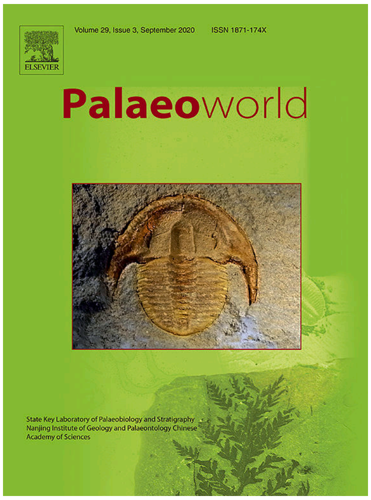

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Diversity of the mostly Mesozoic genus *Mesypochrysa* Martynov, 1927 (Neuroptera: Chrysopidae: Limaiinae) in the lowermost Eocene Fur Formation, Denmark

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Abstract

Three new specimens of the widely distributed Mesozoic genus *Mesypochrysa* Martynov, 1927 (Neuroptera: Chrysopidae: Limaiinae) are reported from the lowermost Eocene Fur Formation, Denmark: two of *M. nielseni* Makarkin and Perkovsky, 2023, and one of *M. frandseni* n. sp. While the venation of their forewings is typical of the genus, their hind wing venation differs significantly from older congeners by two characters: MA and MP are fused distally for a short distance, and MA and the basal branches of RP are strongly zigzagged, characteristic of younger Chrysopinae. *Drakochrysa* Yang and Hong, 1990 is regarded as a junior synonym of *Mesypochrysa*, syn. nov., and accordingly *Drakochrysa sinica* Yang and Hong, 1990 as *Mesypochrysa sinica* (Yang and Hong, 1990), comb. nov. The preoccupied name of *Mesypochrysa sinica* Khramov et al., 2016 is replaced by the new name *M. khramovi*, nom. nov. *Protochrysa brevinervis* Zhang et al., 2020b is transferred to *Mesypochrysa* as *M. brevinervis* (Zhang et al., 2020b), comb. nov.

Keywords: Ypresian; Jutland; green lacewings; taxonomy; new species; new synonymy

1. Introduction

Green lacewings (Neuroptera: Chrysopidae) are medium-sized insects, relatively uniform in appearance. The family includes approximately 1400 extant species and is nearly globally distributed (Oswald and Machado, 2018). It consists of four easily distinguished subfamilies: Apochrysinae, Nothochrysinae, Chrysopinae, and Limaiinae. Only the predominantly tropical Apochrysinae lack fossil record. Fossils of the other three are numerous from the Middle Jurassic to the Pliocene (see Chen et al., 2023; Table 1).

The subfamily Limaiinae includes 39 fossil species in 10 fossil genera (mostly Mesozoic) and probably one extant genus (*Leptochrysa* Adams and Penny, 1992) (see a review of Makarkin and Perkovsky, 2023). Most genera are from the Cretaceous: *Baisochrysa* Makarkin, 1997 (Late Jurassic to Early Cretaceous), *Paralembochrysa* Nel et al., 2005 (Early Cretaceous), *Aberrantochrysa* Khramov, 2018 (Early Cretaceous), *Drakochrysa* Yang and Hong, 1990 (Early Cretaceous), *Limaia* Martins-Neto and Vulcano, 1989 (Early Cretaceous), *Araripechrysa* Martins-Neto and Vulcano, 1989 (Early Cretaceous), *Parabaisochrysa* Lu et al., 2018 (mid-Cretaceous) and *Cretachrysa* Makarkin, 1994 (Late Cretaceous). The genus *Protochrysa* Willmann and Brooks, 1991 is restricted to the early Eocene (Makarkin and Archibald, 2013).

The genus *Mesypochrysa* Martynov, 1927 (= *Caririchrysa* Martins-Neto and Vulcano, 1989; = *Lembochrysa* Ren and Guo, 1996) is the largest in the subfamily with 30 described species (including a new species and new assignments proposed in this paper, see Table 1). Previously, the genus was known only from the Mesozoic (Middle Jurassic to Late Cretaceous), but recently *Mesypochrysa nielseni* Makarkin and Perkovsky, 2023 was described from the lower Eocene Fur Formation based on a forewing. Here, we report three additional specimens of *Mesypochrysa* from this formation, all with both fore- and hind wings: two of *M. nielseni* and the third representing a new species.

2. Locality

The specimens described here come from the marine Fur Formation. This formation, together with the underlying Stolleklint Clay (Ølst Formation), constitutes the Mo-clay of the Limfjord area of northern Jutland, Denmark. There is a considerable body of literature about this Lagerstätte (e.g., Larsson, 1975; Pedersen and Surlyk, 1983; Willumsen, 2004; Pedersen et al., 2012; Rasmussen et al., 2016; Madsen and Rasmussen, 2021). The Fur Formation is the earliest Eocene (Ypresian) in age, deposited over approximately one million years prior to 54.6 Ma (Stokke et al., 2020). The taphonomy of these deposits was discussed by Archibald and Makarkin (2006).

The Fur Formation is one of the most important Ypresian Lagerstätten. Its fossil insects are abundant, with more than 20000 specimens reported (Rust, 1999; Pedersen et al., 2012). To date, more than 200 species of 15 insect orders have been identified from the Mo-clay (Rust, 1998, 1999). Of these, ca. 100 species have been described, and new taxa are added every year (e.g., Manukyan, 2025; Shcherbakov et al., 2025; Simonsen et al., 2025). The order Neuroptera is so far represented by six families: Polystoechotidae, Osmylidae, Mantispidae. Hemerobiidae, Chrysopidae and

Berothidae (Henriksen, 1922; Schlüter, 1982; Willmann and Brooks, 1991; Willmann, 1993; Rust, 1999; Andersen, 2001; Archibald and Makarkin, 2006; Makarkin and Perkovsky, 2023, 2024; Makarkin et al., 2024, 2025a, 2025b). To date, 17 valid species of Neuroptera have been described (including herein), and several others await description.

