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A new genus and species of Nothochrysinae (Neuroptera: Chrysopidae) from the early Eocene Fur Formation, Denmark

VLADIMIR N. MAKARKIN[1*], THOMAS J. SIMONSEN[2] & EVGENY E. PERKOVSKY[3]
[1]*Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch of the Russian Academy of Sciences, Vladivostok, 960022, Russia.*
[2]*Natural History Museum Aarhus, Vilhelm Meyers Allé 10, Aarhus, Denmark.*
t.simonsen@nathist.dk; https://orcid.org/0000-0001-9857-9564
[3]*Natural History Museum of Denmark, Universitetsparken 15, Copenhagen, Denmark.*
perkovsk@gmail.com; https://orcid.org/0000-0002-7959-4379
**Corresponding author. vnmakarkin@mail.ru; https://orcid.org/0000-0002-1304-0461*

Abstract

Triachrysa rusti **gen. et sp. nov.** (Neuroptera: Chrysopidae: Nothochrysinae) is described from the earliest Eocene Fur Formation of Denmark. The three gradate series of crossveins in the forewing distinguishes the new genus from other Nothochrysinae known from this formation. The forewing venation is compared to that of three other genera of Nothochrysinae with three gradate series: the early Eocene *Okanaganochrysa* Makarkin & Archibald, 2013, the latest Eocene *Tribochrysa* Scudder, 1883, and the extant *Triplochrysa* Kimmins, 1952. These four genera are apparently not closely related, and their third (additional) series may have developed independently in these taxa.

Key words: Taxonomy, *Okanaganochrysa*, *Tribochrysa*, *Triplochrysa*, *Triachrysa rusti* **gen. et sp. nov.**

Introduction

The Chrysopidae (green lacewings) comprise one of largest families of Neuroptera with more than 1400 extant species (Oswald & Machado 2018). The family consists of four subfamilies (Apochrysinae, Nothochrysinae, Chrysopinae, and Limaiinae) with numerous fossil species occurring from the Middle Jurassic onwards (Archibald *et al*. 2014; Winterton *et al*. 2019; Chen *et al*. 2023). Of three subfamilies known from the Eocene (*i.e*., Limaiinae, Nothochrysinae, and Chrysopinae), the Nothochrysinae clearly dominate Chrysopidae (see Makarkin & Archibald 2013; Makarkin *et al*. 2022; Makarkin & Perkovsky 2024).

Green lacewings are rather common in the earliest Eocene Fur Formation of Denmark. About 45 specimens are known (partly undescribed) with six valid species of Chrysopidae have been described from there: four species belong to Nothochrysinae (*Cimbrochrysa moleriensis* Schlüter, 1982, *Danochrysa madseni* Willmann, 1993, *Stephenbrooksia multifurcata* Willmann, 1993, and *Furochrysa alisae* Makarkin & Perkovsky, 2024), and two species to Limaiinae (*Protochrysa aphrodite* Willmann & Brooks, 1991 and *Mesypochrysa nielseni* Makarkin & Perkovsky, 2023) (Schlüter 1982; Willmann & Brooks 1991; Willmann 1993; Makarkin & Perkovsky 2023, 2024).

Here, we describe a new genus and species of Nothochrysinae from the Fur Formation in the Henrik Madsen collection of the Fossil and Moclay Museum, Museum Mors.

Material and methods

We examined two specimens, collected at the Ejerslev Mo-clay Pit and Sundby Cliff localities of the Fur Formation in western Limfjord, Denmark. Overviews of this earliest Eocene Danish Lagerstätte have been provided by *e.g*., Larsson (1975), Archibald & Makarkin (2006), Pedersen *et al*. (2012), Rasmussen *et al*. (2016), and Madsen & Rasmussen (2021). Photographs of specimens were taken using a Canon EOS 5D II camera, either with a Canon EF 100 f2.8 USM macro lens or in conjunction with an Olympus SZ60 stereo microscope.

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Venation terminology in general follows Breitkreuz *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; 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.

Abbreviations of institutions: MM, Museum Mors (Fossil and Moclay Museum), Denmark.

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Chrysopidae Schneider, 1851

Subfamily Nothochrysinae Navás, 1910

Genus *Triachrysa* gen. nov.

Type and only species: *Triachrysa rusti* sp. nov.

Diagnosis. Forewing: Costal space strongly narrowed before pterostigmal area; three gradate series in radial space; intramedian cell broad, pentagonal; crossvein 2m-cu connecting MP, CuA located in proximal half of intramedian cell.

