



Nothochrysinæ (Neuroptera: Chrysopidae) from the early Eocene Fur Formation, Denmark, with description of a new genus

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Abstract

Furochrysa alisae **gen et sp. nov.** is described, and *Stephenbrooksia multifurcata* Willmann, 1993 and *Danochrysa madseni* Willmann, 1993 are re-described based on their holotypes and additional specimens from the early Eocene Fur Formation of Denmark. The very long crossvein 1icu between CuA and CuP in the hind wing distinguishes *Furochrysa* **gen. nov.** from all other Nothochrysinæ. The hind wing venation of the holotype of *S. multifurcata* is strongly aberrant; in particular, its MA is deeply forked proximad the origin of RP, while it is not forked proximad the pseudocubitus in other Chrysopidae. The forewing venation of the three examined specimens of *D. madseni* show variability in the branching of the anterior branch of CuP and A2. The chrysopid assemblage of the early Eocene Fur Formation strongly differs from that of the late Paleogene (late Eocene/Oligocene) of Europe, while the nothochrysinæ of the early and late Paleogene of North America do not especially differ.

Key words: Limaiinae, *Stephenbrooksia*, *Danochrysa*, *Furochrysa*, western North America, late Eocene

Introduction

The Nothochrysinæ constitute one of four subfamilies of Chrysopidae (green lacewings): Apochrysinæ, Nothochrysinæ, Chrysopinae, and Limaiinae (e.g., Archibald *et al.* 2014; Winterton *et al.* 2019). This small subfamily is today comprised of 22–23 species in eight to nine genera (Tauber 2019a, b), but was more diverse in the past, with 34 described fossil species in 16 genera in the Cenozoic (Chen *et al.* 2023).

Three valid species of Nothochrysinæ are known from the Fur Formation: *Cimbrochrysa moleriensis* Schlüter, 1982, *Danochrysa madseni* Willmann, 1993 and *Stephenbrooksia multifurcata* Willmann, 1993. Rust (1999) described one more species (*Brooksiochrysa jutlandica*), which differed from these by the presence of three gradate series of crossveins, but this species is invalid, as it appeared in an unpublished dissertation and this name is, therefore, unavailable (ICZN, 1999: Articles 8.1.2 and 8.1.3).

Here, we describe one new genus and species of Nothochrysinæ from the Fur Formation, and re-describe *Stephenbrooksia multifurcata*, also from the Fur Formation, based on two specimens (*i.e.*, the newly found counterpart of the holotype and one additional specimen) and *Danochrysa madseni* based on three specimens (*i.e.*, the holotype and two additional specimens).

Material and methods

The specimens described here were collected in several localities of the Fur Formation in western Limfjord, Denmark (Ejerslev, Svalklit, Gullerup, Sundby). Overviews of this earliest Eocene Danish Lagerstätte may be found in many papers (e.g., Larsson 1975; Archibald & Makarkin 2006; Pedersen *et al.* 2012; Rasmussen *et al.* 2016; Dietrich & Perkovsky 2023; Jenkins Shaw *et al.* 2024). Photographs of NHMD specimens were taken using a Visionary Digital imaging setup with flash lightning and P-51Camlift Driver ver. 2.6.1 to control the camera.

Venation terminology mostly follows Breitreuz *et al.* (2017) except for details (*e.g.*, spaces, veinlets, traces), which follows Oswald (1993). Crossveins are designated by the longitudinal veins to which they connect and are numbered in sequence from the wing base, *e.g.*, 1im, first (basal) crossvein between MA and MP; 2m-cu, second crossvein between MP and CuA.

Abbreviations of wing characters: A1–A3, first to third anal veins; *c1*, *c2*, first and second cubital cells; CuA, anterior cubitus; CuP, posterior cubitus; *im*, intramedian cell; *j*, jugal vein; *jl*, jugal lobe; MA, anterior media; MP, posterior media; Psc, pseudocubitus; Psm, pseudomedia; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; Sc, subcosta.

Acronyms of museums: FM, Fur Museum / Museum Salling, Nederby, Denmark; NHMD, Natural History Museum of Denmark.

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Chrysopidae Schneider, 1851

Subfamily Nothochrysoinae Navás, 1910

Genus *Stephenbrooksia* Willmann, 1993

Stephenbrooksia Willmann, 1993: 241; Peñalver *et al.*, 1995: 486; Nel *et al.*, 2005: 67; Makarkin & Archibald, 2013: 125, 127, 134, 143; Archibald *et al.*, 2014: 191; Makarkin, 2014: 4; Archibald & Makarkin, 2015: 365, 366.

Type and only species: *Stephenbrooksia multifurcata* Willmann, 1993, by original designation.

Emended diagnosis. Both fore- and hind wings: inner series of gradate crossveins arranged in strongly broken or sigmoid line; *im* long, narrow (length/width ratio 4.4–6.3:1); 2m-cu located nearly in middle of *im*; CuP with two long branches (proximal branch simple); A1, A2 forked.

Stephenbrooksia multifurcata Willmann, 1993

(Figs 1–3)

Stephenbrooksia multifurcata Willmann, 1993: 241, 244, Figs 2, 3; Nel *et al.*, 2005: 67; Makarkin & Archibald, 2013: 143, Fig. 2.1; Archibald & Makarkin, 2015: 360 (Table 1).

Type material. Holotype NHMD-624881A & DK 307A (original number GM 2000.4) (part), deposited in the NHMD; NHMD-624881B & DK 307B (original number GM 2000.4) (counterpart), currently deposited in the NHMD; collected by Henrik Madsen. Overlapped fore- and hind wings (basal parts absent in the counterpart).

Additional material. FUM-16651, collected by Ole Burholt, and deposited in the FM. A strongly crumpled incomplete specimen.

Type locality and horizon. Denmark: northern Jutland (Region Nordjylland): Mors Island (Morsø Kommune): Ejerslev. The precise collecting locality of FUM-16651 is unknown. Earliest Eocene (Fur Formation).

Re-description. Holotype (based on the part and counterpart). Forewing 14.0 mm long, 5.2 mm wide. Costal space broad proximally, narrow distally. Most subcostal veinlets simple (five middle veinlets shallowly forked in distal half), relatively densely spaced proximally, very dense distally. Sc well discernible distally, relatively long. RA and its veinlets indiscernible distally, ending on margin before wing apex. Subcostal space narrow; basal subcostal crossvein located slightly proximad origin of RP. RA space moderately broad, with 14 crossveins: basal crossveins with apices slightly inclined to wing base; most distal crossveins with their apices strongly obliquely to wing apex. RP originating close to wing base (at 0.15 length). Anterior trace of RP zigzagged, apically not forked; with 14 pectinate branches, all (except one distal-most) forked, mostly three to four times. Basal crossvein between RP, M (1r-m) long, connecting anterior trace of RP, MA in proximal part of *im* length. M dividing to MA, MP

markedly distad origin of RP. MA probably forked distad Psc; both branches shallowly forked. MP probably deeply forked at Psc; both branches simple. *im* long, narrow (length/width ratio 6.3:1). Crossvein between MA, MP (1*im*) rather short. Psm poorly developed, zigzagged. Crossvein 2*m-cu* connecting *im* and CuA located nearly in middle of *im*. CuA probably with three branches (one forked); continuing into well developed, only slightly zigzagged Psc, which continues into outer gradate series of crossveins. CuP pectinately forked with two long branches; its anterior trace shallowly forked. 1*icu* located near origin of CuP; 2*icu* connecting CuA and anterior trace of CuP (distad origin of distal branch of CuP). 1*c:2c* length ratio 0.26:1. A1 deeply forked. A2 incomplete. A3 not preserved. Two gradate series of crossveins; inner series arranged in strongly broken line, with 13 crossveins distad MA; outer series arranged in smooth line, with 11 crossveins distad RP2.



FIGURE 1. *Stephenbrooksia multifurcata* Willmann, 1993, holotype. A, part (NHMD-624881A); B, counterpart (NHMD-624881B). Scale bars = 2 mm.

Hind wing 10.2 mm long (as preserved; estimated complete length *ca.* 11.5 mm), 4.2 mm wide. Costal space narrow; preserved subcostal veinlets simple, very densely spaced in distal part. Sc indiscernible distally. Subcostal space narrow; crossveins not detected. RA long, indiscernible distally, ending on margin before wing apex. RA veinlets indiscernible. RA space moderately narrow basally, broadening distad; with 11 crossveins inclined obliquely to wing base in proximal half, strongly obliquely to apex in distal half. Anterior trace of RP zigzagged, apically forked; with 11 pectinate branches; RP1-RP7 forked, mostly three times; other branches probably simple. MA basally (slightly proximad origin of RP) dividing into two branches, not fused with RP (connecting by long crossvein 1*r-m*). MA1 forked at Psc; both branches forked again; MA2 forked distad Psc (alternatively: MA2 forked slightly proximad 1*m*, then its anterior branch fused with MA1 for long distance). Psm poorly developed, strongly zigzagged. MP fused with CuA for very short distance; forked distally at Psc, both branches forked again distad Psc. Proximal crossvein between MA, MP (1*m*) very long. CuA pectinate, with three simple branches.

Psc poorly developed, strongly zigzagged. CuP, anal veins not preserved. Two gradate series of crossveins: inner series arranged in strongly broken line, with 11 crossveins distad MA; outer series arranged in smooth line, with 9 crossveins distad MA.

