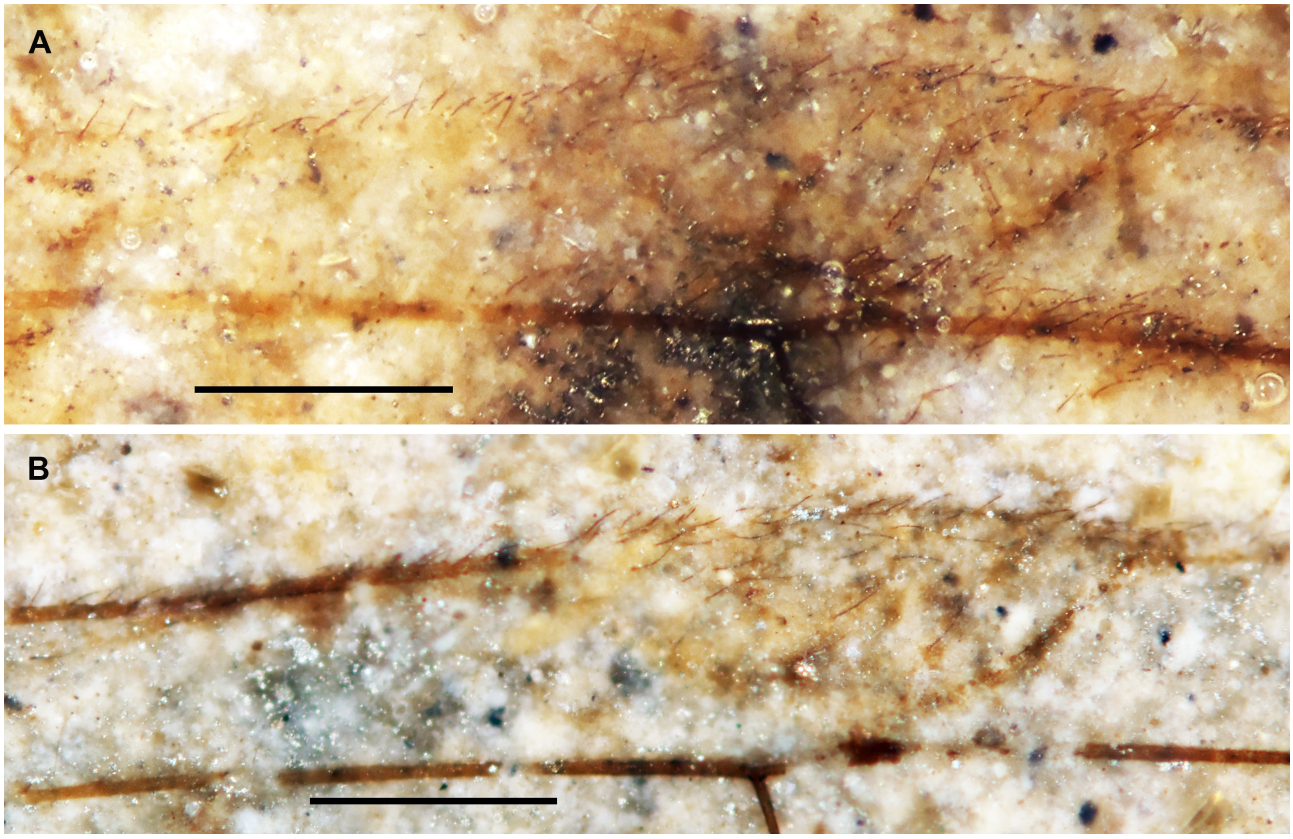

FIGURE 3. Pterostigmata of *Heiemantispa storozhenkoi* **sp. nov.** A, holotype NHMD 2042530 (GM 2025.6a). B, paratype NHMD 2043537 (GM 2025.7).

