



A new species of *Succinoraphidia* Aspöck & Aspöck, 2004 (Raphidioptera: Raphidiidae) from the late Eocene Rovno amber, with venation characteristics of the genus

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Abstract

Succinoraphidia radioni sp. nov. (Raphidiidae) is described from the late Eocene Rovno amber, Ukraine. The genus also includes two species from contemporaneous Baltic amber, i.e., *S. exhibens* Aspöck & Aspöck, 2004 and *S. baltica* (Carpenter, 1957), **comb. nov.** The venation of *Succinoraphidia* is analysed. It possesses several plesiomorphic character states at the family level, and the monotypic subfamily Succinoraphidinae represents a basal group within the family or possibly even a potential stem group of Raphidiidae. All diagnostic character states of *Succinoraphidia* (except the structure of the pterostigma) are found in a few Cretaceous species of the paraphyletic Mesoraphidiidae, but some of these are not found in the extant Raphidiidae.

Key words: Raphidioptera, Raphidiidae, Eocene, Rovno amber, Baltic amber

Introduction

The order Raphidioptera (or snakeflies) is today one of the smallest holometabolous insect orders, comprising ca. 240 species divided into two families, Raphidiidae and Inocelliidae, which are now distributed only in the Northern Hemisphere (Oswald 2018). However, the order was more diverse and widely distributed in the Mesozoic, being represented by Priscaenigmatomorpha (Priscaenigmatidae and Chrysoraphidiidae), Juroraphidiidae and Raphidiomorpha (Metaraphidiidae, Mesoraphidiidae and Baissopteridae) (Liu *et al.* 2014). Raphidiomorpha were often numerous in the Middle Jurassic to Early Cretaceous localities, but became rarer in the Cenozoic.

The oldest Raphidiidae are known from the early Eocene. The four genera from the Eocene are extinct: *Megaraphidia* Cockerell, 1907, *Archiraphidia* Handlirsch, 1910, *Succinoraphidia* Aspöck & Aspöck, 2004, and *Florissantoraphidia* Makarkin & Archibald, 2014 (Aspöck & Aspöck 2004; Makarkin & Archibald 2014). Of these, three genera are from North America and one (*Succinoraphidia*) from Europe. Other fossil species of the family are currently treated in extant genera (Carpenter 1936, 1957; Nel 1993; Engel 2009, 2011).

Snakeflies are very rare in the late Eocene ambers of Europe (i.e., Baltic, Rovno, Bitterfeld and Danish ambers). This is especially true of Raphidiidae: only two species (each represented only by their holotypes) have been described from Baltic amber, i.e., *Raphidia baltica* Carpenter, 1957 and *Succinoraphidia exhibens* Aspöck & Aspöck, 2004. Additionally, there are two other (not reported) specimens of the Baltic amber Raphidiidae.

Previously, Raphidiidae has been mentioned to occur in Rovno amber but without detail (Perkovsky *et al.* 2010). Here, a new species of this family is described from this amber. We found that this species and the two species of Baltic amber Raphidiidae share some venational peculiarities, which allows us to conclude that they belong to the same genus *Succinoraphidia*.

Material and methods

This study is based on a single specimen of Raphidiidae embedded in a relatively large piece of Rovno amber (about 42 x 24 x 19 mm after cutting and polishing), with the following syninclusions: Hymenoptera (one small Scelionidae?), Diptera (four specimens of Chironomidae and legs of Tipuloidea), scales and numerous stellate hairs.

Biotic inclusions of Rovno amber were found in four administrative regions of Ukraine (Rovno, Zhitomir, Volyn and Kiev) and in Brest Region of Belarus (Perkovsky 2017). In the Rovno Region, the majority of inclusions were collected in four administrative districts, i.e., Sarny (Klesov locality), Dubrovitsa, Zarechnoye and Vladimirets (Perkovsky 2017; Perkovsky & Olmi 2018; Radchenko & Perkovsky 2018). The examined snakefly was collected in Vladimirets District near Voronki (see Perkovsky & Olmi 2018).

Rovno amber is the southern coeval of the famous Baltic amber of late Eocene age (Perkovsky *et al.* 2007, 2010; Mänd *et al.* 2018). Its fauna and flora comprise of many taxa common with Baltic amber and ones not distributed north of the southern coast of Subparathetys (e.g., 66% of ant species are common with Baltic amber: Perkovsky 2018). One family, one subfamily, two tribes, and numerous genera (including 19 genera of Hymenoptera) recorded from Rovno amber are unknown from Baltic amber (Perkovsky *et al.* 2010; Legalov *et al.* 2018 and references herein).

The venational terminology follows Makarkin & Archibald (2014). Terminology of wing spaces and details of venation (e.g., veinlets, traces) follows Oswald (1993).

Abbreviations: AA1 to AA3, first to third branches of Analis Anterior; CuA, Cubitus Anterior; CuP, Cubitus Posterior; *doi*, discoidal cells; MA and MP, anterior and posterior branches of Media; RA, Radius Anterior; RP, Radius Posterior; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; ScP, Subcosta Posterior.

Institutional abbreviations: MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.; SIZK, Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine.

Systematic paleontology

Order Raphidioptera Navás, 1916

Suborder Raphidiomorpha Engel, 2002

Family Raphidiidae Latreille, 1810

Subfamily Succinoraphidiinae Aspöck & Aspöck, 2004

Genus *Succinoraphidia* Aspöck & Aspöck, 2004

Type species. *Succinoraphidia exhibens* Aspöck & Aspöck, 2004, by original designation.

