

# The first green lacewings from the late Eocene Baltic amber

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*Pseudosencera baltica* gen. et sp. nov. of Chrysopinae (Chrysopidae, Neuroptera) is described from Baltic amber. Additionally, another species, *Nothochrysa?* sp. (Nothochrysininae), is left in the open nomenclature. *Pseudosencera baltica* gen. et sp. nov. represents the oldest confident record of Chrysopinae. The new genus lacks the apparent forewing intramedian cell, and possesses three character states not found in other Chrysopinae: the simple AA1, the short basal crossvein between M and Cu, and 5–6 rings of setae on the antennal flagellomeres. This genus is probably a specialised form in a basal branch of Chrysopinae, that could not be attributed to any of the known tribes. The specimen of *Nothochrysa?* sp. consists only of fragments of the forewings. The late Eocene Baltic amber represents the oldest horizon where Chrysopinae and Nothochrysininae are found to coexist. It is highly likely that Chrysopidae were extremely rare in these forests.

Key words: Neuroptera, Chrysopinae, Nothochrysininae, Cenozoic, Baltic amber.

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## Introduction

The family Chrysopidae (green lacewings) today is one of the most speciose neuropteran groups with a nearly worldwide distribution. It is divided into four subfamilies: Limaiinae (Middle Jurassic to Paleogene), Nothochrysininae, and Chrysopinae (both Paleogene to Recent), and Aporhysinae (Recent). The fossil Mesochrysoptidae and Corydasialidae were recently considered as chrysopid subfamilies by Engel et al. (2018), but these should be considered as separate families, because they are distinguished from Chrysopidae by many characters (see Makarkin and Menon 2005; Liu et al. 2017). The fossil record of green lacewings is rich, consisting of 64 named species known from the Middle Jurassic to the Pliocene (Archibald and Makarkin 2015; Khramov et al. 2016; Khramov 2018; Lu et al. 2018).

Three rather distinct phases may be identified in the evolutionary history of Chrysopidae: (i) the Mesozoic, when the extinct subfamily Limaiinae dominated (at least from the Middle Jurassic to at least the mid-Cretaceous); (ii) the Paleogene, when Nothochrysininae were dominant among chrysopids; and (iii) the Neogene to Recent, when Chrysopinae became the most dominant group (Archibald et

al. 2014). In the Cenozoic, the late Eocene to the Oligocene was the most interesting period in chrysopid evolution when the transition from the “nothochrysinine” to “chrysopine” phase occurred. However, chrysopids from this interval are poorly studied; nearly all of them belong to Nothochrysininae (e.g., Carpenter 1935; Adams 1967; Nel and Séméria 1986; CoBabe et al. 2002). Only one species from the late Eocene of France is an alleged chrysopine (Séméria and Nel 1990). Therefore, the discovery of other chrysopine species from the late Eocene is of high interest.

Chrysopids occur very rarely in the late Eocene Baltic amber, and hitherto no species had been described. The first mention of a chrysopid specimen in Baltic amber was by Carl Berendt in Göppert and Berendt (1845). Since then this information has been repeated many times (e.g., Hagen 1852; Giebel 1856; Scudder 1885, 1890, 1891; Handlirsch 1907, 1921; Krüger 1923). However, this specimen has never been described (or even illustrated), and it is probably lost now. The first documented record of Chrysopidae from Baltic amber was a photographed adult specimen in Weitschat and Wichard (1998: pl. 55d). The depository of this specimen is unknown, and it has also not been described. Several chrysopid larvae are also known from Baltic amber, but

again none of these have been described (see Scheven 2004; Weitschat 2009; Makarkin and Archibald 2013).

In this paper, we describe the first chrysopids from Baltic amber, a new genus and species and species in open nomenclature. These chrysopids belong to two different subfamilies, Chrysopinae and Nothochrysininae, respectively.

*Institutional abbreviations.*—SMF, Senckenberg Research Institute and Natural History Museum Frankfurt, Germany.

*Other abbreviations.*—AA1–3, first to third anterior analis; CuA, anterior cubitus; CuA1, first (proximal-most) branch of CuA; CuP, posterior cubitus; M, media; MA and MP, anterior and posterior branches of the media; Psc, pseudocubitus; Psm, pseudomedia; RA, anterior radius; RP, posterior radius; RP1–5, first (proximal-most) to fifth branches of RP; ScP, posterior subcosta; 1aa1-aa2, 1aa2-aa3, first (basal) crossvein between AA1 and AA2, AA2 and AA3, respectively; 1im, first crossvein between MA and MP; 1r-m, first (basal) crossvein between R and M; 1scp-r, first (proximal-most) crossvein connecting ScP and R/RA; 1icu, 2icu, first (basal) and second crossveins between CuA and CuP, respectively; 2m-cu, second crossvein between M/MP and Cu/CuA.

## Material and methods

*Specimens.*—This study is based on two specimens from Baltic amber, deposited in the amber collection of the Senckenberg Museum Frankfurt am Main (SF). Line drawings were prepared by Thomas Weiterschan (Figs. 3B, 4) and Vladimir Makarkin (Fig. 6), while photographs were taken by Sonja Wedmann and Thomas Weiterschan using a Leica MZ12.5 stereomicroscope and an attached Nikon D300 digital camera. Extension of depth of focus was

achieved by stacking several photos using Helicon Focus, version 5.3 X 64.