Specimen FUM-16651. Forewing *ca.* 11.6 mm long (as preserved; estimated complete length *ca.* 12.5–13 mm), 4.7 mm wide. Costal space broad proximally, narrow distally. Most subcostal veinlets in proximal half simple (two veinlets forked in left wing), relatively densely spaced; in distal half, veinlets very densely spaced, eight of these forked in right wing, up to five in left wing. Sc relatively long; its distal part not preserved. RA and its veinlets poorly discernible distally, ending on margin before wing apex. Subcostal space narrow; basal subcostal crossvein located slightly distad origin of RP. RA space moderately broad, with 15 crossveins (left wing): proximal crossveins perpendicular to RA; most distal crossveins with their apices strongly oblique to wing apex. Anterior trace of RP zigzagged, apically not forked; with 16 pectinate branches (left wing), all (except one distal) forked, mostly three to four times. Basal crossvein between RP, M (1r-m) long, connecting anterior trace of RP, MA in proximal part of *im* length. M dividing to MA, MP markedly distad origin of RP. MA probably forked distad Psc; one branch shallowly forked. MP probably deeply forked at Psc; both branches forked. *im* long, narrow (length/width ratio 4.4:1). Crossvein between MA, MP (1im) rather short. Psm poorly developed, zigzagged; its proximal-most crossvein (between RP1, MA) ends in distal part of *im*. Crossvein 2m-cu connected *im*, CuA located nearly in middle of *im*. CuA probably with two branches (two forked in right wing); continuing into well developed, only slightly zigzagged Psc, which continues into outer gradate series of crossveins. CuP pectinately forked with two long simple branches. 1icu located near origin of CuP; 2icu connecting CuA and anterior trace of CuP (distad origin of distal branch of CuP). *1c:2c* length ratio 0.2:1. A1, A2 shallowly forked. Two gradate series of crossveins; inner series arranged in strongly broken line, with 14 crossveins distad MA; outer series arranged in more smooth line, with ten preserved crossveins distad RP2.

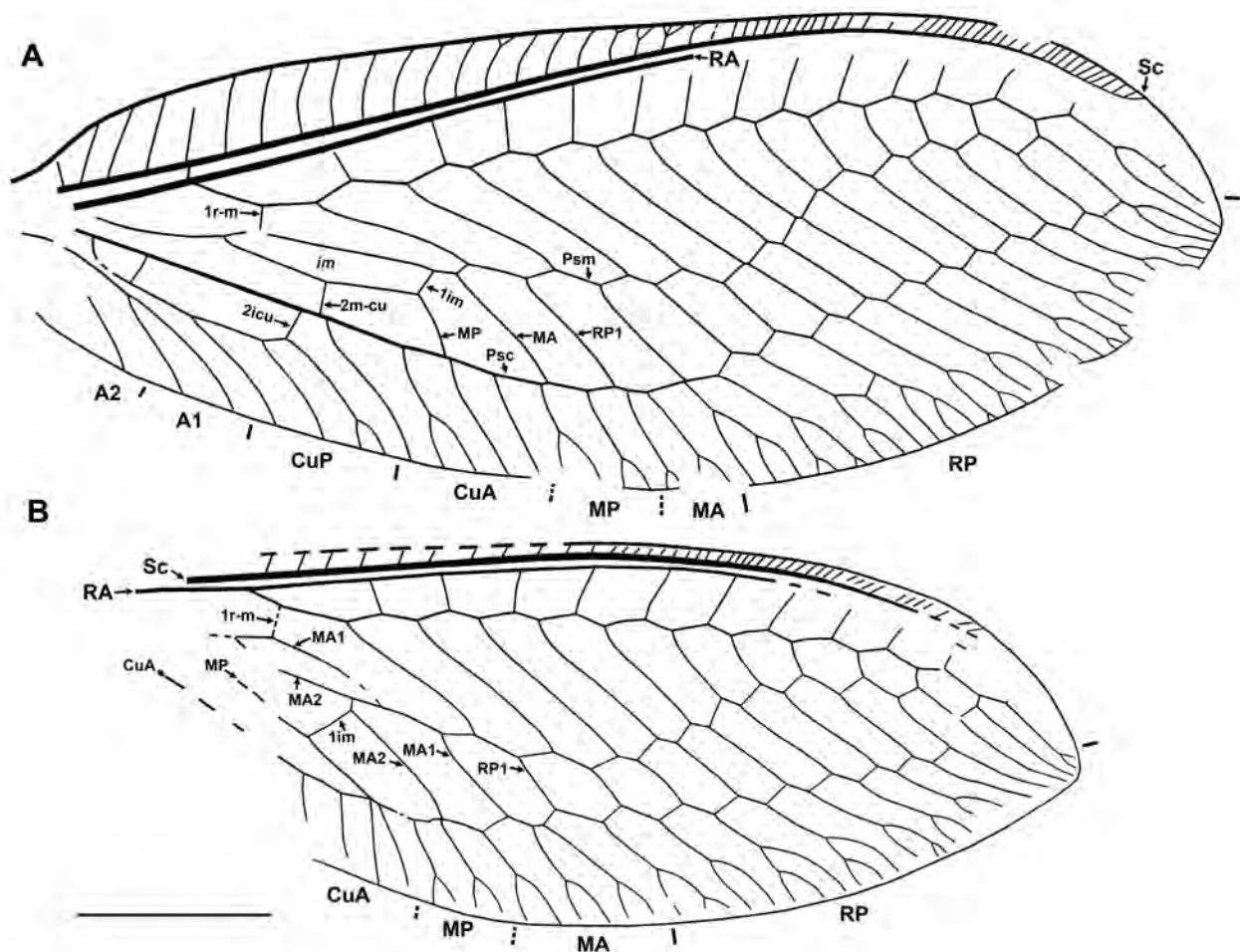


FIGURE 2. *Stephenbrooksia multifurcata* Willmann, 1993, wing venation of the holotype based on the part and counterpart. A, forewing; B, hind wing. Scale bar = 2 mm (both to same scale).

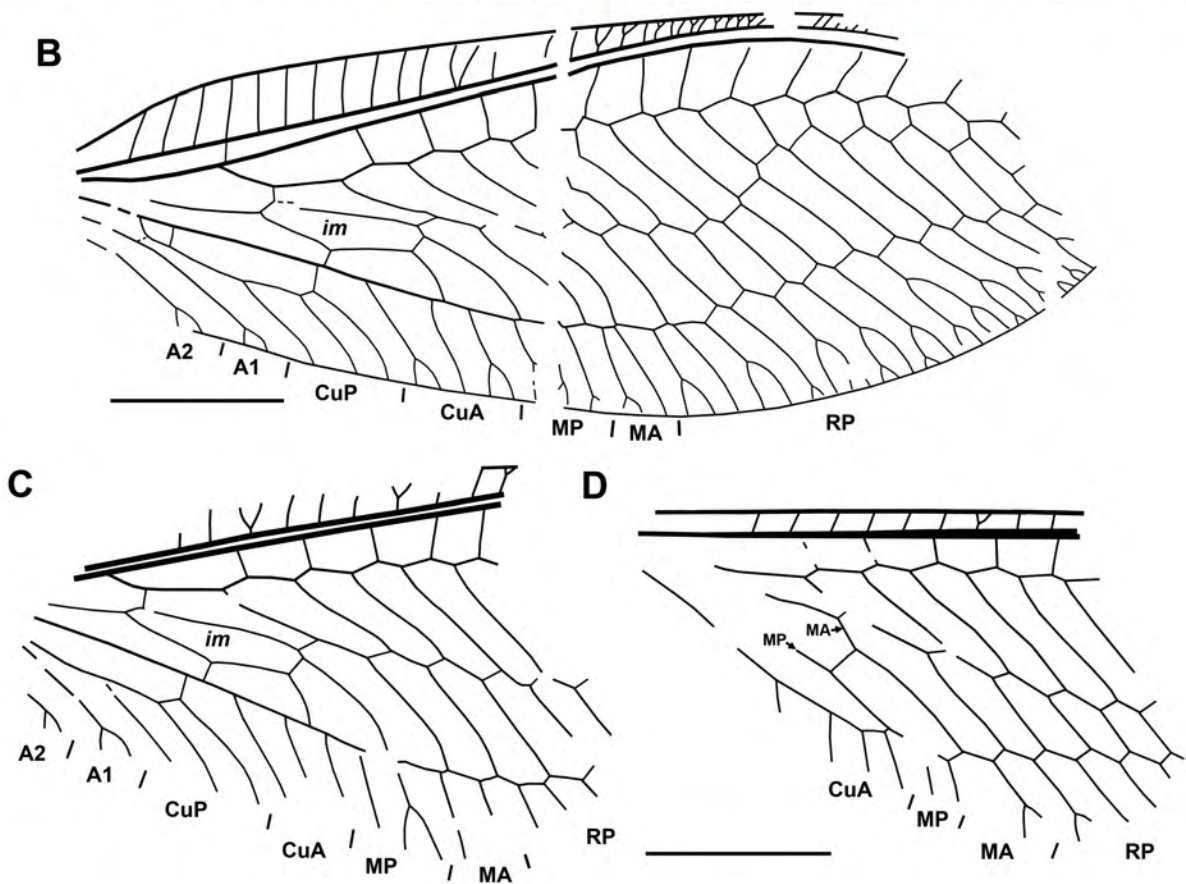
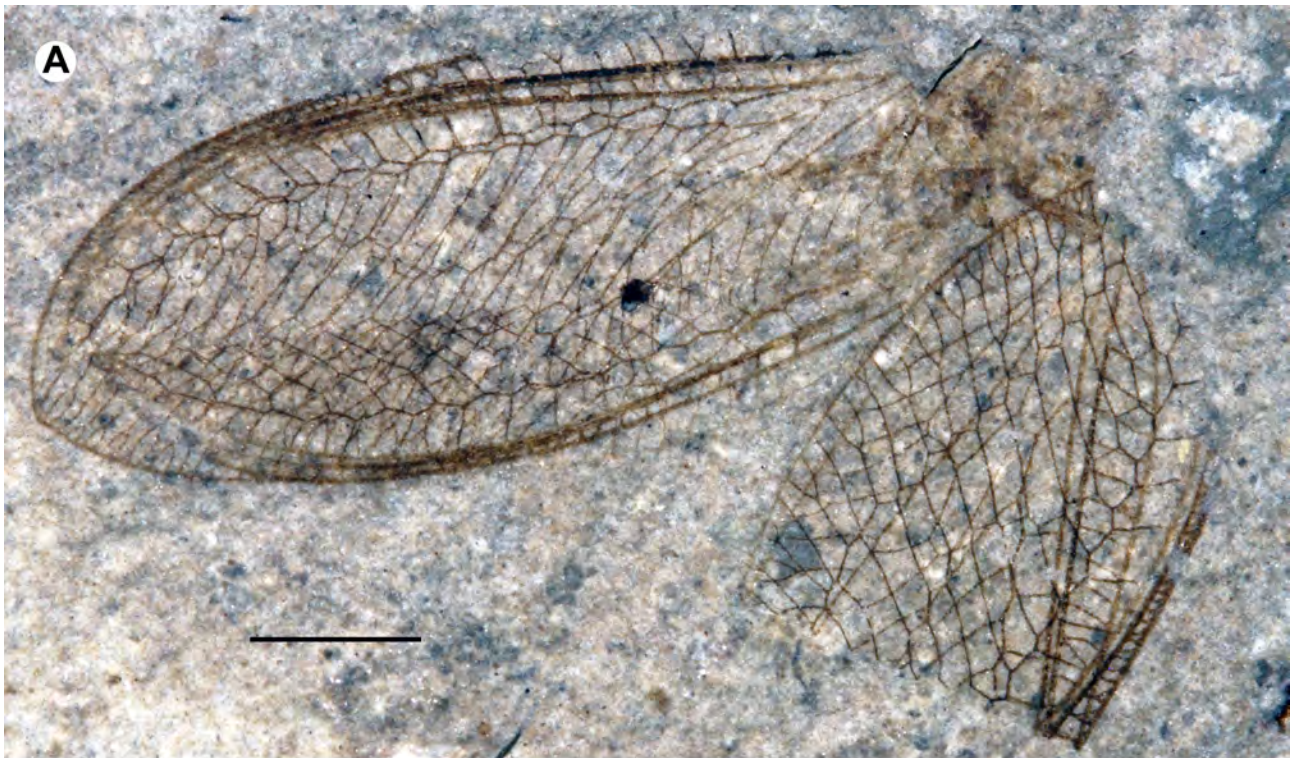