Etymology. From the Greek *tria* [*τρία*], three, and *–chrysa*, a traditional ending for generic names in Chrysopidae, referring to the presence of three gradate series of crossveins in the forewing. Gender: feminine.

Remarks. The new genus is clearly distinguished from other Nothochrysinae (see Discussion).

Triachrysa rusti sp. nov.

(Figs 1–3)

Brooksiochrysa jutlandica Rust, 1999: 284, Pl. 23, Fig. f, *nomen nudum*.

Type material. Holotype MM-14943 (part and counterpart), deposited in the Henrik Madsen collection (number 14M-B2585) of the MM; collected by Henrik Madsen on May 27, 1995. An incomplete forewing with the venation indiscernible in the posterior part.

Paratype MM-14944 (part and counterpart), deposited in the Henrik Madsen collection (number HM 5-B2837) of the MM; collected by Henrik Madsen on July 12, 1995. An incomplete forewing: the posterior basal part is crumpled and folded, and the distal part of the wing is missing.

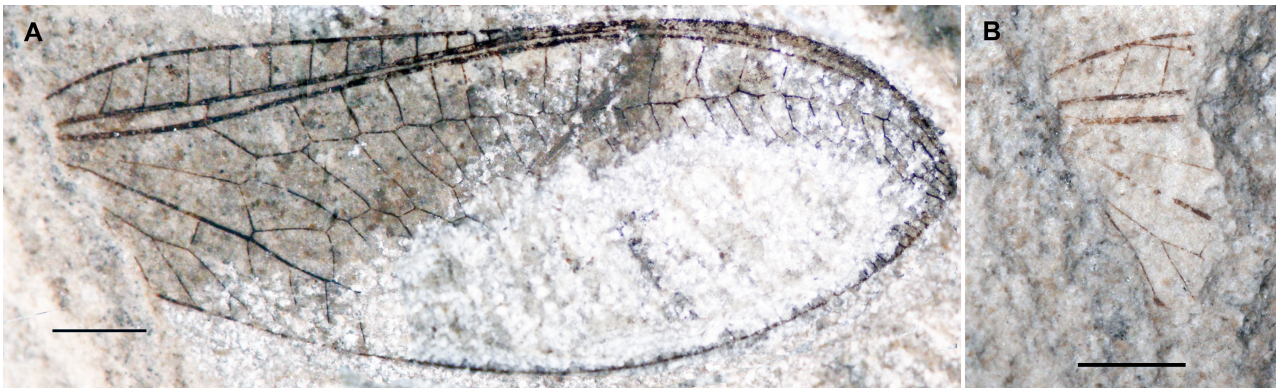

FIGURE 1. *Triachrysa rusti* **gen. et sp. nov.**, holotype MM-14943. A, part (converted to standard view, with apex to the right); B, counterpart. Scale bars = 2 mm.

FIGURE 2. *Triachrysa rusti* **gen. et sp. nov.**, paratype MM-14944. A, part; B, counterpart (converted to standard view, with apex to the right). Scale bars = 2 mm.

Type localities and horizons. Holotype: Denmark: northern Jutland (Region Nordjylland): Mors Island (Morsø Kommune): Ejerslev Mo-clay Pit (ash layer +15). Paratype: Mors Island: Sundby Cliff (ash layers +25 – +30). Fur Formation, lower part of Silstrup Member; earliest Eocene.

Etymology. The specific epithet is a patronym formed from the surname of Jes Rust, a German paleoentomologist, in recognition of his great contributions to the study of Mo-clay insects.

Description. ***Holotype*.** Forewing 19 mm long (as preserved; estimated complete length *ca*. 20.2 mm), 7.2 mm wide. Costal space broad proximally, extremely narrow before pterostigma, then slightly dilated. All subcostal veinlets simple, relatively widely spaced proximally, very dense distally (very poorly preserved). Sc relatively long, poorly discernible distally. RA terminating on margin before wing apex; its veinlets indiscernible distally. Subcostal space narrow; basal subcostal crossveins located opposite origin of RP. RA space broadest medially, with 17 crossveins: basal and distal crossveins perpendicular to RA; medial crossveins with apices slightly inclined to wing apex; one crossvein forked. RP originating relatively close to wing base (at 0.23 length). Anterior trace of RP slightly zigzagged, apically forked; with 21 pectinate branches, mostly preserved only proximally; three distal-most branches simple. 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. Distal parts of MA, MP not preserved. *im*