3. Materials and methods

This study is based on three Fur Formation specimens, one collected at Sundby and another at Vangsgaard pit, both on Mors Island in northern Jutland, and the third at an unknown locality.

The holotype of *Mesypochrysa frandseni* n. sp. was found at Vangsgaard pit in the same concretion with the holotype of *Protheristria roldae* Makarkin et al., 2025b (Mantispidae) (see Makarkin et al., 2025b) and the holotype of the first Eocene roproniid (Perkovsky and Rasnitsyn, in press). The concretion measures approximately 120 cm long, 60 cm wide and 40 cm thick, and contains about 240 insect specimens (Ch. Nielsen, personal communication, November 2025).

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., 1r-m, first crossvein in between RP and M/MA; 2icu, second crossvein between CuA and CuP. Character states of compared taxa are provided in brackets.

Abbreviations: A1–A3, first to third anal veins; CuA, anterior cubitus; CuP, posterior cubitus; *im*, intramedian cell; MA, anterior media; MP, posterior media; Psc, pseudocubitus; Psm, pseudomedia; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; Sc, subcosta.

4. Systematic paleontology

Class Insecta Linnaeus, 1758

Order Neuroptera Linnaeus, 1758

Family Chrysopidae Schneider, 1851

Subfamily Limaiinae Martins-Neto and Vulcano, 1989

Genus *Mesypochrysa* Martynov, 1927

Emended diagnosis: May be distinguished from other genera of the subfamily by a combination of the following forewing character states: distal veinlets of RA short, simple [long, forked in *Protochrysa*]; *im* long (length/width ratio 3.3–6.3), often tapering basally [short (length/width ratio 2.2–2.5), obtuse basally in *Cretachrysa*, *Araripechrysa*]; most branches of RP forked distally [most branches simple in *Limaia*]; crossvein between *im* and CuA located in distal part of *im* or distad *im* [in middle part of *im* in *Araripechrysa*]; two gradate series of crossveins in radial space [three in *Baisochrysa*, *Paralembochrysa*, *Parabaisochrysa*].

Remarks: The venation of *Aberrantochrysa* is similar to that of *Mesypochrysa*. The few characters that distinguish these genera are possibly aberrations.

Mesypochrysa nielseni Makarkin and Perkovsky, 2023

(Figs. 1, 2)

2023 *Mesypochrysa nielseni* – Makarkin and Perkovsky, p. 58, figs. 1–3.

Material examined: Specimen 5-C2335, collected by Henrik Madsen in 1996, and deposited in the Madsen collection in the Madsen collection in Museum Mors; an incomplete overlapped fore- and hind wings. Specimen FUM-N 16652, collected by Ole Burholt, and deposited in Fur Museum; a nearly complete specimen (male) with all wings overlapping.

Locality and horizon: 5-C2335: Denmark: northern Jutland: Mors Island: Sundby; Fur Formation, lower part of the Silstrup Member (ash layers+25 – +30); lowermost Eocene.

FUM-N 16652: Fur Formation (collecting locality unknown).

Description: Specimen 5-C2335 (Fig. 1). Forewing 13.3 mm long as preserved (estimated complete length ca. 14.5 mm), 5.1 mm wide (length/width ratio 2.84). Costal space moderately broad, widest at level of RP origin. All preserved subcostal veinlets simple, rather widely spaced. Apical part of Sc indiscernible. Subcostal space narrow, proximally slightly broadened; basal subcostal crossvein located at level of RP origin. RA long, entering margin slightly before wing apex; several short, closely spaced veinlets preserved apically. RA space slightly broadened medially; with 15 crossveins (of these one forked), all straight (except one). RP originating at obtuse angle. Anterior trace of RP zigzagged, apically shallowly forked; with 10 pectinate branches, all forked once except two (i.e., distal part of RP8 not preserved; RP10 simple); RP7, RP8 fused basally (before inner gradate series). Basal crossvein between RP, M (1r-m) indiscernible, probably connecting anterior trace of RP with at proximal end of *im*. M dividing to MA, MP distad origin of RP. MA, MP probably forked at distad Psc; one branch of MA forked again. *im* long, tapering basally (length/width ratio ca. 3.5). Crossvein between MA, MP (1im) rather long. Psm poorly developed. Crossvein 2m-cu connected *im*, CuA in distal part of *im* (markedly proximad 1im). CuA probably with three simple branches. CuA continuing into well developed, only slightly zigzagged Psc, which continues into outer gradate series of crossveins. Two gradate, smoothly curved series of crossveins: inner series with nine preserved (ten when complete) crossveins distad MA; outer series, with 10 crossveins distad RP2. CuP deeply forked. Two crossveins between CuA, CuP. A1, A2 simple.

Hind wing 12 mm long as preserved (estimated complete length ca.13 mm), ca. 4.6 mm wide. Costal space fragmentarily preserved; subcostal veinlets not preserved (except one). Discernible part of Sc short. Subcostal space narrow; crossveins not detected. RA long, ending on margin nearly at wing apex; few distal veinlets discernible. RA space rather broad, with eleven preserved crossveins in distal part. Anterior trace of RP slightly zigzagged, apically shallowly forked; with 10 pectinate branches (all forked once). Basal part of MA not discernible. Psm poorly preserved, zigzagged. MP fused with MA for short distance at Psc. Proximal crossvein between MA, MP (1im) long. CuA pectinate, with three simple branches. Psc poorly developed. CuA, A1 fused basally. A2 probably simple. Two gradate, smoothly curved series of crossveins: inner series with eight preserved crossveins distad MA (eleven when complete); outer series with eleven crossveins preserved distad MA.