*Terminology.*—We use the general venational terminology of Kukalová-Peck and Lawrence (2004) in the interpretation of Yang et al. (2012, 2014). The venation of Chrysopinae is highly specialized, with numerous fusions (Fig. 1). Correct interpretation of the venation is mainly inferred from the pupal wing tracheation of *Mallada signatus* (Schneider, 1851) and *Chrysopa nigricornis* Burmeister, 1839 (see Tillyard 1916: fig. 5; Comstock 1918: fig. 184). The most important transformations in the venation of Chrysopinae are listed below. (i) In both wings, the aligned sections of MA, MP (only in the forewing of most species), the branches of RP, and the crossveins connecting them form the pseudomedia, and the aligned sections of CuA, MP, MA, the branches of RP, and the crossveins connecting them form the pseudocubitus. (ii) In the forewings of most species of Chrysopinae, MA and MP are fused for some distance to form the intramedian cell (i.e., the proximal-most cell between MA and MP) (see Breitkreuz et al. 2017: fig. 16). However, this cell appears to be absent in several species of Chrysopinae (including *Pseudoscencera baltica* gen. et sp. nov.) and all Apochrysininae. We believe that the intramedian cell is actually present but its posterior side (i.e., proximal part of MP) is fused with CuA and 2m-cu is reduced. In particular, this can be supported by that fact in the extant *Leptochrysa prisca* Adams and Penny, 1992 (which may be the only living Limaiinae; Makarkin and Archibald 2013), the proximal part of MP within the intramedian cell is very close to CuA and 2m-cu is extremely short or reduced (see Adams and Penny 1992: fig. 10). Therefore, we follow Adams (1967: fig. 44), not Breitkreuz et al. (2017: fig. 15B), in the interpretation of the intramedian cell of Apochrysininae and *Pseudoscencera baltica* gen. et sp. nov. (iii) The chrysopine CuA in the hind wing is interpreted to be partially fused

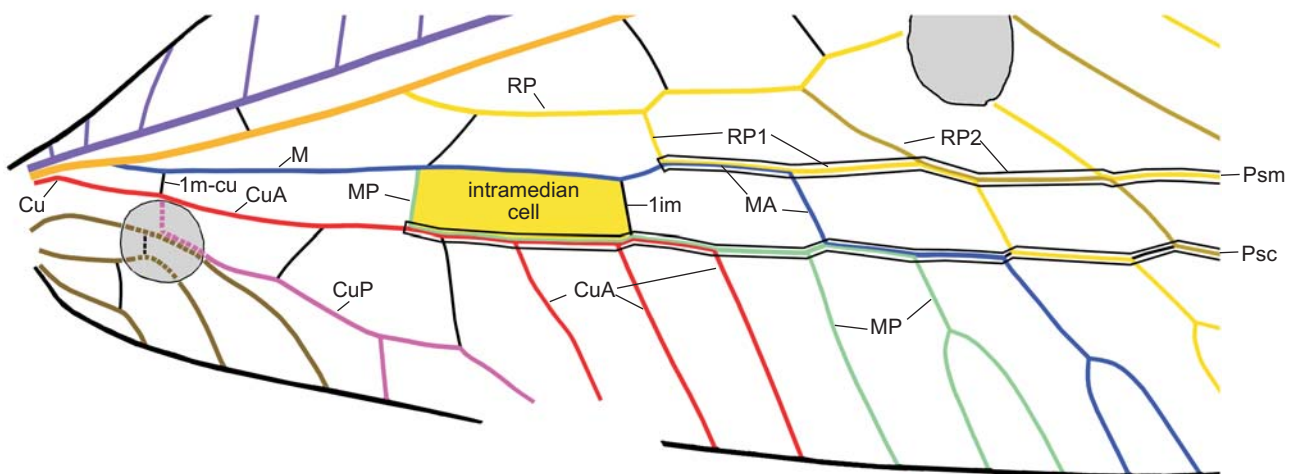


Fig. 1. The intramedian cell, pseudomedia and pseudocubitus in the forewing of green lacewing *Pseudoscencera baltica* gen. et sp. nov. from the late Eocene Baltic amber. Psm and Psc are outlined black in this figure. Abbreviations: 1im, first crossvein between MA and MP; 1m-cu, first (basal) crossvein between M and Cu; CuA, anterior cubitus; CuP, posterior cubitus; M, media; MA and MP, anterior and posterior branches of the media; Psc, pseudocubitus; Psm, pseudomedia; RP, posterior radius; RP1, proximal-most branch of RP; ScP, posterior subcosta.

with MP. Similarly configured CuA in Apochrysinæ is also treated as partially fused with MP (see e.g., Breitkreuz et al. 2017: fig.15B), although the pupal wing tracheation of no species in this subfamily have been examined. (iv) In all Chrysopinæ, MA in the hind wing is basally fused with RP.

Crossveins are designated after the longitudinal veins which they connect and are numbered in sequence from the wing base, e.g., 1scp-r, first (proximal-most) crossvein connecting ScP and R/RA; 2icu, second crossvein between CuA and CuP; 1im, proximal crossvein between MA and MP. Terminology of wing spaces and details of venation (e.g., veinlets) follows Oswald (1993).

## Systematic palaeontology

Order Neuroptera Linnaeus, 1758

Family Chrysopidae Schneider, 1851

Subfamily Chrysopinæ Schneider, 1851

Genus *Pseudoscencera* nov.

*Type species*: *Pseudoscencera baltica* sp. nov.; by monotypy, see below.

*Etymology*: From the Greek adjective *pseudes* [ψευδής], false, and *Scencera*, a genus-group name.

*Diagnosis*.—As for the type species by monotypy.

*Remarks*.—*Pseudoscencera* gen. nov. may be easily distinguished from all other Chrysopinæ by the simple AA1 and the short 1m-cu. Of the genera lacking the apparent intramedian cell (see discussion below), the new genus resembles the subgenus *Scencera* Navás, 1925 (of the genus *Ankylopteryx* Brauer, 1864) more than the genus *Nesochrysa* Navás, 1910 as their hind wings are narrow and have similar venation (see Breitkreuz et al. 2015: fig. 10; New 1980: fig. 78), and the antennae are not longer than the forewing.

*Pseudoscencera baltica* sp. nov.

Figs. 2–4.

*Etymology*: In reference to Baltic amber.

*Holotype*: SMF-Be-2518; an incompletely preserved specimen.

*Type locality*: Baltic amber (precise collecting locality unknown).

*Type horizon*: Late Eocene.

*Diagnosis*.—Antennal flagellomeres with 5–6 rings of setae. In forewing, RA relatively short, entering margin far before wing apex; basal subcostal crossvein (1scp-r) located far proximad origin of RP; single distal subcostal crossvein; apparent intramedian cell absent; Psm well developed, straight; Psc well developed, slightly zigzagged; AA1 simple; basal crossvein 1m-cu short; distal crossvein 2icu very long. In hind wing, MA fused with RP proximally; Psm well developed, straight; CuA partially fused with MP.