Hind wing 7.7 mm long as preserved (approximately 8.1–8.3 mm estimated complete length), approximately 2.2 mm wide. Venation preserved fragmentarily. RP originating at acute angle, with four branches; RP1 originating far from origin of RP; RP1, RP2 distally forked; RP4 probably simple. Two crossveins in RA space preserved. MA distally forked. MP probably with two branches.

Paratype NHMD 2043537 (GM 2025.7). Forewing 8.9 mm long, 2.8 mm wide. Costal space relatively narrow, dilated most at proximal 1/5 length of wing length, narrowed basad and distad. Costal margin markedly concave before pterostigma. Subcostal veinlets simple, widely spaced; humeral veinlet simple with apex directed to wing base. Pterostigma pale, slightly brownish, short; veinlets within it indiscernible. Subcostal space relatively broad, strongly dilated before pterostigma; basal crossvein located opposite origin of RP; distal crossvein short, located in central part of pterostigma. RA distally with two veinlets: one long, distal-most short. RA space with three crossveins: 2ra-rp located distad origin of RP1 so that basal cell between RA, RP long, narrowed proximally; 3ra-rp

located opposite pterostigma; 4ra-rp located distad proximal veinlet of RA. RP originates far from wing base (at approximately 0.25 complete length), its anterior trace rather deeply forked; with five branches, distal-most simple, other forked once. M probably not fused basally with R; forked approximately at level of origin of RP. MA, MP each once forked. Cu forked rather far from wing base. CuA forked once with simple branches. CuP, A1 preserved only basally. First (basal) gradate series of crossveins with two preserved crossveins: 1m-cu rather stout; 1cup-a1 oblique (basal subcostal crossvein may belong to this series). Second series with three crossveins: 2r-m short, connecting stem of RP and MA; 2m-cu long, connecting MP near its origin and CuA nearly opposite 2icu; 2icu long (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 CuA (distal crossvein between RA, RP may belong to this series). Wing maculation probably absent.

Remarks. These two specimens surely belong to the same species as they differ only in small details of venation: in the holotype, crossvein 1r-m is slightly longer, and crossvein 2m-cu is connected to M and Cu near the fork of M, while in the paratype it is connected to MA and CuA slightly distad the fork of M.

Discussion

The preserved venation of the new genus does not allow us to confidently assign it to the subfamily Drepanicinae Enderlein, 1910 or to Calomantispinae Navás, 1914. These subfamilies (along with Mantispinae) have a similar structure of the pterostigma, which is located between Sc and the costal margin (see Lambkin 1986a and Makarkin *et al*. 2025b for further details). The pterostigma of other subfamilies (Symphrasinae, Doramantispinae and Mesomantispinae) is located between Sc+RA or RA and the costal margin.

The rounded pterostigma of *Heiemantispa* **gen. nov.** is very similar to that of Calomantispinae (see Lambkin 1986b: Figs 419, 435; Liu *et al*. 2015: Fig. 12A), but the venation of the new genus is generally similar only to that of *Calomantispa* within subfamily. The venation of two other (American) calomantispine genera is strongly different in that their M is fused with R for a long distance, so that the basal crossvein between M and CuA (1m-cu) connects CuA and R+M (see Reynoso-Velasco & Contreras-Ramos 2019: Fig. 4). In all Drepanicinae and *Calomantispa* (including the new genus), M is basally not fused with R (but they may closely approach), and, therefore, 1m-cu connects CuA and M (rarely at the apparent fusion with R or where R and M approach).

However, *Calomantispa* differs from the new genus by many other characters of venation (*i.e*., except pterostigma): all three species of *Calomantispa* have a strongly dilated costal space [moderately dilated in *Heiemantispa* **gen. nov.**]; there are two to three crossveins between Sc and RA in the pterostigmal area [one in *Heiemantispa* **gen. nov.**]; two to three crossveins between CuA and CuP [one in *Heiemantispa* **gen. nov.**]; and crossvein 2r-m connects RP and the stem of M (or these veins are fused at this point) [connects RP and MA in *Heiemantispa* **gen. nov.**].