Specimen FUM-N 16652, male (Fig. 2). Head, prothorax missing. Mesothorax, metathorax poorly preserved; details not discernible. Mid- and hind legs slender with short setae. Abdomen poorly discernible. Presumed T9 short; shape of ectoproct unclear; presumed S8 long; S9 indiscernible (alternatively, presumed S8 represents fused S8+S9) (Fig. 2B).

Forewing 11.8 mm long, 4.7 mm wide (length/width ratio 2.5). Costal space moderately broad, widest distad level of RP origin. All preserved subcostal veinlets simple, rather widely spaced. Sc short, apex indiscernible. Subcostal space narrow; subcostal crossveins not detected. RA long, entering margin slightly before wing apex; several short, closely spaced veinlets preserved apically. RA space broadened medially, with 11 preserved crossveins (probably 12 when complete). RP originating relatively close to wing base (at 17% complete length), at obtuse angle. Anterior trace of RP zigzagged, apically shallowly forked; with 11 pectinate branches, all forked once. Basal crossvein between RP, M (1r-m) indiscernible; probably very short. M dividing to MA, MP distad origin of RP. MA forked distad Psc; MP probably forked at Psc. *im* long, narrow, tapering basally (length/width ratio ca. 3.6). Crossvein between MA, MP (1im) long. Psm relatively well developed. Crossvein 2m-cu connected *im*, CuA in distal part of *im* (slightly proximad 1im). CuA probably with two simple branches. CuA continuing into well developed, slightly zigzagged Psc, which continues into outer gradate series of crossveins. Two gradate series of crossveins: inner series slightly incurved, with 11 crossveins distad MA; outer series slightly incurved, convergent distally with inner series, with 11 crossveins distad RP1. CuP deeply forked. 2icu connecting CuA, anterior branch of CuP. A1, A2 simple.

Hind wing 9.2 mm long as preserved (estimated complete length *ca*. 10 mm), width ca. 3.8 mm. Costal space fragmentarily preserved with subcostal veinlets incomplete. Discernible part of Sc, RA short. Subcostal space very narrow; crossveins not detected. RA space broad, with seven preserved crossveins. Anterior trace of RP slightly zigzagged; with 9 preserved pectinate branches (all forked once). Psm poorly developed, zigzagged. MP connected with MA by short distal crossvein (2im) at Psc; proximal crossvein (1im) not preserved. CuA pectinately forked with three simple branches. CuP+A1 fragmentarily preserved. Psc poorly developed, zigzagged. Two gradate series of crossveins: inner series with 10 crossveins distad MA (eight preserved); outer series with 11 crossveins preserved distad MP.

Remarks: The wing size and venation of two new specimens are in general concordant with those of *Mesypochrysa nielseni*. The forewing length of the holotype is 14.5 mm, and 11.8–13.3 mm of new specimens. However, their forewing venation is different in number of the RP branches and crossveins in the RA space. These differences may be associated with the different sizes of specimens. Also, the hind wings of new specimens slightly differ by MP being fused with MA for a distance at the pseudocubitus in 5-C2335, while it is connected with MA by short distal crossvein in FUM-N 16652. We consider these differences to be intraspecific. Also, the holotype of *Mesypochrysa nielseni* and specimen 5-C2335 were found in the same ash layers+25 – +30.

This is the youngest known species of the genus.

Mesypochrysa frandseni n. sp.

(Figs. 3, 4)

Etymology: The species is named after one of the collectors of the holotype, John Frandsen (Erslev, Denmark).

Type material: Holotype MGUH 35222 (NHMD-2015714), collected by Dorthe Rold and John Frandsen on February 15, 2025, deposited in the collections of the Natural History Museum of Denmark.

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.

Diagnosis: May be distinguished from other species by a combination of the following. Forewing: RP with 20 branches [10–13 in *M. nielseni*]. Hind wing: MA, MP fused at Psc for a short distance [not fused in other species of the genus except *M. nielseni*]; MA and basal branches of RP strongly zigzagged [at most slightly zigzagged in other species except *M. nielseni*].

Description: Head fragmentarily preserved; only eyes and mouthparts (partially) discernible. Thorax poorly preserved; prothorax short. Mid- and hind legs slender (detail not discernible). Abdomen missing.

Forewing 19.6 mm long, 6.7 mm wide (length/width ratio 2.93). Costal space moderately broad, widest slightly distad level of RP origin. All preserved subcostal veinlets simple, rather widely spaced. Sc short, slightly curved towards RA apically, but apex indiscernible. Subcostal space narrow, proximally broadened; subcostal crossveins not detected. RA long, entering margin slightly before wing apex; several short, closely spaced veinlets preserved apically. RA space broadened medially; with 21 crossveins (of these three forked), some curved in distal half. RP originating relatively close to wing base (at 18% complete length), at obtuse angle. Anterior trace of RP zigzagged, apically shallowly forked; with 20 pectinate branches, all forked once except two (i.e., RP6, RP14) in which proximal branched shallowly forked.

Basal crossvein between RP, M (1r-m) short, connecting anterior trace of RP, MA within *im* near its proximal end. M dividing to MA, MP distad origin of RP. MA probably forked at distad Psc; MP probably simple. *im* long, narrow, tapering basally (length/width ratio ca. 5). Crossvein between MA, MP (1im) rather long. Psm poorly developed. Crossvein 2m-cu connected *im*, CuA at nearly distal end of *im* (slightly proximad 1im). CuA probably with three simple branches. CuA continuing into well developed, only slightly zigzagged Psc, which continues into outer gradate series of crossveins. Two gradate series of crossveins: inner series sinuously curved, with 19 crossveins distad MA; outer series smoothly curved, with 18 crossveins distad RP2. CuP deeply forked. 1icu located far from origin of CuP; 2icu connecting CuA, anterior branch of CuP. *c1*: *c2* length ratio 0.43. A1 simple. A2 incomplete.