*Description*.—*Head*: vertex not elevated; eyes large; ventral border of clypeus slightly concave. Frontal sutures and epistomal suture well developed. Anterior margin of labrum deeply concave. Galea enlarged (long, broad) with short di-

gitus (finger-like apical process). Maxillary palpus five-segmented: two basal segments appear short; third to fifth (terminal) segments elongate (relative length of third to fifth segments: 1.5–1–2.4); terminal segment longest, fusiform. Labial palpus three-segmented; all segments elongate, terminal segment fusiform. Antennae incompletely preserved: scapus rather broad, but short; pedicellus elongate (ca. 1.4 as long as wide), probably very slightly constricted medially (poorly visible); proximal flagellomeres elongate, each probably with 5–6 rings of setae (difficult to count).

Details of thorax not clearly discernible; pronotum dorsally covered with rare long setae. Forelegs and mid-legs shorter than hind legs; all legs covered (especially femur and tibia) with dense, relatively long, fine setae.

*Abdomen*: complete, but poorly preserved.

*Forewing*: 13.2 mm long, 4.6 mm wide (length/width ratio 2.9). Costal space moderately broad for most part, basally and apically narrowed; with simple subcostal veinlets relatively widely spaced, and closely spaced apically. ScP relatively short, entering margin far before wing apex. Subcostal space moderately broad; proximal subcostal crossvein (1scp-r) located very basally, nearly at mid-way from wing base to origin of RP; only one distal crossvein in area of pterostigma detected. Tympanum on basal portion of R not detectable with confidence. RA relatively short, entering margin before wing apex, with 4–5 short, simple distal branches. Origin of RP located relatively close to wing base (at 0.18 of complete length), slightly proximad 2m-cu. Length of RP proximad 1r-m and 1r-m nearly equal. RA space (between RA and RP) relatively narrow, with 13 crossveins. RP strongly zigzagged, with 12 branches, four of them entering Psm; two distal-most branches simple, other branches forked. Basal crossvein 1r-m long, inclined at acute angle to M, connecting RP, M slightly distad fork of M. M appears to originate from R near wing base; forked at nearly a right angle and at level of origin of RP. Apparent intramedian cell absent (actually, it is formally represented by a square formed by the basal crossvein-like part of MP, the proximal part of MP+CuA, the crossvein 1im and the proximal part of MA, see below for details). MA proximally fused with RP1; distally (distad Psc) with two simple branches (left wing) or once forked branches (right wing). MP basally crossvein-like, then fused with CuA; distally (distad Psc) with two simple branches (left wing) or one simple, one forked branch (right wing). Psm well developed, nearly straight. Psc well developed, slightly zigzagged distally. Basal crossvein 1m-cu (“M5”) short, located opposite origin of CuP; 2m-cu absent. CuA partially fused with MP, probably with three long simple branches. CuP once forked, with widely-spaced branches (anterior branch more than twice longer than posterior branch). Two intracubital crossveins: 1icu long, located far proximad basal part of MP; 2icu very long, located distad posterior branch of CuP fork; length of CuP from 2icu to fork nearly equal to branch of CuP fork. Crossvein between CuP, AA1 very short. All anal veins short, simple; AA1 arched; AA2 incurved proximad