FIGURE 3. *Stephenbrooksia multifurcata* Willmann, 1993, specimen FUM-16651. A, specimen as preserved; B, venation of right forewing; C, venation of basal part left forewing; D, venation of basal part left hind wing (C, D converted to standard view, with apex to the right). Scale bars = 2 mm (C, D to same scale).

Hind wing 10.3 mm long (as preserved; estimated complete length *ca.* 11 mm), *ca.* 4.2 mm wide. Costal space narrow; preserved subcostal veinlets simple (one forked), widely spaced in proximal part. Sc, RA poorly discernible distally. Subcostal space very narrow; crossveins not detected. RA space relatively narrow in proximal part, with five preserved crossveins (basal crossveins with apices inclined to wing base). RP with six preserved branches. MA, MP poorly preserved basally (it is unknown if MA fused with RP or not). MA distally poorly preserved; probably forked at Psc (one branch forked again distad Psc). MP not fused with CuA (connected by short crossvein), forked at Psc. Psm poorly developed, strongly zigzagged. Proximal crossvein between MA, MP (1im) long. CuA pectinate, with three branches. Psc poorly developed, strongly zigzagged. CuP, anal veins not preserved. Two gradate series of crossveins, both incomplete.

Remarks. The configuration of the hind wing MA in the holotype of *S. multifurcata* is strongly aberrant. It is deeply forked proximad the origin of RP, but is not forked before its distal branching in any other Chrysopidae, including specimen FUM-16651.

Genus *Furochrysa* gen. nov.

Etymology. From the Fur Formation, referring to the horizon in which the type species is found, and *-chrysa*, a traditional ending for chrysopid names. Gender feminine.

Type and only species: *Furochrysa alisae* gen et sp. nov.

Diagnosis. Both fore- and hind wings: inner series of gradate crossveins arranged in smooth line. Forewing: *im* pentagonal; 2m-cu located nearly in middle of *im*; CuP with one branch; A1, A2 not forked. Hind wing: 1im, 1icu very long.

Remarks. The new genus is most similar to the Danish *Danochrysa* Willmann, 1993, the Danish-North American *Cimbrochrysa* Schlüter, 1982, and *Asiachrysa* Makarkin, 2014 from the Russian Far East by the nearly identical shape of the intramedian cell and the location of 2m-cu nearly in the middle of the intramedian cell. The new genus is easily distinguished from *Danochrysa* by its simple A1 and A2 (both forked in *Danochrysa*), and the once forked CuP (two to three times in *Danochrysa*). The inner gradate series of crossveins is arranged in a strongly broken line in all species of *Cimbrochrysa* and all other Nothochrysinæ known from the Fur Formation, while it is arranged in a smooth line in the new genus. By this character state, *Furochrysa* gen. nov. is similar to *Asiachrysa*, but all veins in the latter genus are widely spaced and RP1 originates far distad 1ra-rp, while it originates proximad 1ra-rp in the new genus.

The very long crossvein between CuA and CuP (1icu) in the hind wing distinguishes *Furochrysa* gen. nov. from all other Nothochrysinæ. Unfortunately, the hind wing venation is unknown in other members of the subfamily from the Fur Formation, but this crossvein is known to be short in North American species of *Cimbrochrysa* (see Makarkin *et al.* 2022: Figs 11C, 13C, D).

The number of the RP branches (18) in the forewing of *Furochrysa* gen. nov. is the greatest among Nothochrysinæ from the Fur Formation.

An additional long crossvein (labelled ma-rp1 in Fig. 5A) between MA and RP1 is here considered to be an aberration (anomaly).

Furochrysa alisae sp. nov.

(Figs 4–5)

Etymology. From the first name of Alisa A. Perkovsky, who found the specimen in collections of the NHMD (an unnumbered part of the former Rettig collection).

Type material. Holotype: MGUH 34321, collected in 2002 by Erwin Rettig and deposited in the NHMD: slightly crumpled and damaged overlapping fore- and hind wings lacking their basal parts.

Type locality and horizon. Denmark: northern Jutland (Region Nordjylland): Mors Island (Morsø Kommune): Svalklit. Earliest Eocene, Fur Formation.

Description. Forewing 13.1 mm long (as preserved; estimated complete length *ca.* 14 mm), *ca.* 4.5 mm wide. Costal space relatively broad proximally, narrow distally. All preserved subcostal veinlets simple, rather widely

spaced proximally, very dense distally. Sc poorly discernible distally, probably rather long (all veinlets figured in Fig. 4A highly likely belong to Sc). RA long, ending on margin markedly before wing apex; its veinlets poorly discernible. Subcostal space narrow; no subcostal crossveins detected. RA space broad, with 16 crossveins: basal crossveins with apices slightly inclined to wing base; most distal crossveins with apices strongly obliquely to wing apex. Anterior trace of RP slightly zigzagged, apically not forked; with 18 pectinate branches: RP1 presumably forked at Psc, both branches again forked once; RP2, RP3 fused proximally (far proximad Psm); RP5 forked twice distally; RP2–RP4, RP6–RP12, RP18 deeply forked once distally; RP13 shallowly forked once distally; RP14–RP17 simple. Basal crossvein between RP, M (1r-m) long, connecting anterior trace of RP, MA near proximal end of *im* length. M dividing to MA, MP markedly distad origin of RP. MA probably forked distad Psc; MP probably deeply forked at Psc. *im* broad (length/width ratio 2.4:1), pentagonal. Crossvein between MA, MP (1im) long. Psm poorly developed, zigzagged. Crossvein 2m-cu connected *im*, CuA located nearly in middle of *im* (slightly in distal portion). CuA probably with three branches. CuA continuing into well developed, only slightly zigzagged Psc, which continues into outer gradate series of crossveins. Two gradate series of crossveins clearly convergent; inner series with 17 crossveins distad MA; outer series with 14 preserved crossveins distad RP2 (16 when complete). Long crossvein present between these series (labelled ma-rp1 in Fig. 2A). CuP incompletely preserved; its anterior branch probably simple; posterior branch probably very fragmentarily preserved. 2icu long. Presumed A1, A2 fragmentarily preserved, simple.