Hind wing 17 mm long as preserved (estimated complete length ca. 18 mm), 5.9 mm wide. Costal space narrow; all preserved subcostal veinlets simple. Discernible part of Sc short, distally slightly thickened. Subcostal space narrow; crossveins not detected. RA long, poorly discernible distally, ending on margin nearly at wing apex; its veinlets indiscernible. RA space broad, broadening medially; with 20 crossveins, some curved in distal half. Anterior trace of RP slightly zigzagged; with 16 preserved pectinate branches (ten forked, other incompletely preserved). MA basally fused with RP. Psm poorly developed, zigzagged. MP fused with MA for some distance. Proximal crossvein between MA, MP (1im) long. CuA, CuP+A1 fragmentarily preserved. Psc poorly developed. Two gradate series of crossveins: inner series arranged in sinuous line, with 16 crossveins distad MA; outer series incomplete, with 8 crossveins preserved distad MA.

Remarks: The fragmentary forewing described previously as ‘Limaiinae gen. et sp. A’ (Makarkin and Perkovsky, 2023, fig. 4) has venation well concordant with that of *Mesypochrysa frandseni* n. sp., and may belong to this species.

5. Discussion

5.1. Characters of Mesypochrysa

5.1.1. Forewing venation

The forewing venation of the genus is rather homogeneous. Besides quantitative differences between the species (e.g., wing size, number of branches RP and subcostal veinlets), there are only small qualitative differences, e.g., in the shape of *im*, the position of the 2m-cu crossvein, the length of RA, the width of the costal space (especially in the distal part), and the branching of RA and the anal veins.

The forewing venation of the oldest known species of the genus from the Middle Jurassic locality of Daohugou (China) is not principally different from that of those from the Upper Jurassic of Karatau (Kazakhstan), the Lower Cretaceous Baissa (Russia: Transbaikalia) and Crato Formation (Brazil), and the Eocene Fur Formation (see Panfilov, 1980; Makarkin, 1997; Martins-Neto, 1997; Nel et al., 2005; Khramov et al., 2016; Wang et al., 2025; this paper). Their forewing RA is long, terminating slightly before to slightly after wing apex, and distal veinlets of RA are relatively long and dense. Species from these localities are also similar in other character states.

The only known species of the genus from the mid-Cretaceous Kachin amber (i.e., *M. coadnata* Chen et al., 2022) differs greatly from these species in its relatively short RA (terminating well before the wing apex) and sparse distal veinlets (Chen et al., 2022, figs. 2, 4, 6). The relatively short RA is also found in *M. miniscula* (Ren and Guo, 1996) from the Lower Cretaceous Yixian Formation (Ren and Guo, 1996, fig. 7).

A1 and A2 are simple in most species of the genus (see Figs. 1, 2), while these are forked in all specimens from the Yixian Formation and some from other Lower Cretaceous localities. The first two species from the Yixian Formation were originally considered to belong to the genus *Lembochrysa* Ren and Guo, 1996, but this genus was later synonymized by Khramov et al. (2016) with *Mesypochrysa*. Indeed, the forewing venation of *Lembochrysa* and *Mesypochrysa* is otherwise nearly identical (see Ren and Guo, 1996, figs. 7, 8; Nel et al., 2005, fig. 13.1; Zhang et al., 2020a, figs. 1, 2).

The important character state of *Mesypochrysa* is the short Sc terminating on RA. It is easily seen in two species, the Early Cretaceous *M. chrysopa* Makarkin, 1997 and the Middle Jurassic *M. paucinervis* Wang, Yang and Ren in Wang et al., 2025 (Makarkin, 1997, fig. 13; Wang et al., 2025, fig. 1b). The terminal part of Sc is poorly or not discernible in many other species as their pterostigmata are often dark to very dark. These veins are fully separate in all other extant and Cenozoic Chrysopidae. Interestingly, Sc and RA are similarly not fused distally in extant Hemerobiidae, but fused in many of their Mesozoic taxa (e.g., Klimaszewski and Kevan, 1986, fig. 2; Ponomarenko, 1992, fig. 4; Liu et al., 2022, fig. 3; Nakamine et al., 2022, fig. 2B).

5.1.2. Hind wing venation

The hind wing venation of *Mesypochrysa* is apparently more varied than that of the forewings. Unfortunately, the hind wings of many Limaiinae are unknown or at most incompletely preserved. Below, three characters are analyzed in detail.

5.1.2.1. The basal fusion of MA and RP

The hind wing MA and RP of *Mesypochrysa frandseni* n. sp. are fused for some distance, and MA is originating on RP. This character state often occurs in Chrysopidae and is found in some representatives of *Mesypochrysa* (*M. minuta* Makarkin, 1997, *M. chrysopa* Makarkin, 1997, *M. curvimedia* Makarkin, 1997, *M. minima* Makarkin, 1997, *M. magna* Makarkin, 1997, *M.* cf. *chrysopoides* Ponomarenko, 1992, and *M. criptovenata* Martins-Neto and Vulcano, 1989), and *Parabaisochrysa* (Makarkin, 1997, figs. 5, 14, 16, 18; Martins-Neto, 1997, fig. 4; Nel et al., 2005, fig. 13.2; Lu et al., 2018, figs. 2C, D, 3B), most Nothochrysinae (including the oldest known species *Sinonothochrysa zhangi* Huang and Nel in Huang et al., 2022 from the Paleocene of China) and Apochrysinae, and all Chrysopinae.