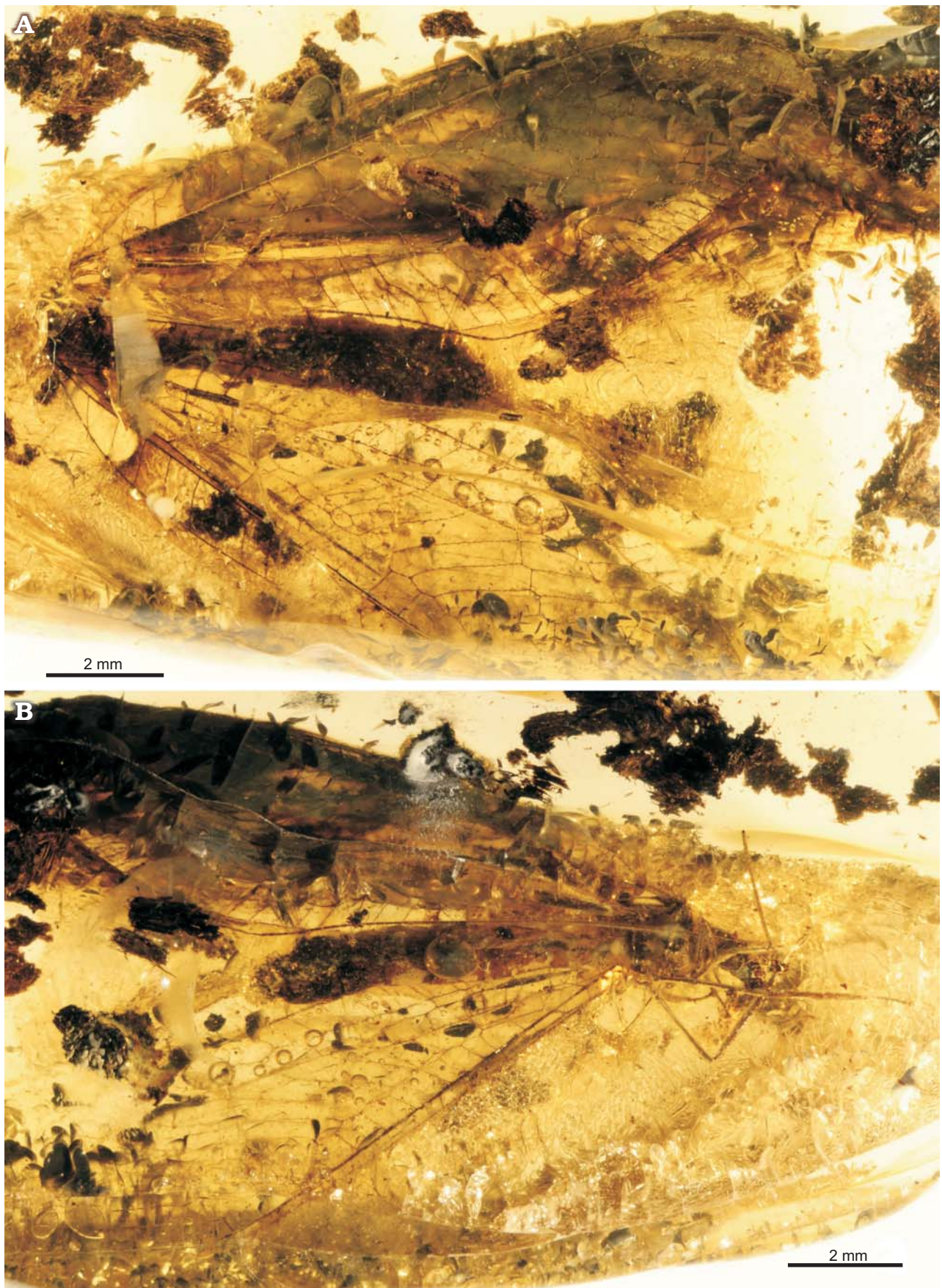


Fig. 2. Green lacewing *Pseudoscencera baltica* gen. et sp. nov. from the late Eocene Baltic amber. Holotype (SMF-Be-2518) in dorsal (A) and lateral (B) views.

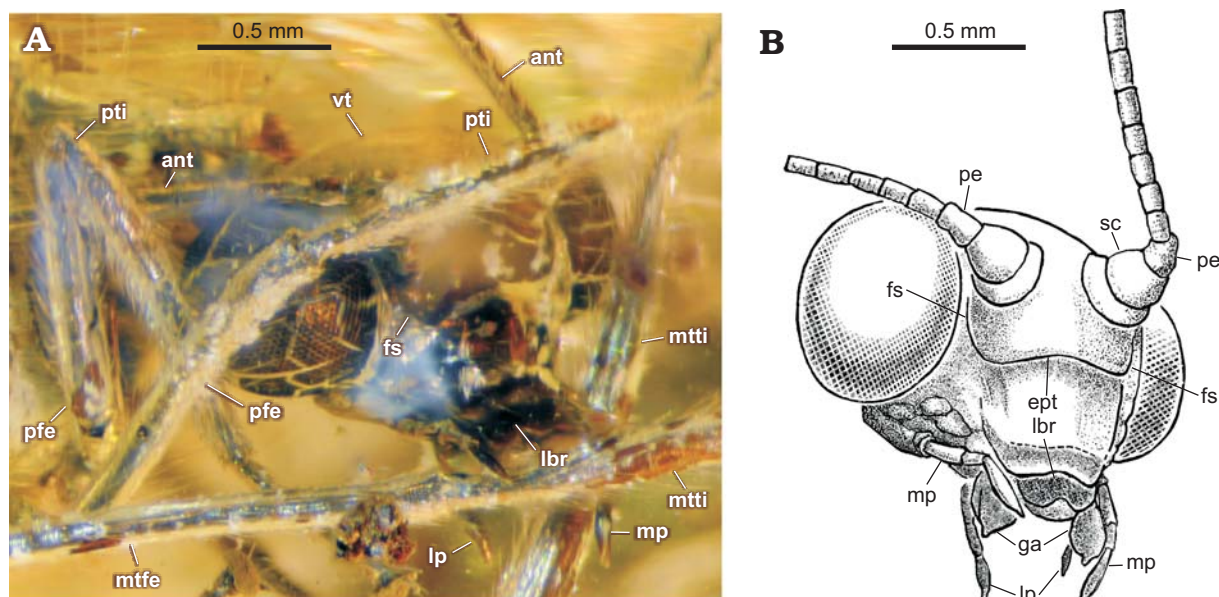


Fig. 3. Green lacewing *Pseudoscencera baltica* gen. et sp. nov. from the late Eocene Baltic amber. Head and legs of the holotype SMF-Be-2518. **A.** Photograph, fronto-lateral view. **B.** Line drawing of the head, latero-frontal view. Abbreviations: ant, antenna; ept, epistomal suture; fs, frontal suture; ga, galea; lbr, labrum; lp, labial palpus; mp, maxillary palpus; mtfe, metafemur; mtti, metatibia; pe, pedicellus; pfe, profemur; pti, protibia; sc, scapus; vt, vertex.

1aa1-aa2, arched after; AA3 incurved proximad 1aa2-aa3, nearly straight after. Two crossveins between anal veins: 1aa1-aa2 rather short; 1aa2-aa3 long. Two complete gradate series of crossveins, slightly divergent distally; 8 crossveins in inner series anterior to Psm; 10 crossveins in outer series anterior to Psc (i.e., RP3). Wing membrane apparently hyaline throughout.

*Hind wing*: markedly narrower than forewing; 11.0 mm long as preserved (estimated complete length ca. 11.8–12.0 mm), ca. 3.1 mm wide. Costal space narrow, with simple subcostal veinlets relatively widely spaced before pterostigmal region (basally relatively closely spaced). Termination of ScP, RA not preserved. Subcostal space narrow; subcostal crossveins not detected. RP originates relatively near wing base, strongly zigzagged, with 11 preserved branches, four of them entering Psm. Psm well developed, straight. M basally not fused with R, forked slightly distad origin of RP. MA basally crossvein-like (oblique), then fused with RP for considerable distance; probably simple. MP probably simple. Psc well developed, slightly zigzagged. CuA fused with MP for some distance; one preserved branch (CuA1) originated before fusion with MP. Two gradate series of crossveins (incompletely preserved).

*Remarks.*—A chrysopid specimen figured by Weitschat and Wichard (1998: pl. 55d) appears to be conspecific with *Pseudoscencera baltica* gen. et sp. nov. as its venation is nearly identical with that of the holotype. This specimen was previously treated as probably belonging to Belonopterygini (a tribe of Chrysopinae) by Makarkin and Archibald (2013) and Archibald et al. (2014), but the phylogenetic relationships of *Pseudoscencera baltica* gen. et sp. nov. are obscure, what is discussed below. Its antennae (if they are completely

preserved, what is rather likely) are markedly shorter than the forewing (nearly two-thirds).