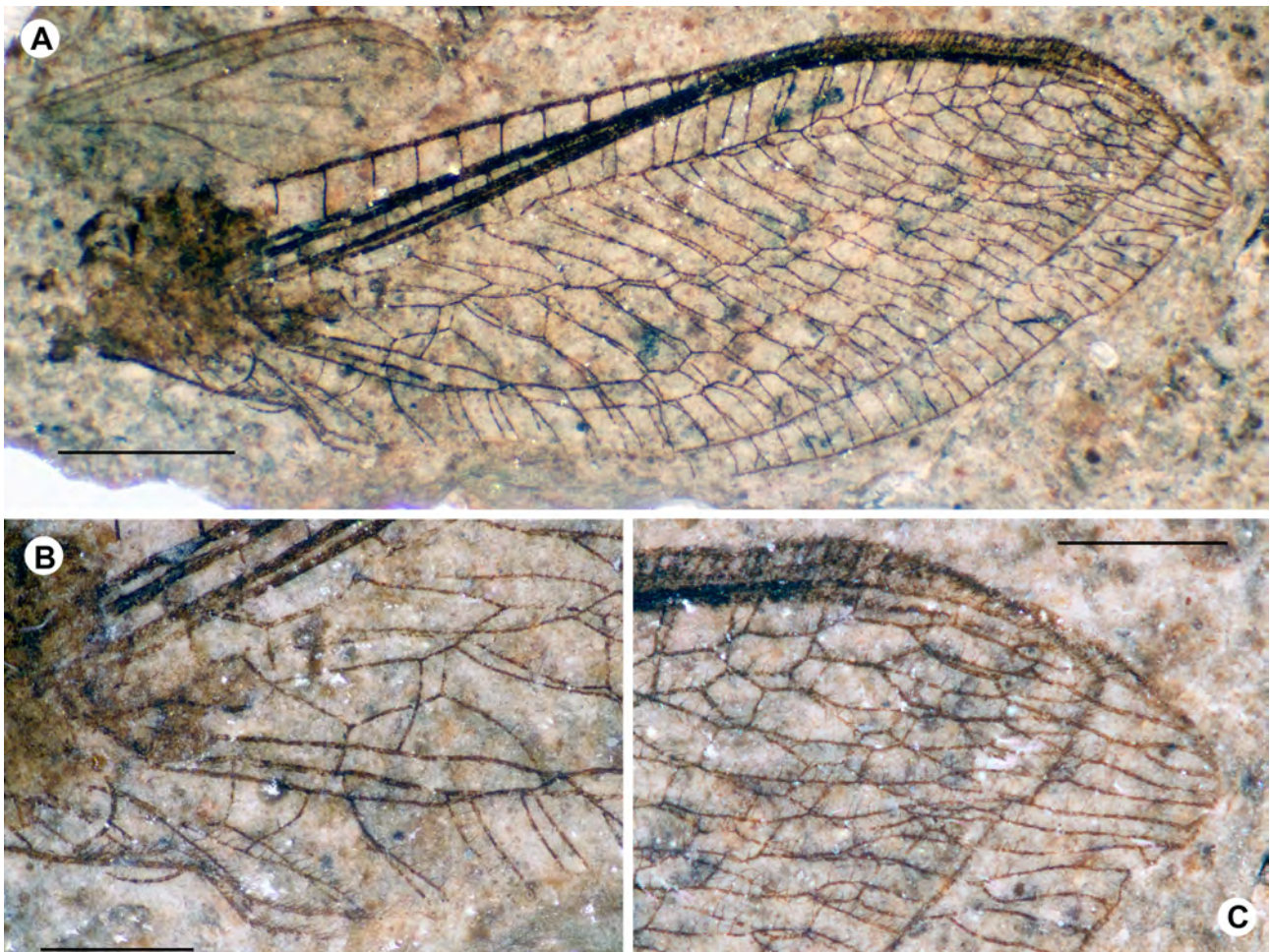


FIGURE 4. *Furochrysa alisae* gen. et sp. nov., holotype MGUH 34321. A, specimen as preserved; B, basal part of wings; C, apical part of wings. Scale bars = 2 mm (A), 1 mm (B, C).

Hind wing *ca.* 11.5 mm long, *ca.* 4.0 mm wide. Costal space narrow; preserved subcostal veinlets simple, widely spaced. Sc indiscernible distally. Subcostal space narrow; crossveins not detected. RA long, ending on margin well before wing apex. RA veinlets poorly discernible. RA space moderately broad; crossveins strongly oblique in distal half. RP with 17 branches; RP1, RP3–RP13 forked once; RP2 forked twice, RP14–RP17 simple. MA, MP basally not preserved (it is unknown if MA fuses with PR). MA presumably forked distad Psc. MP presumably fused with

CuA for very short distance; forked distally at Psc with both branches simple. Intramedial space broad; proximal crossvein between MA, MP (1im) very long. Psm relatively well developed, zigzagged. CuA presumably pectinate, with three branches. Psc relatively well developed, zigzagged. CuP simple. Crossvein between CuA, CuP (1icu) very long. A1, A2, A3 simple. Two gradate series of crossveins arranged in smooth line: inner series with 15 crossveins distad MA; outer series with 14 crossveins distad MA.

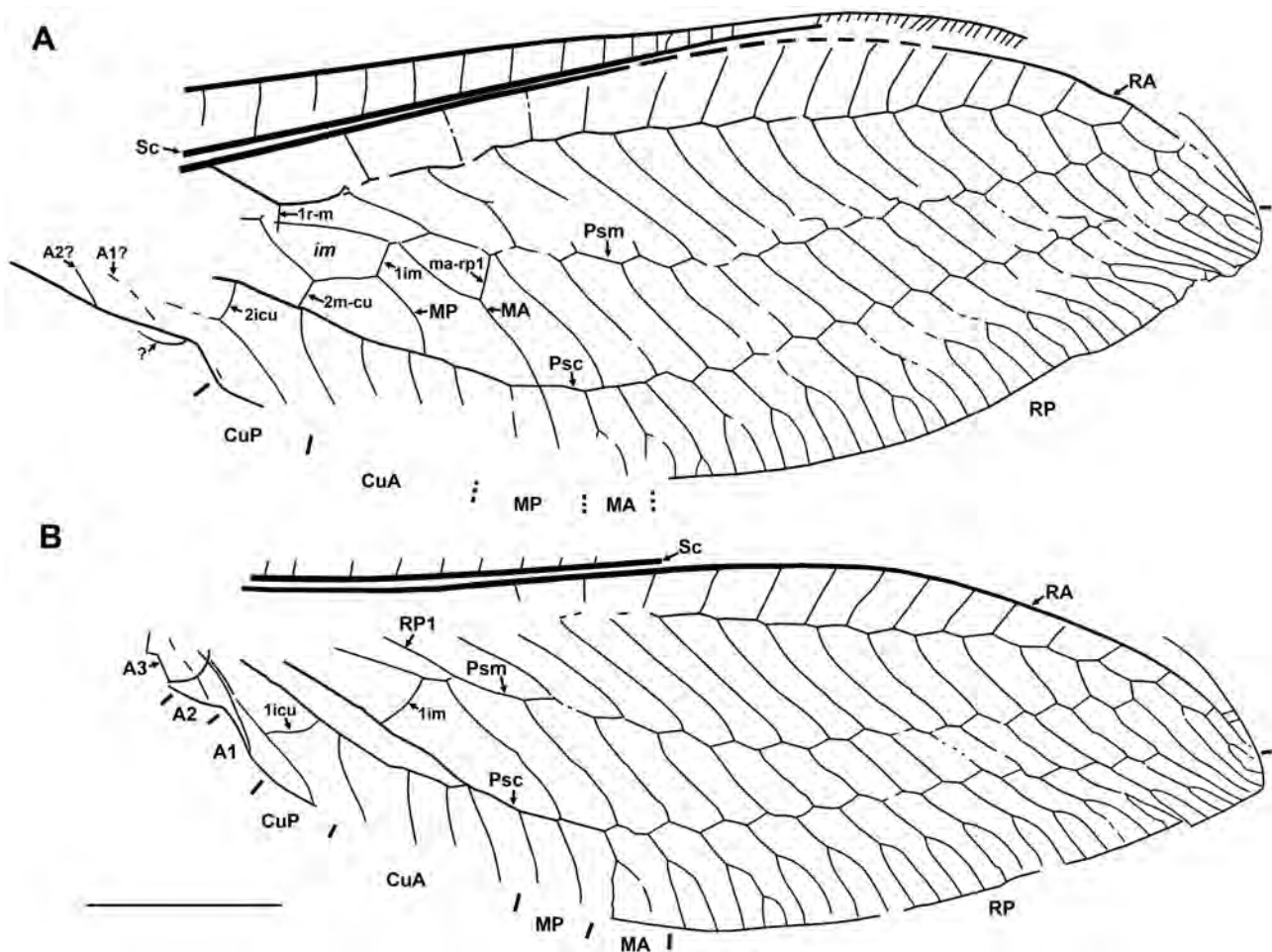


FIGURE 5. The venation of *Furochrysa alisae* gen. et sp. nov., holotype MGUH 34321. A, forewing; B, hind wing. Scale bar = 2 mm (both to same scale).

Danochrysa Willmann, 1993

Danochrysa Willmann, 1993: 240; Peñalver *et al.*, 1995: 486; Nel *et al.*, 2005: 67; Makarkin & Archibald, 2013: 125, 127, 134; Archibald *et al.*, 2014: 191; Makarkin, 2014: 4; Archibald & Makarkin, 2015: 365, 366.

Type and only species: *Danochrysa madseni* Willmann, 1993, by original designation.

Emended diagnosis. Forewing: inner series of gradate crossveins arranged in strongly broken or sigmoid line; *im* elongated, pentagonal (length/width ratio 3.1–4:1); 2m-cu located nearly in middle of *im*; CuP with two pectinate branches (proximal branch often forked); A1 forked; A2 mainly forked (rarely simple).

Danochrysa madseni Willmann, 1993

(Figs 6–9)

Danochrysa madseni Willmann, 1993: 240, 244, Figs 1, 4; Nel *et al.*, 2005: 67; Makarkin & Archibald, 2013: 143, Fig. 2.3; Archibald & Makarkin, 2015: 360.

Type material. Holotype: NHMD-624880A, B & DK 306A, B (formerly No. 14-2296) (part and counterpart), deposited in the NHMD. A nearly complete specimen with crumpled left wings.

Additional material. FUM-11100, collected by Erwin Rettig, and deposited in the FM; four wings, all crumpled except one forewing. FUM-13748, collected by Erwin Rettig, and deposited in the FM; a nearly complete forewing overlaying parts of poorly preserved hind wing.