broad, pentagonal (length/width ratio 2.1:1). Crossvein between MA, MP (1im) rather long. Psm poorly developed, zigzagged. Crossvein 1m-cu poorly preserved, located proximad origin of CuP; 2m-cu (between *im* and CuA) short, located in proximal part of *im*. CuA probably with four simple branches; continuing into well developed, only slightly zigzagged Psc (only its proximal part preserved). CuP deeply forked once; its anterior trace shallowly forked. 1icu long, located near origin of CuP; 2icu connecting CuA and anterior trace of CuP much proximad 2m-cu. *1c*:*2c* length ratio 0.25:1. 1A fragmentarily preserved; 2A, 3A not preserved. Three gradate series of crossveins: in additional (third) series, four proximal crossveins preserved (between RP3 to RP7); in inner series, three proximal crossveins preserved (between MA to RP3); five distal crossveins (between PR14 to RP20) may belong to either inner or additional series; in outer series, four distal preserved crossveins (between stem of RP to RP18).

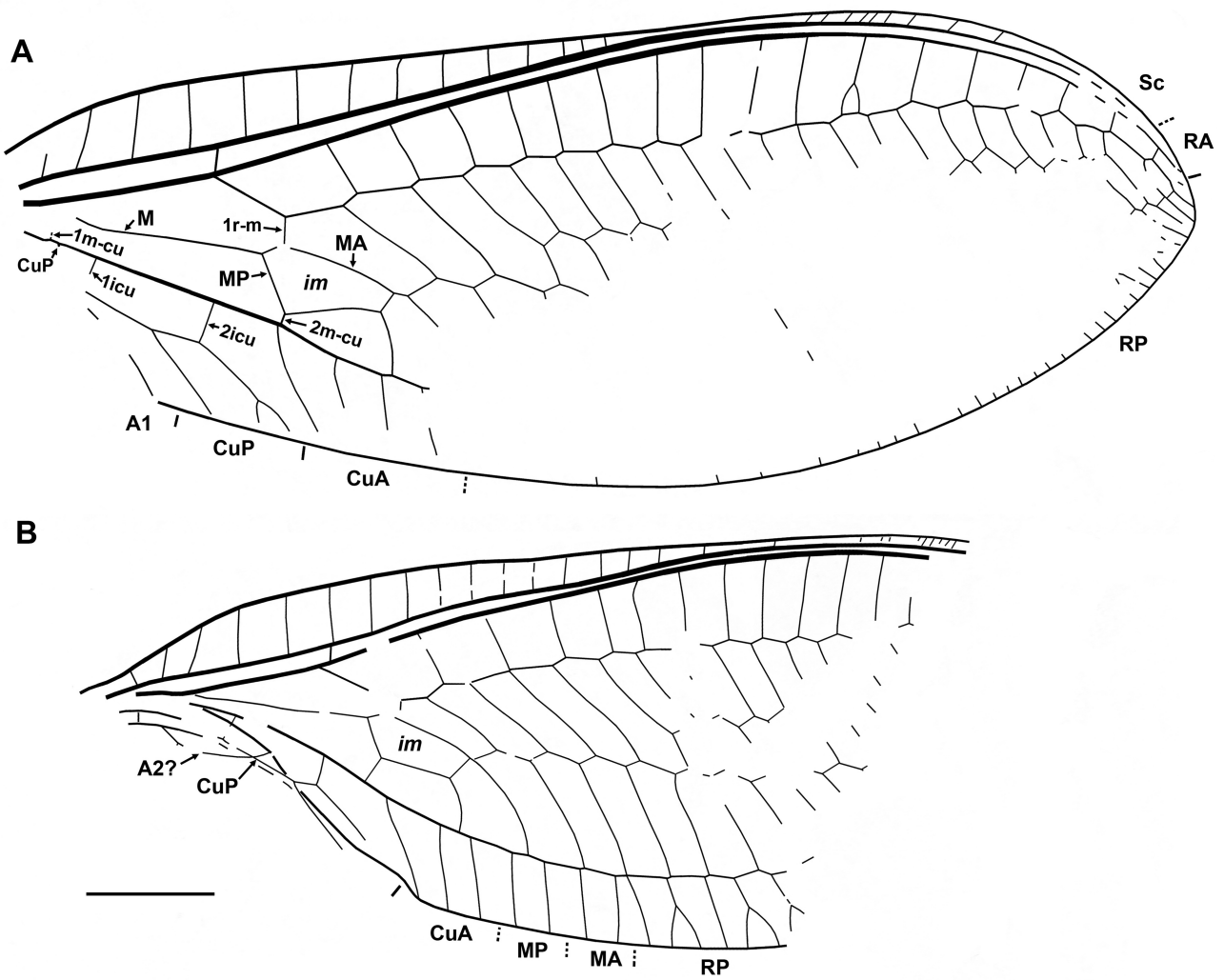

FIGURE 3. Forewing venation of *Triachrysa rusti* **gen. et sp. nov.** A, holotype MM-14943; B, paratype MM-14944. Scale bars = 2 mm (both to same scale).