*Stratigraphic and geographic range.*—Late Eocene Baltic amber.

Subfamily Nothochrysinæ Navás, 1910

*Nothochrysa?* sp.

Figs. 5, 6.

*Material.*—SMF-Be-2464; two fragmentarily preserved forewings from late Eocene of Baltic amber (precise collecting locality unknown).

*Description.*—Forewing ca. 10.5 mm long as preserved (ca. 15–16 mm estimated). Distal part of costal space narrow. ScP long. Distal subcostal veinlets closely spaced, several forked. Subcostal space distally rather broad, with several distal crossveins (five detected). RA long, almost reaching wing apex; with four distal veinlets. RA space relatively narrow, with 16 preserved crossveins. RP with 19 preserved branches; of these, five entering into Psm. Psm, Psc probably well developed, slightly zigzagged. Space between Psm, Psc very broad distally. Psm continues into inner gradate series, which consists of 12 crossveins (left wing). Psc continues into outer gradate series, which consists of 15 crossveins (left wing).

*Remarks.*—The new species is assigned to Nothochrysinæ due to the presence of two features characteristic of the subfamily: Psm continues into the inner gradate series of crossveins, and ScP and RA are long. In Chrysopinae, Psm continues distad the inner gradate series, and ScP and RA are much shorter. It is tentatively assigned to the genus *Nothochrysa* for the following reasons: the wings are rather large possessing numerous RP branches (about

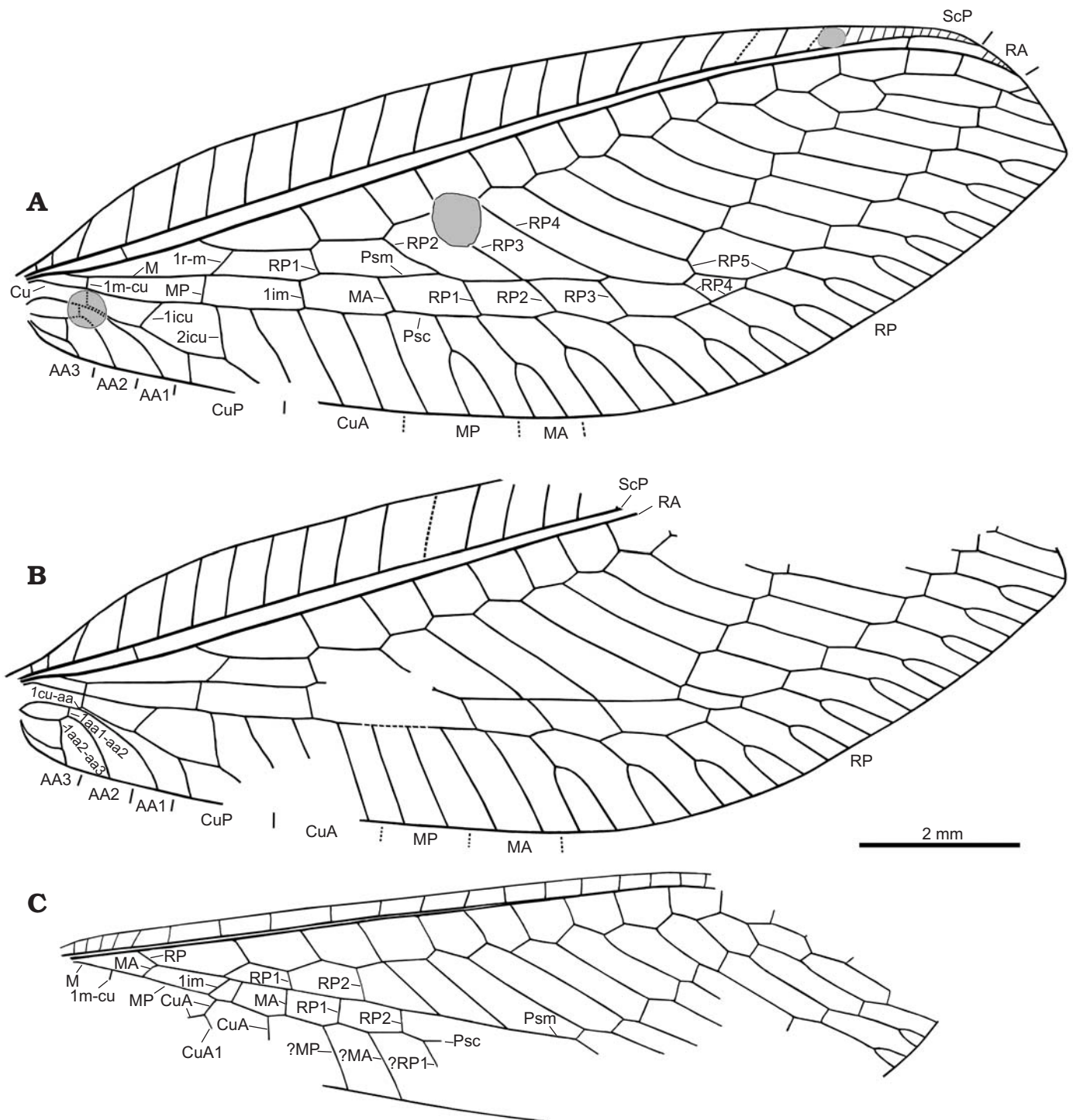


Fig. 4. Green lacewing *Pseudoscencera baltica* gen. et sp. nov. from the late Eocene Baltic amber. Wing venation of the holotype SMF-Be-2518, right (A) and left (B) forewing, left hind wing (C). B, C converted to right dorsal view. Abbreviations: 1aa1-aa2, first crossvein between AA1 and AA2; 1aa2-aa3, first crossvein between AA2 and AA3; 1icu, first (basal) crossvein between CuA and CuP; 2icu, second crossvein between CuA and CuP; 1cu-aa, first crossvein between CuP and AA1; 1im, first crossvein between MA and MP; 1m-cu, first (basal) crossvein between M and Cu; AA1-3, first to third anterior analis; CuA, anterior cubitus; CuA1, first (proximal-most) branch of CuA; CuP, posterior cubitus; M, media; MA and MP, anterior and posterior branches of the media; Psc, pseudocubitus; Psm, pseudomedia; RA, anterior radius; RP, posterior radius; RP1-5, first (proximal-most) to fifth branches of RP; ScP, posterior subcosta.