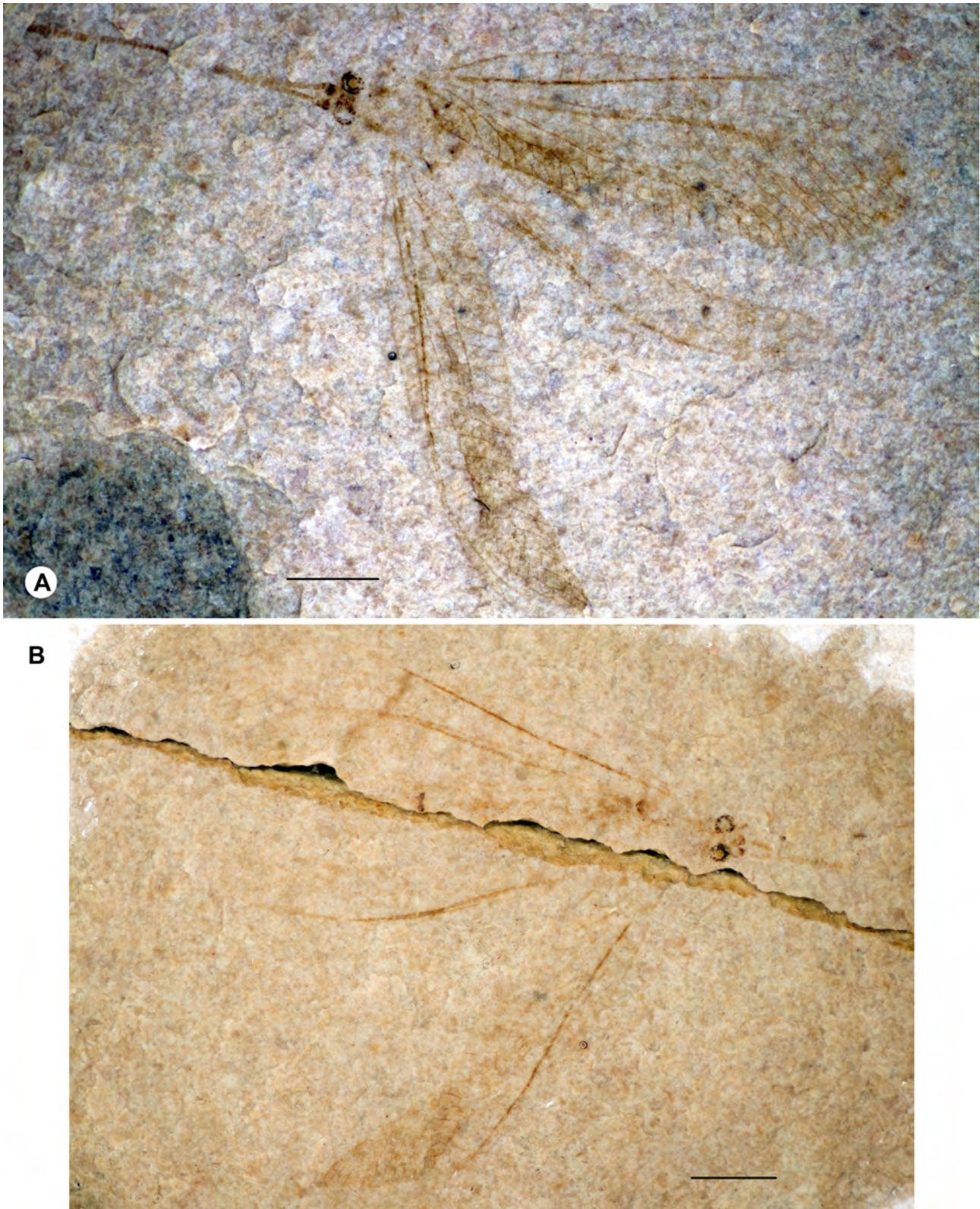


FIGURE 6. *Danochrysa madseni* Willmann, 1993, holotype. A, part (NHMD-624880A); B, counterpart (NHMD-624880B). Scale bars = 2 mm.

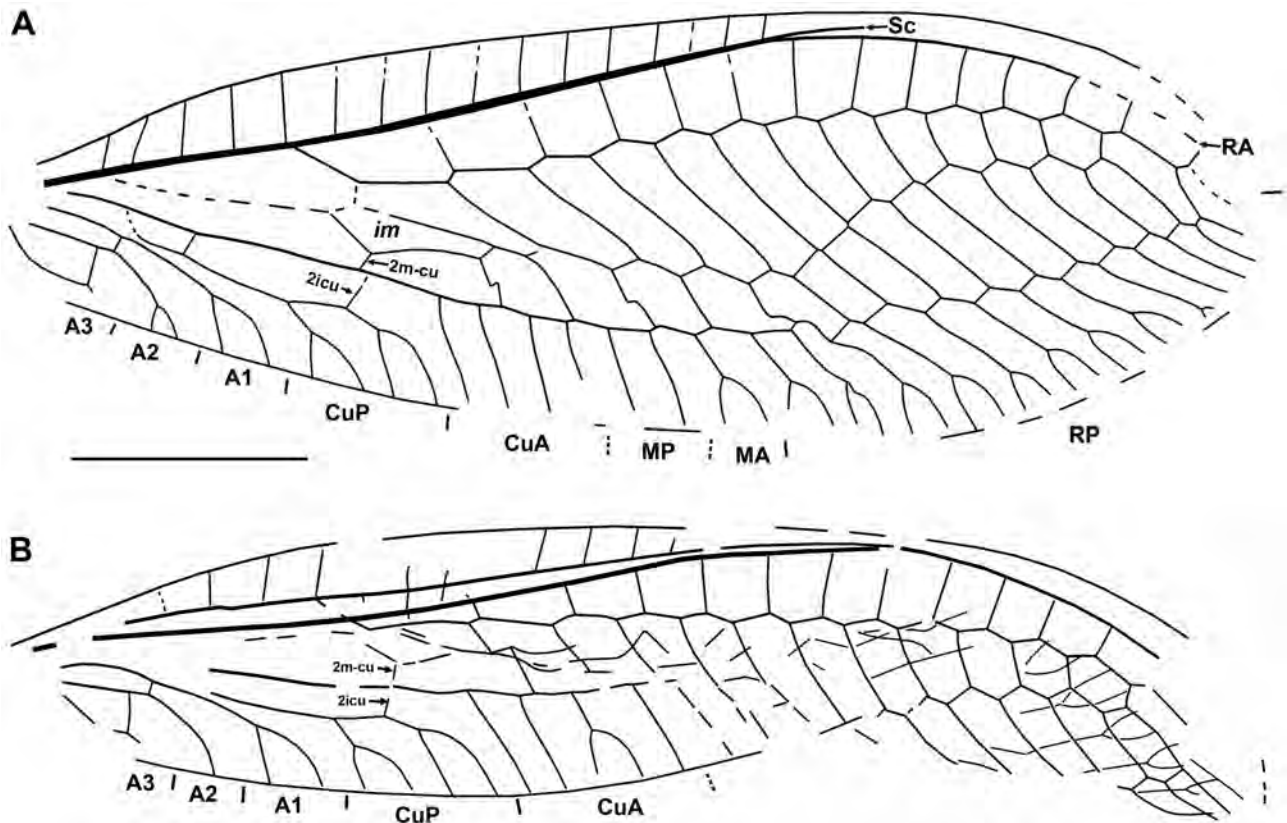


FIGURE 7. The forewing venation of *Danochrysa madseni* Willmann, 1993, holotype NHMD-624880. A, right wing; B, left wing. Scale bar = 2 mm (both to same scale).

Type locality and horizon. Denmark: northern Jutland (Region Nordjylland): Mors Island (Morsø Kommune): Sundby. The locality of FUM-11100: Morsø Kommune: Gullerup, 56.886741°N, 8.731003°E; the precise collecting locality of FUM-13748 is unknown. Earliest Eocene, Fur Formation.

Re-description. Holotype NHMD-624880 (Figs 6, 7). Head with well preserves eyes; antennae: scapus enlarged, dark; pedicellus much smaller, dark; flagellum paler (apical parts not preserved). Thorax, abdomen very poorly discernible; lateral margins of pronotum appears darkish.

Forewing *ca.* 10.7 mm long, 3.5 mm wide. Costal space moderately broad. All preserved subcostal veinlets simple, rather widely spaced. Sc relative long, indiscernible distally. RA distally and its veinlets indiscernible. Subcostal space moderately narrow; subcostal crossveins not detected (see Remarks). RA space moderately broad, with 13 preserved crossveins, all nearly perpendicular to RA. RP originating relatively far from wing base (at 0.24 wing length). Anterior trace of RP zigzagged (apical part not preserved), with 13 pectinate branches. RP1–RP8 relatively deeply forked; RP9 shallowly forked; RP10–RP13 probably simple. Crossvein between MA, MP (1im) rather long, ends on *im* in its proximal part. M dividing to MA, MP markedly distad origin of RP. MA probably forked distad Psc. MP probably forked at Psc. *im* rather narrow, pentagonal (length/width ratio 4:1). Crossvein between MA, MP (1im) short. Psm poorly developed, zigzagged. Crossvein 2m-cu in proximal part of *im*. CuA probably with three branches (forked once in left wing); continuing into well developed, only slightly zigzagged Psc, which continues into outer gradate series of crossveins. 2icu located distad 2m-cu (right wing) or nearly opposite it (left wing). *Ic:2c* length ratio 0.3:1. CuP with two branches; proximal one deeply forked. A1 rather deeply forked. A2 shallowly forked (right wing), and simple (left wing). A3 probably simple. Crossvein between A1, A2 rather short; between A2, A3 long. Two gradate series of crossveins: inner series arranged in strongly broken (sigmoid) line, with 12 crossveins distad MA; outer series arranged in smooth line, with 11 crossveins distad RP2.

Hind wing venation very poorly preserved.

Specimen FUM-11100 (Fig. 8). Forewing 11.2 mm long, *ca.* 4 mm wide. Costal space moderately broad. All preserved subcostal veinlets simple, widely spaced proximally and medially. Sc relative long, indiscernible distally. RA ending on margin slightly before wing apex; its veinlets poorly discernible. Subcostal space narrow;

no subcostal crossveins detected. RA space relatively broad, with 13 crossveins, approximately perpendicular to Sc. RP originating relatively far from wing base (at 0.23 wing length). Anterior trace of RP zigzagged, apically not forked; with 13 pectinate branches. RP1–RP3, RP5, RP7–RP8 forked once; RP4 forked twice; RP6, RP9–RP13 simple. Crossvein between MA, MP (1m) rather long, ends on *im* slightly distad fork of M. M dividing to MA, MP markedly distad origin of RP. MA presumably forked distad Psc. MP presumably forked at Psc; both branches simple in right wing; basal branch deeply forked, distal branch simple in left wing. *im* rather broad, pentagonal (length/width ratio 3.1:1). Crossvein between MA, MP (1m) rather short. Psm poorly developed, zigzagged. Crossvein 2m-cu connected *im*, CuA in middle of *im*. CuA presumably with three branches (basal branch forked in left wing); continuing into well developed, only slightly zigzagged Psc, which continues into outer gradate series of crossveins. CuP with two simple branches. A1, A2 forked. A3 simple. Crossvein between A2, A3 long. Two gradate series of crossveins: inner series arranged in sigmoid line, with 12 crossveins distad MA; outer series arranged in more or less smooth line, with 12 crossveins distad RP2.