Thus, the venation of both *Calomantispa* and *Nolima* greatly differs from that of the new genus and shares with it only the rounded pterostigma (except other features characteristic of most Mantispidae). Despite significant differences in the venation, *Calomantispa* and *Nolima* are grouped together as a single subfamily based on the presence of bifid claws and some genital features (Lambkin 1986a). It is possible, however, that this subfamily is paraphyletic, and *Calomantispa* may belong to the subfamily Drepanicinae. But it needs a more detailed examination.

On the other hand, the preserved venation of *Heiemantispa* **gen. nov.** agrees well with that of Drepanicinae. The structure of its rounded pterostigma does not principally differ from that of other genera of the subfamily. Of fossil taxa, the venation of *Heiemantispa* **gen. nov.** is most like that of *Protheristria* Makarkin *et al*., 2025a from the Fur Formation (*cf*. Figs 4A and 4E). A re-examination of the holotype of *Protheristria roldae* shows that the forewing Sc is located closer to the costal margin than was depicted in Figure 3A of Makarkin *et al*. (2025a) (see our new figure 4E); the earlier depicted Sc (Makarkin *et al*. 2025a: Fig. 3A) actually belongs to the hind wing. The forewing venation of the new genus may be distinguished from *Protheristria* by the following character states (except the simple CuP): the pterostigma is more rounded [clearly elongate in *Protheristria*]; RA distad the pterostigma is not curved posteriorly and has two distal veinlets [RA distad the pterostigma is clearly curved posteriorly, with three veinlets in *Protheristria*]; RP originates at a more acute angle [more obtuse angle in *Protheristria*]; the basal cell between RA, RP is longer (length/width ratio 4.4–5.0), and is proximally narrowed [shorter (length/width ratio 3.8), proximally wide in *Protheristria*].

Of the extant genera, both (*Heiemantispa* **gen. nov.** and *Protheristria*) are most like *Theristria*. The venation of some *Theristria* species is generally similar to that of these fossil Danish genera, but their pterostigmata differ by being very dark with two to nine extremely short subcostal crossveins in the pterostigmal region in *Theristria* [pterostigmata are pale with one subcostal crossveins in *Heiemantispa* **gen. nov.** and *Protheristria*].