20); the well-developed Psm and Psc; two series of gradate crossveins; and the long ScP and RA. Of the known nothochryesine genera, this set of character states is only present in *Nothochrysa*.

The genus *Nothochrysa*, with five extant species, is distributed in Europe, North Africa, Turkey, China, and North America (Adams 1967; Aspöck et al. 2001; Yang et al. 2005; Kovanci and Canbulat 2007). Two fossil species

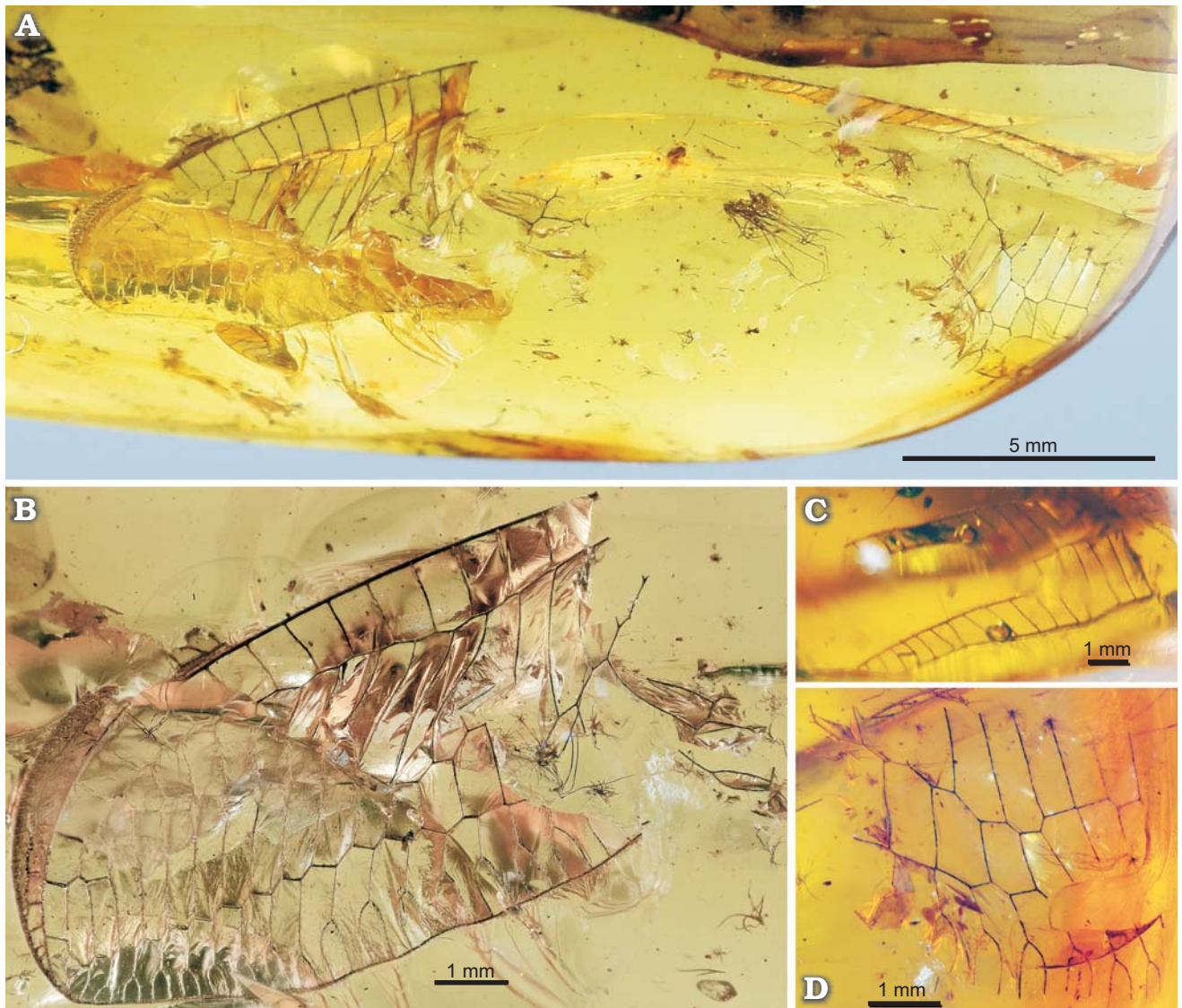


Fig. 5. Green lacewing *Nothochrysa?* sp. from the late Eocene Baltic amber. SMF-Be-2464, general view (A), left forewing (B), costal space of right forewing (C), fragment of right forewing (D).

are known: *Nothochrysa stampieni* Nel and Séméria, 1986 from the Oligocene (late Rupelian/basal Chattian) of Aix-en-Provence (France), and *N. praeclara* Statz, 1936 from the early Miocene (Aquitanian) or latest Oligocene (Chattian) of Rott (Germany). The forewing venation of these fossil species is rather similar to that of the Baltic amber species.

## Discussion

Imaginal chrysopids occur extremely rarely in Baltic amber. We have information only on five specimens: four Chrysopinae and one Nothochrysiniae. Three of them most probably belong to *Pseudosencera baltica* gen. et sp. nov.: the holotype, the specimen reported by Weitschat and Wichard (1998: pl. 55d) mentioned above, and an unpublished specimen (in a private collection; VM personal observation). A fourth chrysopine specimen is in general simi-

lar to *P. baltica* gen. et sp. nov. but its wings are incomplete, and therefore its congeneric and conspecific status cannot be confirmed (in a private collection; VM personal observation). A single known nothochrysinine specimen is described above; it is too fragmentary to discuss further. However, *Pseudosencera baltica* does possess features that allow it to be discussed in detail. It is noteworthy that all the extant chrysopids, to which *Pseudosencera* gen. nov. is most similar, occur in tropical regions (see below). Therefore, we may presume that this genus is a thermophilic element in the Baltic amber neuropteran assemblage.