Hind wing venation poorly preserved.

Specimen FUM-13748 (Fig. 9). Forewing 11 mm long (as preserved; estimated complete length *ca.* 11.5 mm), *ca.* 4.0 mm wide. Costal space moderately broad. Preserved subcostal veinlets simple, rather widely spaced proximally and medially. Sc indiscernible in distal half. RA probably ending on margin before wing apex; its veinlets poorly discernible. Subcostal space moderately broad; basal subcostal crossveins (1sc-r) located slightly proximad origin of RP. RA space relatively broad, with 13 preserved crossveins, more or less perpendicular to Sc. RP originates relatively far from wing base. Anterior trace of RP slightly zigzagged (its distal part not preserved). RP with 13 preserved branches; most of them probably forked once distally (except probably for two to three distal-most). Crossvein between MA, MP (1m) rather long, ends on *im* in proximal 1/5 of its anterior length. M dividing to MA, MP slightly distad origin of RP. MA probably forked distad Psc. MP probably forked at Psc. *im* rather narrow, pentagonal (length/width ratio 3.6:1). Crossvein between MA, MP (1m) short. Psm poorly developed, zigzagged. Crossvein 2m-cu connected *im*, CuA located nearly in middle of *im* (slightly in proximal portion). CuA probably with four simple branches; continuing into well developed, only slightly zigzagged Psc, which continues into outer gradate series of crossveins. CuP with two branches; anterior branch forked. A1 deeply forked. A2 shallowly forked. A3 strongly curved, simple. Crossvein between A2, A3 long. Two gradate series of crossveins: inner series arranged in sigmoid line, with 13 crossveins distad MA; outer series arranged in more smooth line, with seven preserved crossveins distad RP3 (presumed ten in life). One additional crossvein between these series, located between RP9, RP10.

Hind wing venation almost indiscernible.

Remarks. The veins visible in the subcostal space of the left forewing (Fig. 7C) are likely not true subcostal crossveins. The RA and subcostal spaces overlap each other in this area, and these may be crossveins of the RA space.

The forewing venation of three examined specimens of *D. madseni* shows some variability. The anterior branch of CuP is forked in three wings (Figs 7A, B, 9B), and simple in one wing (Fig. 8C); similarly, A2 is forked in three wings (Figs 7A, 8C, 9B), and simple in one wing (Fig. 7B). The crossvein 2m-cu is located proximad 2icu in the holotype right wing (Fig. 7A), oppositely to 2icu in the holotype left wing (Fig. 7B), but distad it in three other wings (Figs 8B, C, 9B). This is related to the position of the crossvein 2m-cu relative to the length of the intramedian cell, *i.e.*, mainly in its middle, but in the proximal part in one wing (Fig. 7A).

An additional crossvein between RP9 and RP10 (labelled “add.irp” in Fig. 9B) in FUM-13748 is here considered an aberration (anomaly).

Genus *Cimbrochrysa* Schlüter, 1982

Cimbrochrysa Schlüter, 1982: 258; Schlüter, 1984: 7; Willmann & Brooks, 1991: 126, 130; Willmann, 1993: 242, 244; Peñalver *et al.*, 1995: 486; Nel *et al.*, 2005: 67; Makarkin & Archibald, 2013: 127; Archibald *et al.*, 2014: 191; Makarkin, 2014: 4; Archibald & Makarkin, 2015: 365, 366; Makarkin *et al.*, 2022: 312.

Type species: *Cimbrochrysa moleriensis* Schlüter, 1982, by original designation.

Emended diagnosis. Forewing: inner series of gradate crossveins arranged in strongly broken line; *im* pentagonal (length/width ratio 3.7:1); 2m-cu located nearly in middle of *im*; CuP with one branch; A1, A2 probably simple.

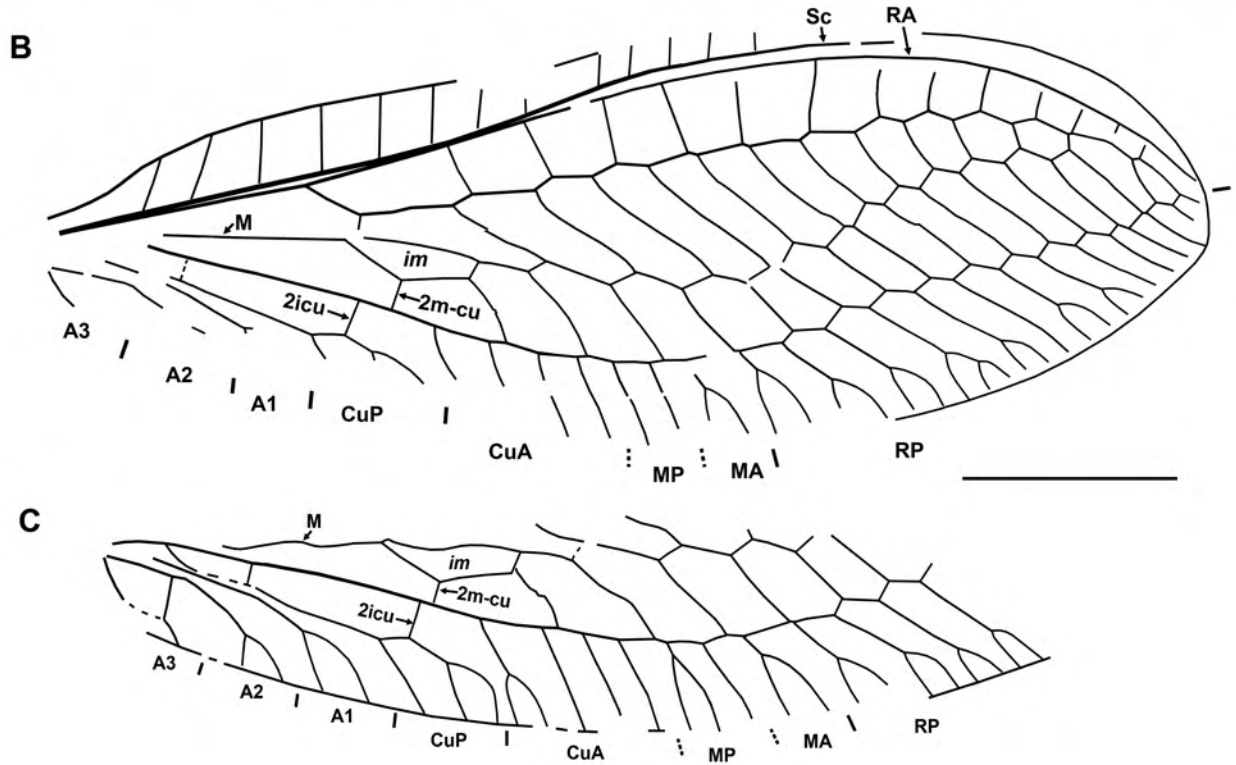


FIGURE 8. *Danochrysa madseni* Willmann, 1993, specimen FUM-11100. A, specimen as preserved; B, venation of right forewing; C, venation of left forewing. Scale bars = 2 mm (B, C to same scale).

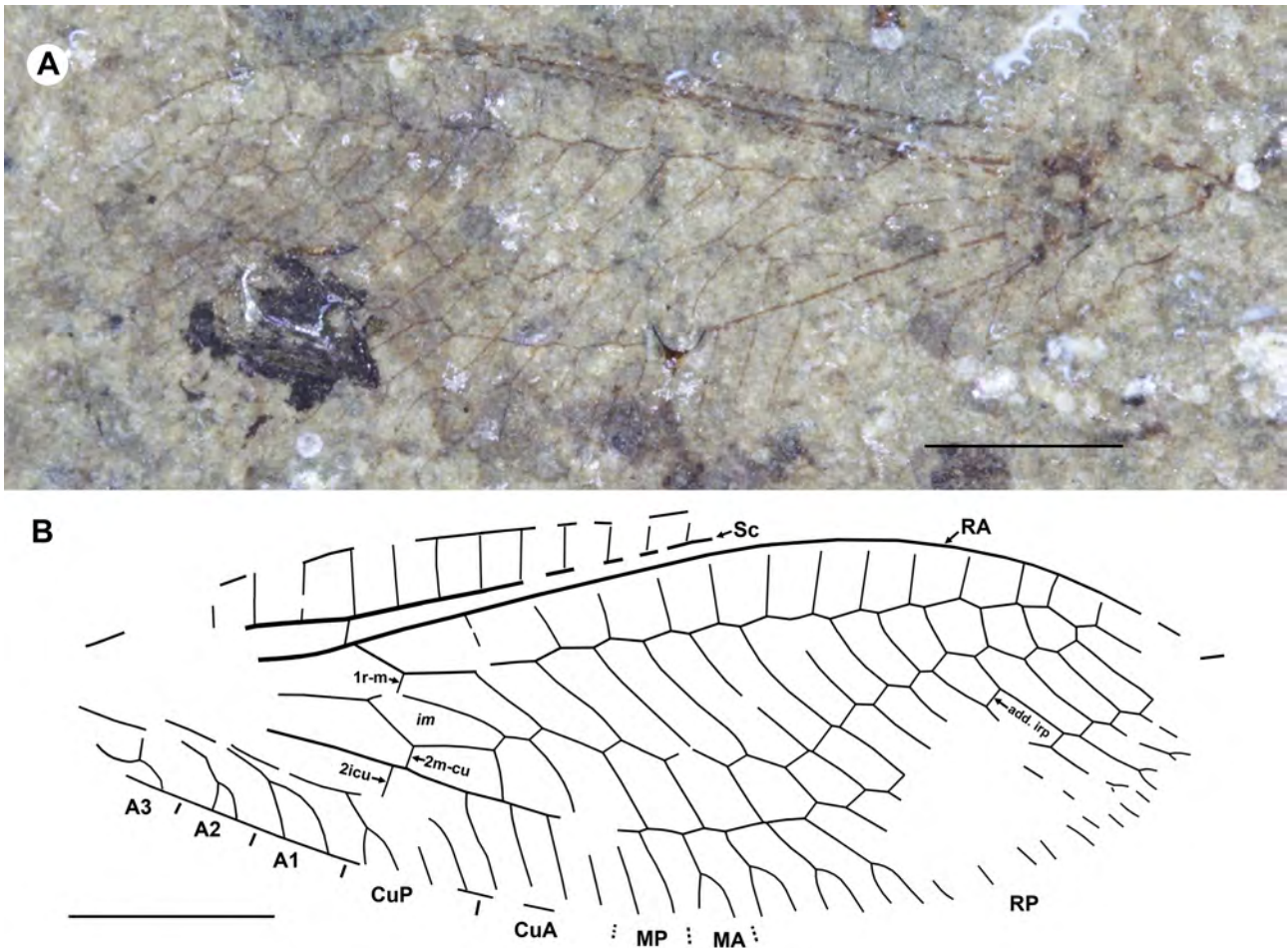


FIGURE 9. *Danochrysa madseni* Willmann, 1993, specimen FUM-13748. A, specimen as preserved; B, venation of forewing. Scale bars = 2 mm.