***Paratype*.** Forewing 13.9 mm long (as preserved; estimated complete length *ca*. 17.2 mm), 6.2 mm wide. Costal space broad proximally, very narrow distally. All preserved subcostal veinlets simple, relatively widely spaced proximally, very densely spaced distally. Sc, RA before pterostigma thickened. Subcostal space narrow; basal subcostal crossvein located slightly distad origin of RP. RA space broadened towards apex, with 12 preserved crossveins: proximal crossveins perpendicular to RA; distal crossveins with their apices slightly oblique toward wing apex. Anterior trace of RP zigzagged, with 13 preserved branches; three proximal branches (of five preserved) forked once; distal portions of other branches not preserved. Basal crossvein between RP, M (1r-m) relatively long, connecting anterior trace of RP with MA in proximal part of *im* length. M dividing to MA, MP markedly distad origin of RP. MA, MP probably forked at Psm; all their branches distad Psc simple. *im* pentagonal, rather broad (length/width ratio 2.9:1). Crossvein between MA, MP (1im) long. Psm poorly developed, zigzagged; its proximal-most

crossvein (between RP1, MA) ends just distad *im*. Crossvein 2m-cu rather long, connecting *im*, CuA in proximal part of *im*. CuA probably with three simple branches; continuing into well developed, only slightly zigzagged Psc, which continues into outer gradate series of crossveins. CuP deeply forked once; both branches nearly parallel. 1icu long; 2icu connecting CuA and anterior trace of CuP (much proximad 2m-cu). Anal veins crumpled and forded; presumed 2A simple. Three gradate series of crossveins: additional series going anterior and parallel to inner series possesses four preserved crossveins; preserved part of inner series arranged in straight zigzagged line, with nine preserved crossveins distad MA; two-three proximal crossveins preserved in outer series.

Remarks. This species was described by Rust (1999) as *Brooksiochrysa jutlandica* Rust, but this 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). We could not locate the Rust's specimens.

The forewing venation of the holotype and paratype is slightly different, but we consider this as intraspecific variability. The shape of the intramedian cell and the length of crossvein 2m-cu markedly differs in these specimens. The forking of two veins (*i.e*., one of crossveins between RA and RP, and the anterior branch of CuP) in the holotype are obviously anomalies, often observed in extant species of the family.