This condition is obviously derived. The plesiomorphic condition occurs rarely in Chrysopidae when M is divided into MA and MP, and MA is connected with RP by a crossvein. It is found in some Limaiinae (*Mesypochrysa reducta* Panfilov, 1980, *M. miniscula* and *M. coadnata* Chen et al., 2022; *Baisochrysa*; *Protochrysa*; and *Leptochrysa*: Panfilov, 1980, fig. 113; Willmann and Brooks, 1991, fig. 2; Ren and Guo, 1996, fig. 7b; Makarkin, 1997, fig. 22; Tauber, 2019, figs. 2b, 6b; Chen et al., 2022, figs. 2B, 4C), and a few Nothochrysinae (*Archaeochrysa* Adams, 1967; *Stephenbrooksia* Willmann, 1993; and some *Triplochrysa* Kimmins, 1952: New, 1980, fig. 22: Makarkin et al., 2022, fig. 2B; Makarkin and Perkovsky, 2024, fig. 2B). Of these, only two genera are extant (i.e. *Leptochrysa* and *Triplochrysa*), others are from the Eocene or older.

This state is unknown in the limaiine *Limaia*, *Araripechrysa*, *Cretachrysa*, and *Aberrantochrysa*.

5.1.2.2. The distal fusion of MA and MP

The distal fusion of the hind wing MA and MP for a short distance as found in both species of *Mesypochrysa* from the Fur Formation has not been previously documented in the genus or subfamily. However, it is characteristic of younger subfamilies, present in most Nothochrysinae (e.g., Makarkin et al., 2022, figs. 9C, D, 11C, 13C, D, 16C, D, 19D, 22C, D, 25C, D, 28) and all Chrysopinae and Apochrysinae. This condition is obviously derived.

These veins are not fused in other Limaiinae and few Nothochrysinae, e.g., two genera from the Fur Formation (*Furochrysa* Makarkin and Perkovsky, 2024 and *Stephenbrooksia* Willmann, 1993) (Makarkin and Perkovsky, 2024, figs. 3D, 5B), and the plesiomorphic Eocene/Oligocene genus *Archaeochrysa* (Makarkin and Archibald, 2013, figs. 15.6, 16.6, 18.6; Makarkin et al., 2022, fig. 2B).

5.1.2.3. The strongly zigzagged MA and basal branches of RP

The MA and the basal branches of RP are at most slightly zigzagged in most species of *Mesypochrysa* (e.g., Makarkin, 1997, fig. 14; Wang et al., 2025, fig. 4d, f), but strongly zigzagged in two Fur Formation species at the Psm: parts of MA and RP1 forming the Psm are aligned; they are parallel distad the Psm and go at a strong angle to it. A similar condition occurs in most Nothochrysinae (e.g., Makarkin et al., 2022, figs. 2B, 9C, D, 11C, D), and all Chrysopinae and Apochrysinae. The strongly zigzagged MA and the basal branches of RP are obviously derived states for the two species.

5.1.3. Genital segments of Mesypochrysa

Male genital segments are described in four species of Limaiinae, all belong to *Mesypochrysa*: *M.* cf. *intermedia* Panfilov, 1980 from the Middle Jurassic of Daohugou (Khramov et al., 2016, fig. 2B), *Mesypochrysa* sp. from the Upper Jurassic of Karatau (Khramov et al., 2016, fig. 1D), *M. cannabina* Khramov, 2018 from the Lower Cretaceous of Khasurty (Russia: Transbaikalia) (Khramov, 2018, fig. 2D), and

M. nielseni (this paper). Their terminal segments are plesiomorphic (unmodified); the 8th and 9th sternites are not fused; and the 9th tergite is very short. Unfortunately, the male genital segments of *M. nielseni* are poorly visible; in general, they are most similar to those of *M. cannabina* in the poorly discernible 9th sternite and ectoproct (Fig. 2B). However, the 8th and 9th sternites of *M. nielseni* may be fused as is typical for younger subfamilies (especially Apochrysinae and Chrysopinae), but this requires confirmation.

The female genital segments have been described in only one fossil species of Limaiinae, the mid-Cretaceous *M. coadnata* (Chen et al., 2022, figs. 1D, 3D, 5E), and in the extant *Leptochrysa prisca* Adams and Penny, 1992 (Tauber, 2019, figs. 8, 9). These are similarly constructed in both: the 8th and 9th tergites are plesiomorphically not fused (fused in some Nothochrysinae, and all Chrysopnae and Apochrysinae), and the 9th tergite is expanded ventro-caudally. The structure of the female genital segments of Limaiinae and most Nothochrysinae are similar.

5.2. General consideration

The only subfamily of Chrysopidae known from the Mesozoic is Limaiinae, although the taxonomic position of the two Cretaceous genera (i.e., *Araripechrysa* and *Paralembochrysa*) is considered unclear (see Makarkin and Perkovsky, 2023). The forewing venation of both Fur Formation species is typical for the genus, but their hind wing venation differs considerably from that of their congeners (above). Their hind wing MA and MP are fused distally for a short distance, and MA and the basal branches of RP are strongly zigzagged. These two apomorphic features are not found in other representatives of *Mesypochrysa* and could allow us to assign the Fur Formation species to a new genus, but we consider this premature.

The presence of the three hind wing apomorphic character states mentioned above in the Fur Formation species is concordant with an evolutionary tendency within the family. These conditions are rare (or not present) in Limaiinae, but characteristic of younger subfamilies, especially Chrysopinae and Apochrysinae. A similar situation is found in the Fur Formation Mantispidae. The *Danomantispa* Makarkin et al., 2025a is the only drepanicine genus possessing a pterostigma very similar to that of more advanced Mantispinae (Makarkin et al., 2025a).