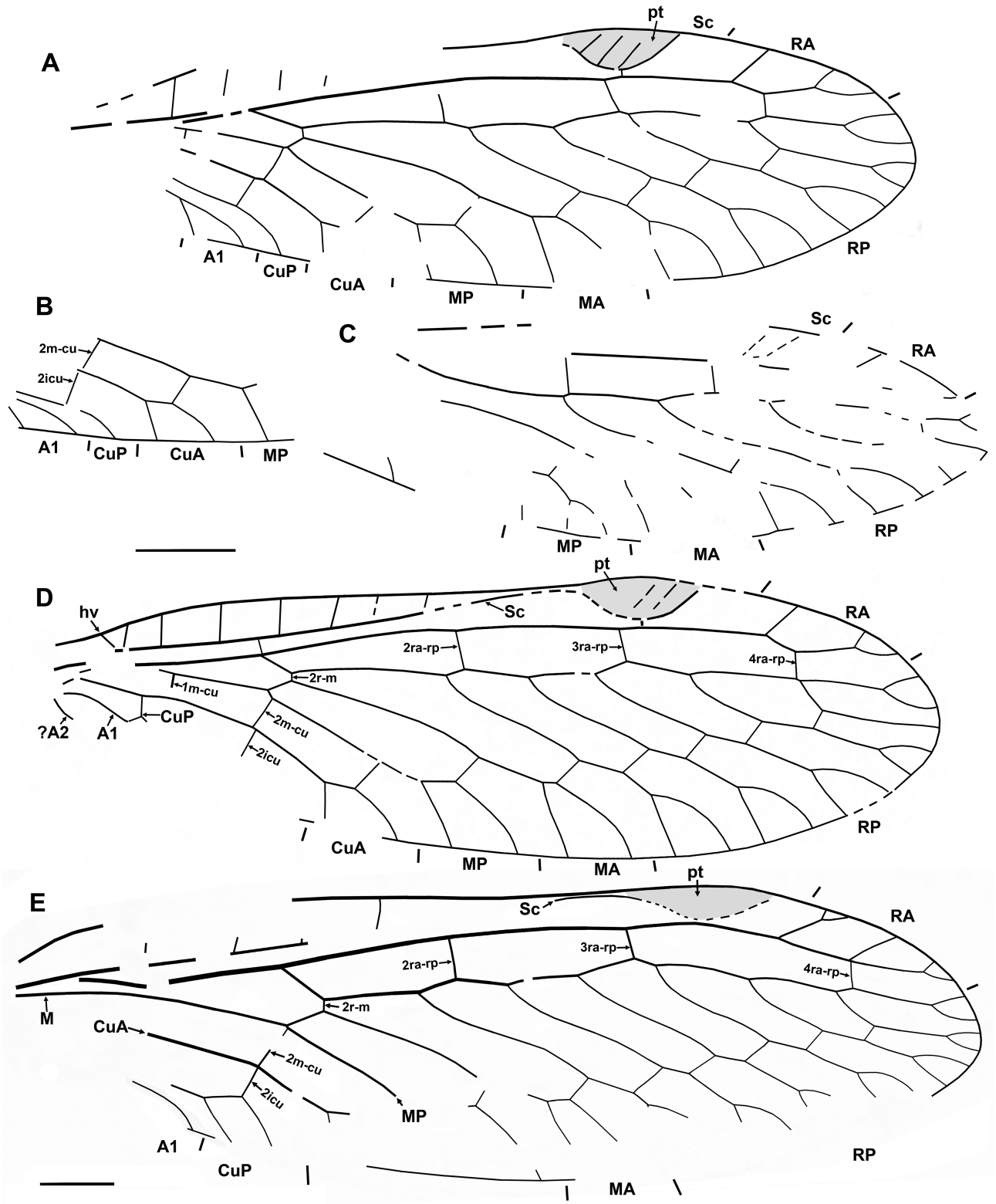

FIGURE 4. Wing venation of *Heiemantispa storozhenkoi* **sp. nov.** (A–D) and *Protheristria roldae* Makarkin *et al*., 2025 (E). A–C, holotype NHMD 2042530 (GM 2025.6a): A, right forewing; B, left forewing; C, right hind wing; D, paratype NHMD 2043537 (GM 2025.7), forewing; E, holotype MGUH 35093 (GM 2025.1), forewing (re-drawn from Makarkin *et al*., 2025a with slightly changed venation in the pterostigmal area, see the text). Scale bars = 1 mm (A–D to same scale).

The forewing CuP of *Heiemantispa* **gen. nov.** is simple. It is deeply forked in the vast majority of Mantispidae, and its shallowly forked or simple states occur extremely rarely. We know of only a few species with such a structure of CuP: the mid-Cretaceous *Rhachisymphrasis raehlei* Makarkin & Staniczek, 2026 (Symphrasinae); the Oligocene *Prosagittalata oligocenica* Nel, 1989 and the extant *Leptomantispa chaos* Hoffmann, 2002 (both Mantispinae), and the extant genus *Nolima* Navás, 1914 (Calomantispinae) (Nel 1989: Fig. 3; Hoffmann 2002: Fig. 587; Reynoso-Velasco & Contreras-Ramos 2019: Fig. 4A; Makarkin & Staniczek 2026: Fig. 6A).

Wing venation shows that *Heiemantispa* **gen. nov.** and *Protheristria* are more closely related to each other than either is to *Danomantispa* Makarkin *et al*., 2025b. The former two genera may theoretically belong to Calomantispinae. This is quite possible, but it is more likely that all three genera belong to the subfamily Drepanicinae. Unfortunately, the body is not preserved in specimens of all three species of mantispids from the Fur Formation, and further comparisons and relationships between them cannot yet be determined.

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