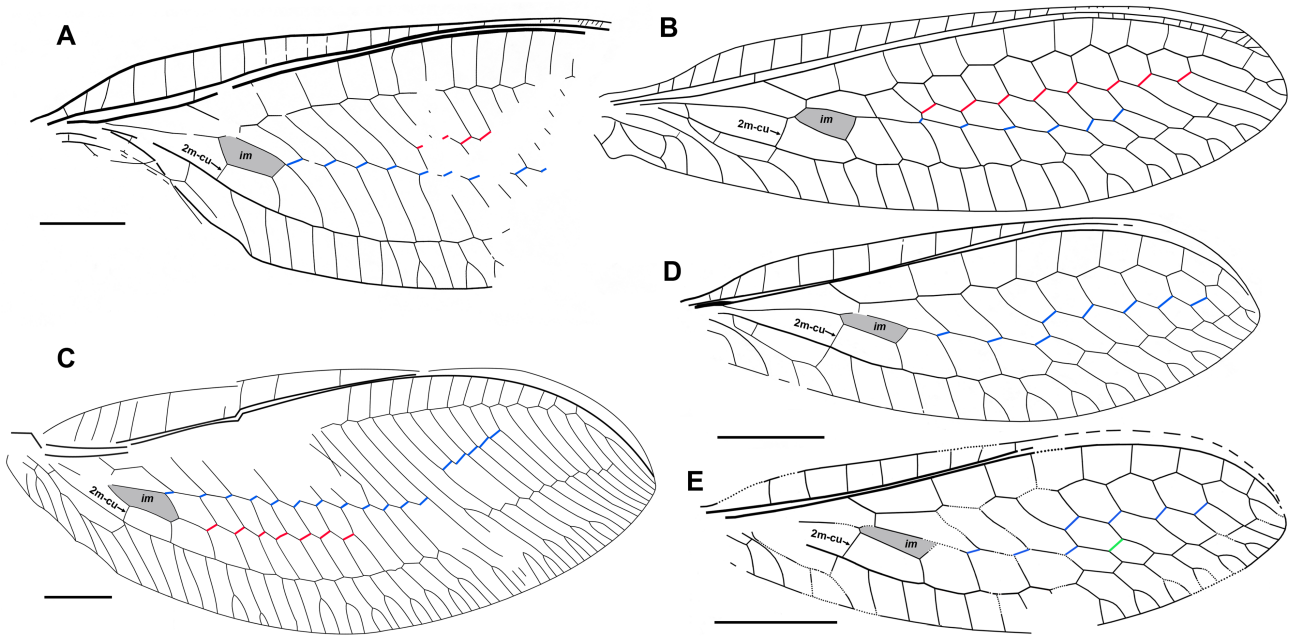

FIGURE 4. Forewing venation of Nothochrysinae with three gradate series. A, *Triachrysa rusti* **gen. et sp. nov.** (paratype); B, *Triplochrysa kimminsi* New, 1980 (re-drawn from New, 1980: Fig. 21; scale bar was not provided, the forewing 13–14 mm long); C, *Okanaganochrysa coltsunae* Makarkin & Archibald, 2013 (re-drawn from Makarkin & Archibald, 2013: Fig. 4.2); D, *Tribochrysa firmata* Scudder, 1890, paralectotype (re-drawn from Makarkin *et al.,* 2022: Fig. 28); E, *T. firmata*, lectotype (re-drawn from Makarkin *et al.,* 2022: Fig. 25A). The additional (third) series is shown by red, the inner series by blue, the additional crossvein in the inner series by green. Scale bars = 2 mm.

Discussion

Triachrysa **gen. nov**. is assigned with certainty to the subfamily Nothochrysinae due to the shape of the intramedial cell, the proximal location of the crossvein 2m-cu, and the long Sc. It is the fourth genus in this subfamily possessing three gradate series of crossveins. The three previously known genera are: the early Eocene *Okanaganochrysa* Makarkin & Archibald, 2013 (one species from McAbee, British Columbia, Canada), the latest Eocene *Tribochrysa* Scudder, 1883 (two species from Florissant, Colorado, U.S.A.), and the extant *Triplochrysa* Kimmins, 1952 with two species from easternmost Australia (New 1980: Figs 13, 21; Brooks & Barnard 1990: Fig. 567; Makarkin & Archibald, 2013: Figs 4.2, 4.4; Makarkin *et al*. 2022: Fig. 28). Other described Chrysopidae from the Fur Formation have two gradate series.

The new genus clearly differs from *Okanaganochrysa* by its inner gradate beginning at the intramedial cell and the additional series located between the inner and outer series (Fig. 4C); from *Triplochrysa* by the location of

2m-cu proximad the intramedial cell (Fig. 4B); and from *Tribochrysa* by its very long 2m-cu located in the very proximal part of the intramedial cell (Figs 4D, E).

In most Nothochrysinae (and in chrysopids in general) there are two gradate series of crossveins in the forewing radial space: inner and outer series (see Breitkreuz *et al*. 2017: Fig. 16). The forewings of two nothochrysine genera have more than three series, *i.e*., the early Eocene *Adamsochrysa* Makarkin & Archibald, 2013 from McAbee and Republic (Washington, U.S.A.), and the extant *Dictyochrysa* from Australia and Tasmania (New 1980: Figs 42, 44; Makarkin & Archibald 2013: Figs 6–12).

The four genera with three gradate series of crossveins are apparently not closely related, and their third (additional) series may have evolved independently in these taxa. Indeed, in the new genus the additional series is located anterior to the inner series (Fig. 4A). Such a placement is also found in *Triplochrysa* (Fig. 4B). But these genera strongly differ by other forewing characters, mainly the position of crossvein 2m-cu as proximad the intramedian cell. This is characteristic only of some Pliocene to extant genera (see Archibald & Makarkin 2015). In *Okanaganochrysa*, the additional series is located between the inner and outer series (Fig. 4C). In *Tribochrysa* the additional (third) series is only apparent. The inner series is normally arranged in a strongly broken line in that genus (Fig. 4D). However, in one specimen of *Tribochrysa firmata* Scudder, 1890, an additional crossvein opposite another crossvein (Figs 4E, green crossvein) is present in this series. Consequently, it seems like there are three series in this specimen.

Triachrysa **gen. nov**. is also distinguished from most other Nothochrysinae from the Fur Formation by its extremely narrowed costal space before the pterostigmal area. The exception is *Cimbrochrysa* Schlüter, 1982 in which this area of the costal space is also extremely narrowed judging from the original description of Schlüter (1982). In this, the new genus is similar to most other genera of the subfamily.

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