An analysis of characters of *Pseudosencera* gen. nov. shows that this genus cannot be assigned to Limaiinae and Nothochrysiniae from its venation. Its most striking feature is the absence of the apparent forewing intramedian cell (actually, the intramedian cell is present, but MP is fused with CuA within it, see above). This character state is obviously apomorphic within Chrysopidae (see Brooks and Barnard

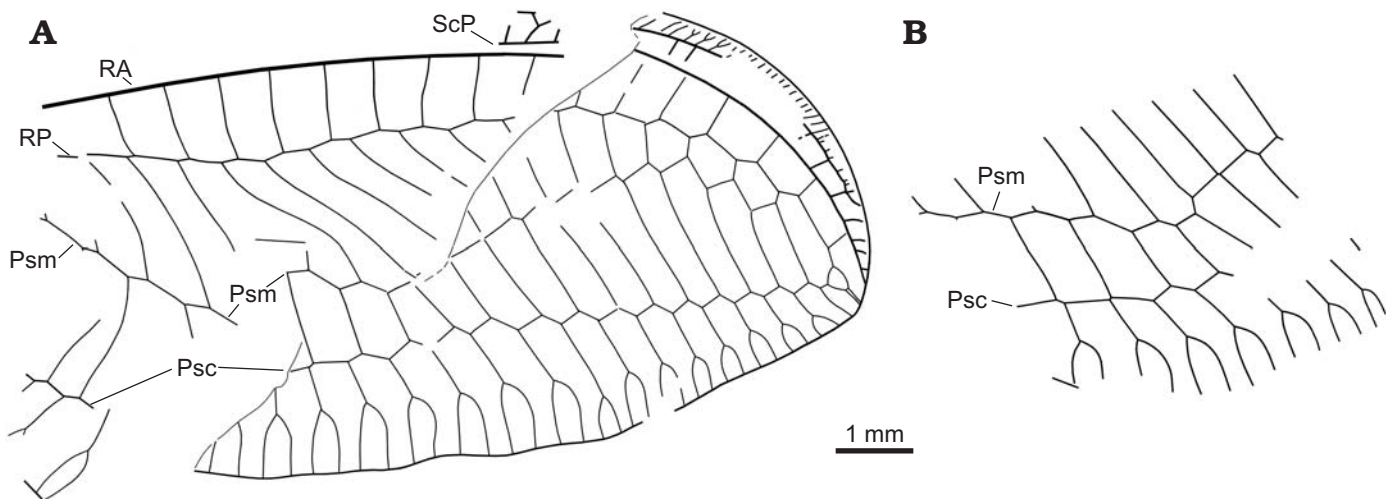


Fig. 6. Green lacewing *Nothochrysa?* sp. from the late Eocene Baltic amber. Wing venation of the SMF-BE-2464, left (A, converted to right dorsal view) and right (B) forewing. Abbreviations: Psc, pseudocubitus; Psm, pseudomedia; RA, anterior radius; RP, posterior radius; ScP, posterior subcosta.

1990: 120), and occurs in two subfamilies: in all species of Apochrysinæ and in four extant species of Chrysopinæ: *Belonopteryx arteriosa* Gerstaecker, 1863 from Brazil and Argentina and two species of the genus *Nesochrysa* from Madagascar, i.e., *Nesochrysa seyrigi* (Navás, 1934) and *N. grandidieri* (Navás, 1913) (all Belonopterygini), and a single species of *Sencera* from southeastern Asia to Australia (Ankylopterygini) (see Navás 1913; Brooks and Barnard 1990; Breitkreuz et al. 2015).

Although *Pseudosencera* gen. nov. shares with Apochrysinæ the absence of the apparent forewing intramedian cell, the venation of the latter otherwise strongly differs from that of this genus. Firstly, the basal crossvein 1scp-r is present in *Pseudosencera* gen. nov. (and in the vast majority of other Chrysopinæ), however it is lost in all Apochrysinæ as well as in the enigmatic genus *Nothancyla* Navás, 1910, which was recently confirmed to belong to Chrysopinæ (Dai et al. 2016). Also, other forewing character states of Apochrysinæ are not present in the new genus: e.g., the costal space is broad distally; the subcostal veinlets are closely spaced; Psm continues into the inner gradate series of crossveins; numerous crossveins are present anterior of the inner gradate series (often arranged into one or several additional gradate series); RP originates very close to the wing base. Further, MA in the hind wing in most Apochrysinæ is not fused with the stem of RP (at most only touches it) (see e.g., Kimmins 1952: figs. 4–7, 9–11; Winterton and Brooks 2002: figs. 9, 10, 15), and the antennae are longer than the forewing in all Apochrysinæ.

Of the four apomorphies of Apochrysinæ proposed by Brooks (1997), i.e., Psm and Psc close together; the basal subcostal crossvein absent; the pedicel constricted, and antennal setae arranged in five rings, only the latter is found in *Pseudosencera* gen. nov. However, this condition occurs also in many Nothochrysinæ and is probably plesiomorphic. Of the numerous synapomorphies of Apochrysinæ (exclusive of *Nothancyla*) proposed by Winterton and Brooks

(2002), only one character is detected in *Pseudosencera* gen. nov., i.e., the elongate setae on the femur and tibia. This feature, however, is too weak to support its assignment to this subfamily. Therefore, an apochrysinæ affinity of *Pseudosencera* gen. nov. is very unlikely.

The general wing venation of *Pseudosencera* gen. nov. is similar to that of Chrysopinæ. In particular, this affinity is supported by the location of the crossvein 1scp-r in the forewing: this crossvein is situated more basally in Chrysopinæ (as found in *Pseudosencera* gen. nov.) than in Limaiinæ and Nothochrysinæ. The arrangement of the inner gradate series in the forewing of the new genus is also characteristic of Chrysopinæ. The venation of the hind wing of *Pseudosencera* gen. nov. is typical for Chrysopinæ.