The situation with *Mesypochrysa* is similar to that of *Chrysopa* Leach, 1815, s.l. For over a centuary this genus *sensu lato* was considered cosmopolitan, comprising many species now represented by separate genera. The forewing venation of most of these genera (e.g., *Chrysopa* s.str., *Apertochysa* Tjeder, 1966, *Cunctochrysa* Hölzel, 1970) is practically identical, differing only by coloration of the body and veins, and by male genitalia.

Chrysopa s.l. was a collective genus, and it is very likely that *Mesypochrysa* is also such. Its occurrences in localities with different climates across the world appears to indicate this. However, to resolve this issue, it is necessary to find and examine the genitalia of a large number of species.

5.3. Taxonomic notes

Drakochrysa (with the only species *D. sinica* Yang and Hong, 1990) has been described from the Lower Cretaceous Laiyang Formation of China. Its holotype is most probably lost. The wing venation of *D. sinica* was inadequately depicted (Yang and Hong, 1990, figs. 4, 5), but the published photograph is rather good (Yang and Hong, 1990, pl. 1). Based on this photograph, we can see that its visible venation is typical for *Mesypochrysa*; all diagnostic character states are present in the species. Its forewing venation is most similar to that of *M. miniscula*. Therefore, *Drakochrysa* is a synonym of *Mesypochrysa*, syn. nov. *D. sinica* is here transferred to this genus as *Mesypochrysa sinica* (Yang and Hong, 1990), comb. nov. However, later *Mesypochrysa sinica* Khramov et al., 2016 was described from another locality in China (Daohugou). We propose to replace this preoccupied species name by a new name in honor of one of the authors who described it, Alexander V. Khramov: *Mesypochrysa khramovi*, nom. nov.

The venation of *Protochrysa brevinervis* Zhang et al., 2020b is typical for that of *Mesypochrysa* and similar to that of other Yixian Formation species of the genus in the forked A1 and A2. The only difference from other species is that some of the RA veinlets are forked. In several other undescribed specimens of *Mesypochrysa* from the Yixian Formation some of these veinlets are also forked (VNM, personal observation). Therefore, we propose to transfer the species to *Mesypochrysa* as *M. brevinervis* (Zhang et al., 2020b), comb. nov.

6. Conclusion

The discovery of two species of *Mesypochrysa* from the lowermost Eocene Fur Formation is very important. While the venation of the forewings is typical of the genus, their hind wing venation is different from all older (Mesozoic) congeners by at least two character states: their hind wing MA and MP are fused distally for a short distance, and MA and the basal branches of RP are strongly zigzagged. These features are characteristic of younger subfamilies, especially Chrysopinae and Apochrysinae, i.e., they are concordant with the trend in venational evolution within the family.

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Figure captions

Fig. 1. *Mesypochrysa nielseni* Makarkin and Perkovsky, 2023, specimen 5-C2335. (A) Part (converted to standard right view). (B) Counterpart. (C) Forewing venation. (D) Hind wing venation (fused MA and MP in red). Abbreviations: A1, A2, first and second anal veins; CuA, anterior cubitus; CuP, posterior cubitus; *im*, intramedian cell; MA, anterior media; MP, posterior media; Psc, pseudocubitus; Psm, pseudomedia; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; Sc, subcosta; 1icu, first crossvein between CuA and CuP; 1im, first crossvein between MA and MP; 1m-cu, first crossvein between M and Cu; 2icu, second crossvein between CuA and CuP; 2m-cu, second crossvein between M and Cu. Scale bars = 2 mm (C, D to same scale).

Fig. 2. *Mesypochrysa nielseni* Makarkin and Perkovsky, 2023, specimen FUM-N 16652. (A) Specimen as preserved. (B) Apex of abdomen (lateral view). (C) Forewing venation. (D) Hind wing venation. etc, ectoproct; S8, 8th sternite; T9, 9th tergite. Abbreviations: A1, A2, first and second anal veins; CuA, anterior cubitus; CuP, posterior cubitus; *im*, intramedian cell; MA, anterior media; MP, posterior media; Psc, pseudocubitus; Psm, pseudomedia; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; 1icu, first crossvein between CuA and CuP; 1im, first crossvein between MA and MP; 2icu, second crossvein between CuA and CuP; 2m-cu, second crossvein between M and Cu. Scale bars = 2 mm (A), 1 mm (B–D) (C, D to same scale).

Fig. 3. *Mesypochrysa frandseni* n. sp., holotype MGUH 35222. (A) Part. (B) Counterpart. Scale bars = 2 mm.

Fig. 4. Wing venation of *Mesypochrysa frandseni* n. sp., holotype MGUH 35222. (A) Forewing. (B) Hind wing (fused MA and MP in red). Abbreviations: A1, A2, first and second anal veins; CuA, anterior cubitus; CuP, posterior cubitus; *im*, intramedian cell; MA, anterior media; MP, posterior media; Psc, pseudocubitus; Psm, pseudomedia; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; Sc, subcosta; 1icu, first crossvein between CuA and CuP; 1im, first crossvein between MA and MP; 1m-cu, first crossvein between M and Cu; 2icu, second crossvein

between CuA and CuP; 2m-cu, second crossvein between M and Cu. Scale bar = 2 mm (both to same scale).