Species included. *Cimbrochrysa moleriensis* from the earliest Eocene Fur Formation, Denmark; *C. americana* Makarkin *et al.*, 2022, *C. major* Makarkin *et al.*, 2022, both from the latest Eocene Florissant Formation, Colorado, U.S.A.

Remarks. The North American specimens were assigned to this genus due to the similarity of their forewing venation to that of the type species. However, the configurations of A1 and A2 in the holotype are poorly preserved (either might be forked), and these veins are simple in the North American specimens. The angulate hind margin of the holotype forewing figured by Schlüter (1982: Fig. 1b) is false judging from its photograph; the holotype forewing is oval as normal for Chrysopidae.

The hind wing venation of *C. moleriensis* was not described, although it is preserved judging from Schlüter's photograph (1982: Fig. 1a). The hind wing MA is proximally fused with RP in both American species (Makarkin *et al.* 2022: Figs 9C, D, 11C, D, 13C, D). However, this character state is not included in the genus diagnosis as its condition in the holotype is unknown.

Cimbrochrysa moleriensis Schlüter, 1982

Cimbrochrysa moleriensis Schlüter, 1982: 260, 261, Figs 1a, b; Schlüter, 1984: 3, 4, Fig. 2; Martins-Neto & Vulcano, 1989: 190, Fig. 1C; Sèmèria & Nel, 1990: 30; Willmann, 1990: 7, 1993: 242; Willmann & Brooks, 1991: 126, 130, Fig. 3d; Nel *et al.*, 2005: 67; Makarkin & Archibald, 2013: 143, Fig. 2.2; Archibald & Makarkin, 2015: 360; Makarkin *et al.*, 2022: 313.

Type material. Holotype: No. FM 448/74. An almost complete forewing and hind wing overlapped.

Type locality and horizon. Denmark: northern Jutland (Region Nordjylland): Mors Island (Morsø Kommune): Gullerup. Earliest Eocene, Fur Formation.

Remarks. Neither the holotype nor any other specimen of *Cimbrochrysa moleriensis* is found in any museum (FM, NHMD). Therefore, the description of Schlüter (1982) is the only information for the species. Rust (1999) assigned a forewing (MM 5-B2388) to it; however, the holotype and that specimen are surely not conspecific, as crossvein 2m-cu is located in the basal half of the intramedian cell in MM 5-B2388, as mentioned by Rust (1999), but this crossvein is located nearly in its middle in all other known Fur species of Nothochrysoidea, including *C. moleriensis* (2m-cu is located the proximal half of the intramedian cell in the right forewing of the holotype of *D. madseni*, but it is shifted distally in the left wing). Based on the proximal location of 2m-cu, MM 5-B2388 might belong to a genus similar to one of the North American genera, e.g., *Palaeochrysa* Scudder, 1883, *Lithochrysa* Carpenter, 1935 or *Archaeochrysa* Adams, 1967. Unfortunately, Rust (1999) did not provide a photograph of MM 5-B2388.

Discussion

The Nothochrysoidea clearly dominated the Eocene Chrysopidae, constituting the Nothochrysoidea Phase in the history of the family (see Archibald *et al.* 2014). Four of their species are known from the Fur Formation, each belonging to a different genus: *Cimbrochrysa*, *Danochrysa*, *Stephenbrooksia*, and *Furochrysa* **gen. nov.** This is oldest known assemblage of the subfamily, although its oldest record is *Sinonothochrysa zhangi* Huang & Nel in Huang *et al.*, 2022 from the Paleocene of China.

The forewing venation of all Fur Nothochrysoidea is rather similar by some features, e.g., the position of the crossvein 2m-cu in the middle of the intramedian cell, and the inner series of gradate crossveins are arranged in a strongly broken or sigmoid line in most species.

The chrysopid assemblage of the early Eocene Fur Formation differs strongly from that of the late Eocene/Oligocene of Europe. The former includes only extinct genera of Nothochrysoidea and Limaiinae (Makarkin & Perkovsky 2023). In contrast, the only extant nothochrysoidean genus *Nothochrysa* McLachlan, 1868 was recorded from the late Paleogene (late Eocene/Oligocene): one specimen from late Eocene Baltic amber preliminarily assigned to *Nothochrysa* (Makarkin *et al.* 2018) and three fossil species of the genus described from the Oligocene/early Miocene of France and Germany (Statz 1936; Nel & Séméria 1986; Ngô-Muller *et al.* 2019). In addition, three species of Chrysopidae have been described from the late Eocene of Europe: one from Monteils (France) and two from Baltic amber, including one belonging to the Chrysopini (Séméria & Nel 1990; Makarkin *et al.* 2018; Chen *et al.* 2023).

The early Eocene nothochrysoidean assemblage from western North America is very different from that from the Fur Formation. It is represented by five genera (seven species), not occurring in Europe: *Adamsochrysa* Makarkin & Archibald, 2013 (two species), *Okanaganochrysa* Makarkin & Archibald, 2013 (one species), *Pseudochrysopa* Makarkin & Archibald, 2013 (one species), *Archaeochrysa* Adams, 1967 (two species) and *Lithochrysa* Carpenter, 1935 (one species) (Makarkin & Archibald 2013; Archibald & Makarkin 2015, 2017). The forewing venation of these genera is more diverse than that of the Fur Formation nothochrysoidea: the large *Adamsochrysa* with rather dense venation on the one hand, and the small *Pseudochrysopa* with the specialized, reduced venation on the other hand.

The small assemblage of middle Eocene Nothochrysoidea from western North America (Kishenehn Formation, Montana) includes two genera (three species): *Minimochrysa latialata* Jepson & Makarkin, 2023 (the smallest known chrysopid species), *Palaeochrysa greenwalti* Jepson & Makarkin, 2023 and *P. minor* Jepson & Makarkin, 2023.

The late Eocene assemblage of Nothochrysoidea from western North America (Florissant) is represented by six genera: *Archaeochrysa* (three species), *Dyspetochrysa* Adams, 1967 (one species), *Cimbrochrysa* (two species), *Lithochrysa* (four species), *Palaeochrysa* (one species), and *Tribochrysa* Scudder, 1883 (two species) (Makarkin *et al.* 2022). Of these, three are known from the early and middle Eocene of North America (*Archaeochrysa*, *Lithochrysa*, and *Palaeochrysa*); one from the Fur Formation (*Cimbrochrysa*); and *Dyspetochrysa* may be a synonym of *Archaeochrysa*. Therefore, only *Tribochrysa* is endemic to the Florissant Formation.

The only nothochrysinine known from the post-Eocene North America is *Archaeochrysa creedi* (Carpenter, 1935) from the late Oligocene Creede Formation, Colorado. Eleven specimens were assigned to this species (Carpenter 1935; Carpenter in Carpenter *et al.* 1938; Adams 1967). No Chrysopinae were recorded from the Paleogene of North America.

Therefore, the nothochrysinines of the late Paleogene (late Eocene/Oligocene) in North America do not much differ from that of its older horizons. The strong differences in the chrysopid assemblages between the late Eocene Baltic amber in Europe and Florissant in North America are particularly striking.

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References

- Adams, P.A. (1967) A review of the Mesochrysininae and Nothochrysininae (Neuroptera: Chrysopidae). *Bulletin of the Museum of Comparative Zoology*, 135, 215–238.
- 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>
<https://doi.org/10.1017/S1477201906001945>
- Archibald, S.B. & Makarkin, V.N. (2015) A new species of *Archaeochrysa* Adams (Neuroptera: Chrysopidae) from the early Eocene of Driftwood Canyon, British Columbia, Canada. *Canadian Entomologist*, 147 (4), 359–369.
<https://doi.org/10.4039/tce.2014.53>
- Archibald, S.B. & Makarkin, V.N. (2017) A new fossil green lacewing (Neuroptera: Chrysopidae) from the early Eocene Driftwood Canyon, Canada. *Zootaxa*, 4324 (2), 397–400.
<https://doi.org/10.11646/zootaxa.4324.2.13>
- Archibald, S.B., Makarkin, V.N., Greenwood, D.R. & Gunnell, G.F. (2014) The Red Queen and Court Jester in green lacewing evolution: bat predation and global climate change. *Palaios*, 29 (5), 385–391.
<https://doi.org/10.2110/palo.2013.089>
- 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>
- Carpenter, F.M. (1935) Tertiary insects of the family Chrysopidae. *Journal of Paleontology*, 9, 259–271.
- Carpenter, F.M., Snyder, T.E., Alexander, C.P., James, M.T. & Hull, F.M. (1938) Fossil insects from the Creede Formation, Colorado. Part 1. Introduction, Neuroptera, Isoptera and Diptera. *Psyche*, 45 (2/3), 105–118, 1 pl.
<https://doi.org/10.1155/1938/46082>
- Chen, Z.L., Gao, Y.H., Makarkin, V.N. & Liu, X.Y. (2023) First green lacewing species of the tribe Chrysopini (Insecta: Neuroptera: Chrysopidae: Chrysopinae) from the Eocene Baltic amber and Miocene Mexican amber. *Palaeoentomology*, 6 (6), 651–664.
<https://doi.org/10.11646/palaeoentomology.6.6.7>
- Dietrich, C.H. & Perkovsky, E.E. (2023) First leafhopper from the early Eocene Fur Formation of Denmark representing a new genus of Cicadellinae (Hemiptera: Cicadomorpha). *Palaeoentomology*, 6 (5), 447–450.
<https://doi.org/10.11646/palaeoentomology.6.5.2>
- Hagen, H.A. (1866) Hemerobidarum Synopsis synonymica. *Stettiner Entomologische Zeitung*, 27, 369–462.
- Huang, D.Y., Lian, X.N., Jouault, C., Gao, J. & Nel, A. (2022) First green lacewing (Insecta: Neuroptera: Chrysopidae) from the Paleocene Sanshui Basin of Guangdong, South China. *Historical Biology*, 34 (4), 704–712.
<https://doi.org/10.1080/08912963.2021.1943381>
- ICZN (1999) *International Code of Zoological Nomenclature. 4th edition*. International Trust for Zoological Nomenclature, London, xxix + 305 pp.