However, the following three character states of *Pseudosencera* gen. nov. are not found in other Chrysopinæ.

(i) The simple (non-forked) AA1. This condition often occurs in Mesozoic Limaiinæ (e.g., *Mesypochrysa* Martynov, 1927 and *Parabaisochrysa* Lu, Wang, Ohl, and Liu, 2018; Makarkin 1997: figs. 1, 2; Khramov et al. 2016: fig. 3; Lu et al. 2018: fig. 2), and many Nothochrysinæ, from the Eocene (e.g., *Palaeochrysa* Scudder, 1885; *Asiachrysa* Makarkin, 2014; some *Tribochrysa* Scudder, 1885; some *Archaeochrysa* Adams, 1967) and extant (all genera except *Nothochrysa* and *Dictyochrysa* Esben-Petersen, 1917). On the other hand, AA1 is forked in some other Mesozoic Limaiinæ (e.g., Ren and Guo 1996: figs. 7, 8), some Nothochrysinæ, all species of Chrysopinæ, and all genera of Apochrysinæ (however, the simple AA1 occurs in some species of the latter). It should be noted that AA1 is also forked in the closely related Mesozoic family Mesochrysopidae (see Makarkin and Menon 2005). Therefore, the forked AA1 is very probably plesiomorphic at the level of Chrysopoidea and Chrysopidae, but the simple AA1 evolved several times, possibly independently.

(ii) The short basal crossvein 1m-cu in the forewing is another characteristic feature of *Pseudosencera* gen. nov. Such a short 1m-cu occurs in more basal Limaiinæ and



Nothochrysinæ, but it is long to very long in all extant Chrysopinæ. All “crossveins” between Psm and Psc in Apochrysinæ are short to very short as these veins are closely running over the entire length (see e.g., Winterton and Brooks 2002: figs. 5, 8, 10, 12, 14). Therefore, it seems to be incorrect to compare the length of 1m-cu in the specialised apochrysinæ venation with that in the more “normal” venation of other subfamilies. The condition found in *Pseudoscencera* gen. nov. is very probably plesiomorphic in Chrysopidae.

(iii) Five to six rings of setae are found on the antennal flagellomeres of *Pseudoscencera* gen. nov., where four rings are present in other Chrysopinæ (Brooks 1997). But this condition, as found in *Pseudoscencera* gen. nov., is plesiomorphic: setae on flagellar segments are arranged in five to six rings in more basal Nothochrysinæ, and in five rings in Apochrysinæ (Brooks and Barnard 1990); the setation of flagellomeres is unknown in the Mesozoic Limaiinæ.

These three character states hamper the determination of the tribal affinity of *Pseudoscencera* gen. nov. Molecular analyses of the tribal phylogeny of Chrysopinæ are inconclusive, they support different relationships among the four tribes: “(Belonopterygini + (Ankylopterygini + Leucochrysinini)) + Chrysopini” (Winterton and de Freitas 2006) or “(Belonopterygini + Leucochrysinini) + (Ankylopterygini + Chrysopini)” (Jiang et al. 2017). The latter relationship of tribes was supported also by morphological data (Brooks 1997).

The absence of the apparent forewing intramedian cell is known in species of two tribes, Belonopterygini and Ankylopterygini. Judging from the proposed phylogenies mentioned above, this character state may have evolved independently. The character states of *Pseudoscencera* gen. nov. are more similar to those of Ankylopterygini, but we cannot assign it to this tribe due to the presence of the above discussed three character states. Because two of these are plesiomorphic and not present in other Chrysopinæ, we may assume that this new genus represents a basal branch of this subfamily. On the other hand, the absence of the apparent forewing intramedian cell and the simple AA1 are apomorphic features indicating that *Pseudoscencera* gen. nov. is a specialised genus of a basal branch of Chrysopinæ.

Hitherto, the only described Paleogene species of a presumed Chrysopinæ was *Paleochrysa monteilsensis* Séméria and Nel, 1990 from the late Eocene Monteils Formation, France. The species is known from an incomplete forewing. Its chrysopine affinity is based on the arrangement of the inner gradate series of crossveins, which is typical for this subfamily. But the long ScP and RA and the rectangular shape of the intramedian cell are more characteristic of Nothochrysinæ. Therefore, the subfamily affinity of *P. monteilsensis* should be considered as preliminary.

All other known fossil Chrysopinæ are known from the Miocene (Handschin 1937; Barbu 1939; Makarkin 1991; Engel and Grimaldi 2007). Most of these species were assigned to the extant genus *Chrysopa* Leach, 1815, sensu lato. It means that their venation generally resembles that

of *Chrysopa* sensu stricto and similar chrysopine genera which are distinguished from one another mainly by their genitalia. However, there are small differences in the venation between these genera, which allow assignment of three species of *Chrysopa* sensu lato from the middle Miocene of Stavropol (southern Russia) to three extant genera of Chrysopini: *Chrysoperla* Steinmann, 1964, *Suarisus* Navás, 1914, and *Chrysopa* sensu stricto (Makarkin 1991). Of course, these assignments are questionable as they cannot be supported by the study of genitalia.

One species of *Leucochrysa* McLachlan, 1868 has been described from the Miocene Dominican amber (Engel and Grimaldi 2007). So, fossil representatives of two tribes of Chrysopinæ are known, Chrysopini and Leucochrysinini, but no species of Belonopterygini and Ankylopterygini are known, to which *Pseudoscencera* gen. nov. is most similar.

## Conclusions

The late Eocene Baltic amber is the oldest locality where Chrysopinæ and Nothochrysinæ are found to coexist. Chrysopinæ are represented by a species of specialised genus, which is the oldest confident record of the subfamily, possessing at least two plesiomorphic conditions not recorded in the extant taxa. In general, it is puzzling that green lacewings are so rare in Baltic amber, especially considering their habit of resting on plants (trees, in particular). Even the aquatic larvae of the Neuropteran family Nevrothidae, which also pupate in water, occur more frequently in Baltic amber than chrysopids. Therefore, we may reasonably assume that Chrysopidae were indeed rare in the late Eocene ecological communities of the Baltic amber forest.

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