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Figure 1

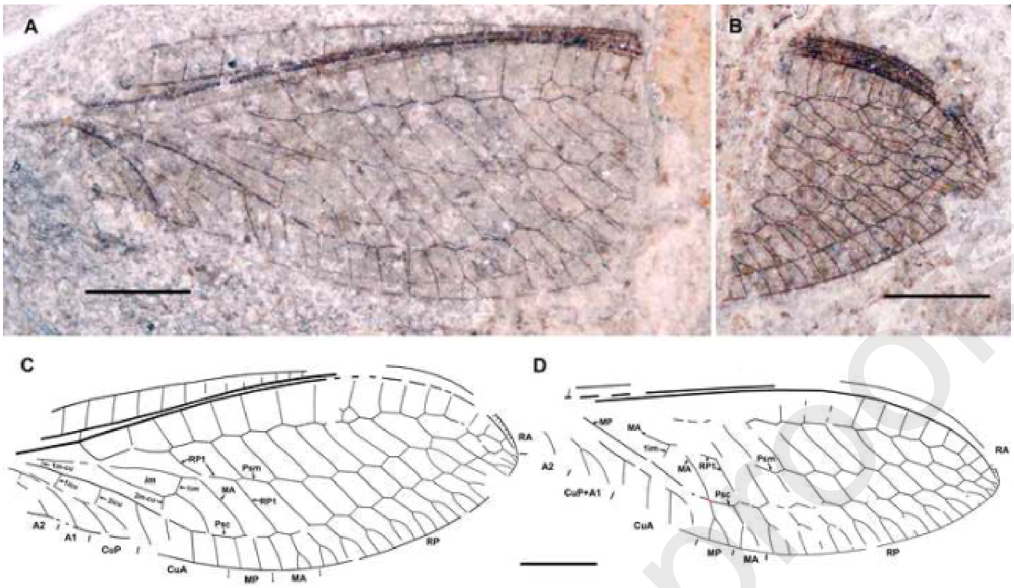

Figure 2

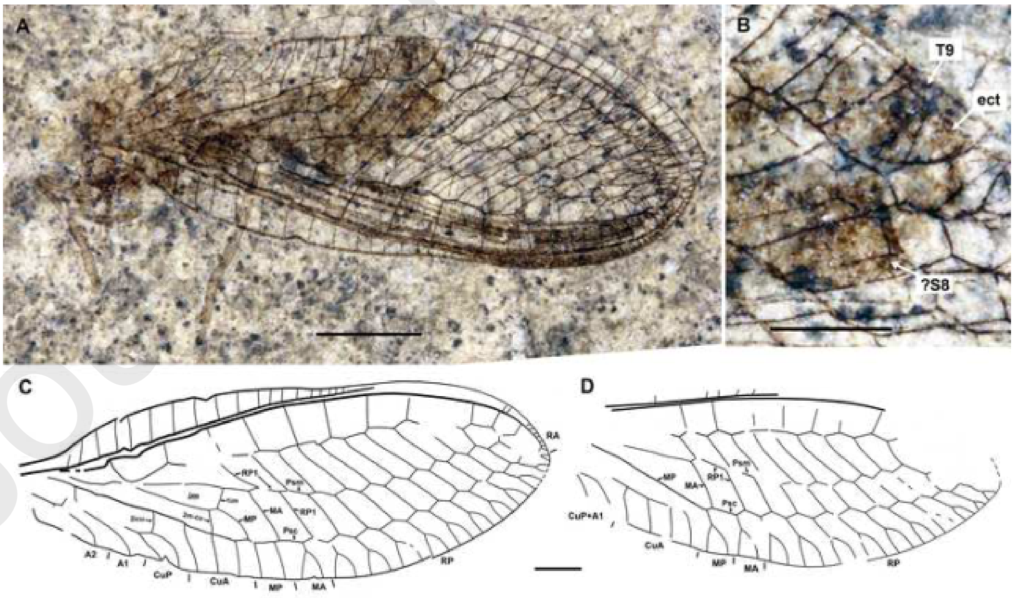

Figure 3

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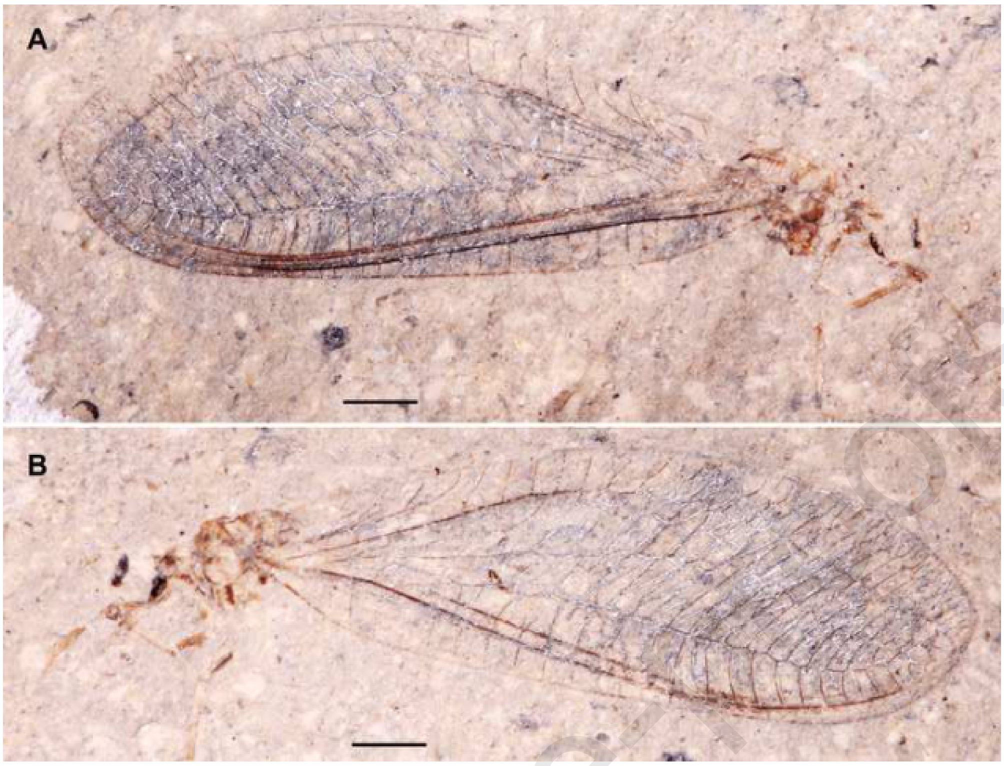