- Jenkins Shaw, J., Nielsen, C. & Perkovsky, E.E. (2024) A pinophiline rove beetle (Coleoptera: Staphylinidae: Paederinae) from the early Eocene Fur formation, Denmark. *Entomologiske Meddelelser*, 90 (1), 61–70.
- Jepson, J.E. & Makarkin, V.N. (2023) Fossil Neuropterida (Insecta: Neuroptera and Raphidioptera) from the middle Eocene Kishenehn Formation, Montana, USA. *Zootaxa*, 5306 (4), 427–444.
<https://doi.org/10.11646/zootaxa.5306.4.2>
- 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.
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10th ed. Vol. 1. Salvii, Holmiae*, 824 pp.
<https://doi.org/10.5962/bhl.title.542>
- Makarkin, V.N. (2014) A new fossil green lacewing (Neuroptera: Chrysopidae) from the Eocene Tadushi Formation, eastern Sikhote-Alin. *Far Eastern Entomologist*, 272, 1–7. [<https://www.biosoil.ru/FEE/Publication/418>]
- Makarkin, V.N., Antell, G. & Archibald, S.B. (2022) A revision of Chrysopidae (Neuroptera) of the late Eocene Florissant Formation, Colorado, with description of new species. *Zootaxa*, 5133 (3), 301–345.
<https://doi.org/10.11646/zootaxa.5133.3.1>
- Makarkin, V.N. & Archibald, S.B. (2013) A diverse new assemblage of green lacewings (Insecta: Neuroptera: Chrysopidae) from the early Eocene Okanagan Highlands, western North America. *Journal of Paleontology*, 87 (1), 123–146.
<https://doi.org/10.1666/12-052R.1>
- Makarkin, V.N. & Perkovsky, E.E. (2023) New Limaiinae (Neuroptera: Chrysopidae) from the early Eocene Fur Formation, Denmark, including an unexpected finding of a Mesozoic genus. *Zootaxa*, 5383 (1), 57–66.
<https://doi.org/10.11646/zootaxa.5383.1.4>
- Makarkin, V.N., Wedmann, S. & Weiterschan, T. (2018) The first green lacewings from the late Eocene Baltic amber. *Acta Palaeontologica Polonica*, 63 (3), 527–537.
<https://doi.org/10.4202/app.00504.2018>
- Martins-Neto, R.G. & Vulcano, M.A. (1989) Neurópteros (Insecta: Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. I - Família Chrysopidae. *Anais da Academia Brasileira de Ciências*, 60 (2), 189–201, 1 pl. [for 1988]
- McLachlan, R. (1868) A monograph of the British Neuroptera-Planipennia. *Transactions of the [Royal] Entomological Society of London*, 16, 145–224.
<https://doi.org/10.1111/j.1365-2311.1868.tb00622.x>
- Navás, L. (1910) Crisópidos (Ins. Neur.) nuevos. *Brotéria (Zoológica)*, 9 (1), 38–59.
- Nel, A., Delclòs, X. & Hutin, A. (2005) Mesozoic chrysopid-like Planipennia: a phylogenetic approach (Insecta: Neuroptera). *Annales de la Société entomologique de France, New Series*, 41, 29–68.
<https://doi.org/10.1080/00379271.2005.10697440>
- Nel, A. & Séméria, Y. (1986) Une nouvelle espèce de Chrysopide fossile du Stampien supérieur (Oligocène) d’Aix-en-Provence *Notochrysa* [sic] *stampieni* n. sp. (Neuroptera, Chrysopidae, Notochrysinae [sic]). *Neuroptera International*, 4 (1), 23–30.
- Ngô-Muller, V., Blot, K. & Nel, A. (2019) A second species of *Notochrysa* from the latest Oligocene of France (Insecta: Neuroptera: Chrysopidae). *Palaeoentomology*, 2 (2), 111–114.
<https://doi.org/10.11646/palaeoentomology.2.2.2>
- Oswald, J.D. (1993) Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). *Journal of the New York Entomological Society*, 101, 143–299.
- 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.
- Peñalver, E., Nel, A. & Martínez-Delclòs, X. (1995) New Nothochrysinae from the Spanish Miocene (Neuroptera, Chrysopidae). *Bulletin de la Société entomologique de France*, 100 (5), 481–487.
<https://doi.org/10.3406/bsef.1995.17194>
- Rasmussen, J.A., Madsen, H., Schultz, B.P., Sylvestersen, R.L. & Bonde, N. (2016) The lowermost Eocene deposits and biota of the western Limfjord region, Denmark—Field Trip Guidebook. *2nd International Mo-clay Meeting at Muse@um, Skive and Fossil and Mo-clay Museum, Museum Mors, Nykøbing Mors, Denmark*, 2–4 November 2016, 1–35.
- Rust, J. (1999) *Biologie der Insekten aus dem ältesten Tertiär Nordeuropas*. Habilitationsschrift zur Erlangung der venia legendi für das Fach Zoologie in der biologischen Fakultät der Georg-August-Universität, Göttingen, 482 pp., 34 pls.
- Schlüter, T. (1982) *Cimbrochrysa moleriensis* n. g. n. sp. und *Hypochrysa hercyniensis* n. sp., zwei fossile Chrysopidae-Arten (Insecta: Planipennia) aus dem europäischen Tertiär. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1982 (5), 257–264.
<https://doi.org/10.1127/njgpm/1982/1982/257>
- Schlüler, T. (1984) Phylogeny of Chrysopidae. In: Canard, M., Séméria, Y. & New, T.R. (Eds.), *Biology of Chrysopidae*. Dr. W. Junk Publishers, The Hague, etc., pp. 1–8.
- Schneider, W.G. (1851) *Symbolae ad monographiam generis Chrysopae, Leach*. Hirt, Vratislaviae, 178 pp.
- Scudder, S.H. (1883) The tertiary Lake Basin at Florissant, Colo., between South and Hayden Parks. *Annual Report of the United States Geological and Geographical Survey of the Territories*, 12, 271–293.
<https://doi.org/10.3133/70159191>

- Séméria, Y. & Nel, A. (1990) *Paleochrysopa monteilsensis* gen. et sp. nov., a new fossil of Chrysopidae from the Upper Eocene Formation of Monteils (France), with a review of the known chrysopid fossils (Insecta: Neuroptera). In: Mansell, M.W. & Aspöck, H. (Eds.), *Advances in Neuropterology. Proceedings of the Third International Symposium on Neuropterology*. South African Department of Agricultural Development, Pretoria, pp. 27–32.
- Statz, G. (1936) Ueber neue Funde von Neuropteren, Panorpaten und Trichopteren aus den tertiären Schiefer von Rott am Siebengebirge. *Decheniana: Verhandlungen des Naturhistorischen Vereins des Rheinlande und Westfalens*, 93, 208–255.
- Tauber, C.A. (2019a) South American Nothochrysinæ (Neuroptera, Chrysopidae): I. Description of *Nothochrysa ehrenbergi* sp. nov. *ZooKeys*, 866, 1–18.
<https://doi.org/10.3897/zookeys.866.35394>
- Tauber, C.A. (2019b) South American Nothochrysinæ (Neuroptera, Chrysopidae): II. Redescription of *Leptochrysa prisca* Adams & Penny. *ZooKeys*, 866, 19–38.
<https://doi.org/10.3897/zookeys.866.35396>
- Willmann, R. (1990) Insekten aus der Fur-Formation von Dänemark (Moler, ob. Paleozän / unt. Eozän ?). 1. Allgemeines. *Meyniana*, 42, 1–14.
- Willmann, R. (1993) Insekten aus der Fur-Formation von Dänemark (Moler, ob. Paleozän / unt. Eozän?). 8. Zwei neue Vertreter der Chrysopidae (Neuroptera). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1993 (4), 239–245.
<https://doi.org/10.1127/njgpm/1993/1993/239>
- Willmann, R. & Brooks, S.J. (1991) Insekten aus der Fur-Formation von Dänemark (Moler, ob. Paleozän / unt. Eozän?). 6. Chrysopidae (Neuroptera). *Meyniana*, 43, 125–135, 2 pls.
- Winterton, A.L., Gillung, J.P., Garzón-Orduña, I.J., Badano, D., Breitzkreuz, L.C.V., Duelli, P.R., Engel, M.S., Liu, X.Y., Machado, R.J.P., Mansell, M., Mochizuki, A., Penny, N.D., Tauber, C.A. & Oswald, J.D. (2019) Evolution of green lacewings (Neuroptera: Chrysopidae): an anchored phylogenomics approach. *Systematic Entomology*, 44, 514–526.
<https://doi.org/10.1111/syen.12347>