Figure 4

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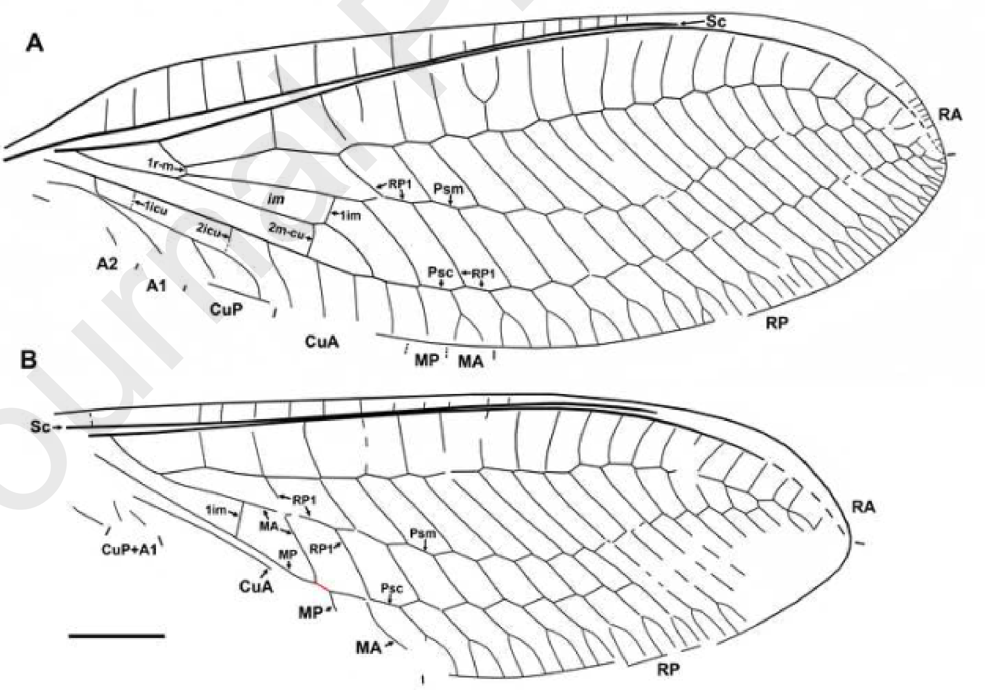

Table 1. A list of species of *Mesypochrysa*.

	Species	Locality	Age
1	*M. angusta* Wang, Yang and Ren in Wang et al., 2025	Daohugou, China	late Middle Jurassic (Bathonian/Callovian)
2	*M. khramovi*, nom. nov.	same	same
3	*M. paradoxica* Wang, Yang and Ren in Wang et al., 2025	same	same
4	*M. paucinervis* Wang, Yang and Ren in Wang et al., 2025	same	same
	M. cf. *intermedia*: Khramov et al., 2016	same	same
5	*M. intermedia* Panfilov, 1980 = *M. makarkini* Nel et al., 2005	Karatau, Kazakhstan	Late Jurassic (Oxfordian/Kimmeridgian)
6	*M. latipennis* Martynov, 1927	same	same
7	*M. reducta* Panfilov, 1980	same	same
8	*M. polyclada* Panfilov, 1980	same	same
9	*M. minuta* Jepson et al., 2012	Purbeck, England	Early Cretaceous (Berriasian)
10	*M. cannabina* Khramov, 2018	Khasurty, Russia	Early Cretaceous (late Barremian)
11	*M. naranica* Khramov, 2018	same	Same
12	*M. angustialata* Makarkin, 1997	Baissa, Russia	Early Cretaceous (Barremian/Aptian)
13	*M. chrysopa* Makarkin, 1997	same	same
14	*M. curvimedia* Makarkin, 1997	same	same
15	*M. falcata* Makarkin, 1997	same	same
16	*M. magna* Makarkin, 1997	same	same
17	*M. minima* Makarkin, 1997	same	same
18	*M. binervis* Zhang, Shi and Ren in Zhang et al., 2020a	Yixian Formation, China	Early Cretaceous (Barremian/Aptian)
19	*M. brevinervis* Zhang et al., 2020b, comb. nov.	same	same

	M. cf. *chrysopoides*: Nel et al., 2005	same	same
20	*M. miniscula* (Ren and Guo, 1996)	same	same
21	*M. polyneura* (Ren and Guo, 1996)	same	same
22	*M. pusilla* Zhang, Shi and Ren in Zhang et al., 2020a	same	same
23	*M. sinica* (Yang and Hong, 1990), comb. nov.	Laiyang Formation	Early Cretaceous (Barremian/Aptian)
24	*M. confusa* (Martins-Neto and Vulcano, 1989)	Crato Formation, Brazil	Early Cretaceous (late Aptian)
25	*M. criptovenata* (Martins-Neto and Vulcano, 1989)	same	same
26	*M. skulda* (Martins-Neto, 2003)	same	same
27	*M. chrysopoides* Ponomarenko, 1992	Bon-Tsagan, Mongolia	Early Cretaceous (Aptian/Albian)
28	*M. coadnata* Chen et al., 2022	Kachin amber, Myanmar	Late Cretaceous (earliest Cenomanian)
29	*M. nielseni* Makarkin and Perkovsky, 2023	Fur Formation, Denmark	earliest Eocene
30	*M. frandseni* n. sp.	same	same