Diagnosis based on wing venation. In fore- and hind wings, [1] pterostigma elongate with one incorporated branch (veinlet) of RA; [2] RA distad pterostigma not forked; [3] RP distad crossvein 3ra-rp not forked; [4] crossvein 3ra-rp located distad pterostigma. In hind wing, [5] crossvein 1r-m long, longitudinal; [6] AA1 and CuP fully separate; [7] crossvein between AA1+2 and AA3 present.

Species included. Three species from the late Eocene of Europe: *S. exhibens* and *S. baltica* (Carpenter, 1957), **comb. nov.** (both from Baltic amber); *S. radioni* **sp. nov.** from Rovno amber.

Comments. The genus *Succinoraphidia* differs from other genera of the family by male genitalia in which the gonapophyses 9 are completely free and bear a subapical hook; these character states are found in *S. exhibens* (Aspöck & Aspöck 2004). However, other known specimens (i.e., the holotypes of *S. baltica* and *S. radioni* **sp. nov.**, and two not reported specimens of this genus from Baltic amber) are represented by females. Nevertheless, the venation of all these specimens is so similar that their assignment to the same genus is undoubted. In particular, their wings possess some character states not occurring in other genera of Raphidiidae [characters 3, 6, 7].

***Succinoraphidia radioni* sp. nov.**

Figs 1–4

Diagnosis. In both fore- and hind wings, ScP relatively long, length between termination of ScP and proximal end of pterostigma twice shorter than length of pterostigma [this length slightly longer than length of pterostigma in *S. baltica*]; pterostigma distinctively paler in proximal part, darker in distal part [somewhat darker proximally in *S. exhibens*]; in hind wing, anterior trace of MP with three pectinate branches [two branches in *S. exhibens*].

Description. Female. Body poorly discernible. Prothorax relatively broad. Ovipositor long, with oval gonostyli (Fig. 3).

Forewing oval, 8.7 mm long, 2.7 mm wide. Costal space moderately dilated at 1/5 wing length; all four subcostal veinlets simple, widely spaced (additional incomplete veinlet between two basal veinlets in right wing). ScP relatively long, terminating on costal margin at about 0.55 wing length; length between termination of ScP and proximal end of pterostigma twice shorter than length of pterostigma. Subcostal space broad, with two crossveins: basal crossvein 1scp-r located distad seeming origin of M; distal crossvein 2scp-r at proximal end of pterostigma. Pterostigma elongate, paler proximad proximal branch of RP (light-brown), darker distad (brown). Anterior trace of RA not forked distally, strongly bent posteriorly after origin of distal branch, terminating at margin before wing apex; with two branch (veinlet): proximal branch located within pterostigma (part of pterostigma proximad this branch longer than distad); distal one nearly straight, located at distal end of pterostigma. RA space (between RA, RP) with two crossveins: 2ra-rp long, located slightly proximad proximal end of pterostigma; 3ra-rp shorter, located well distad end of pterostigma. RP originates far from wing base (at about 0.48 complete wing length), with two branches: RP1 deeply forked at outer gradate series of crossveins; RP2 simple. Anterior trace of RP not forked distally. One crossvein between branches of RP as part of outer gradate series (irp), connecting anterior branch of RP1, RP2 at its origin. Three crossveins between RP, MA: 1r-m, 2r-m connect anterior trace of RP, MA; 3r-m connects RP1 and anterior branch of MA. M appear fused basally with R for considerable distance, then actually fused with CuA for short distance; forked distad origin of RP. MA once deeply forked. MP fused with CuA for considerable distance, then pectinately branched, with two simple branches. Two intramedian crossveins form two *doi*. Cu dividing into CuA, CuP rather far from wing base. CuA crossvein-like before fusion with M, perpendicular to Cu, then fused with M for very short distance, not forked distally. CuP simple, aligned with Cu and nearly parallel to distal part of CuA. Crossvein between CuA, CuP (icu) long; crossvein between CuP, AA1 short. Anal veins not forked distally; no crossvein between these. AA2, AA3 fused basally; then AA2 bent to AA1 and fused with it for short distance; free distal part of AA3 short.

Hind wing ca. 7.5 mm long, 2.6 mm wide. Costal space narrow; subcostal veinlets poorly discernible. ScP relatively long, terminating on costal margin at about 0.63 wing length; length between termination of ScP and proximal end of pterostigma nearly twice shorter than length of pterostigma. Subcostal space with one distal crossvein 2scp-r at proximal end of pterostigma. Pterostigma elongate, slightly lighter than in forewing; paler proximad proximal branch of RP, darker distad. Anterior trace of RA not forked distally, strongly bent posteriorly after origin of distal branch, terminating at margin before wing apex (slightly distad than in forewing); with two branch (veinlet): proximal branch located within pterostigma (part of pterostigma proximad this branch longer than distad); distal one nearly straight, located at distal end of pterostigma. RA space with three crossveins: 1ra-rp located nearly opposite to 2r-m; 2ra-rp located somewhat proximad proximal end of pterostigma; short 3ra-rp located well distad termination of pterostigma, connecting anterior traces of RA and RP. RP originates relatively close to wing base (at ca. 0.35 complete wing length), with two branches. RP1 deeply forked outer gradate series of crossveins; RP2 simple. One crossvein between branches of RP as part of outer gradate series. Three crossveins between RP, M/MA; 1r-m long, slightly sinuate, connecting anterior trace of RP and M near its seemingly origin; 2r-m connects RP1 and anterior trace of MA; 3r-m as part of outer gradate series connecting RP1 before fork and anterior branch of MA. M appears fused basally with R, forked into MA, MP distad well origin of RP. MA deeply forked distally; MP pectinately branched, with three branches. Two crossveins between MA and MP (1im, 2im) form two cells (*1doi*, *2doi*), nearly equal in length; length/width ratio of *2doi* 1.7 (left wing) to 2.1 (right wing). Two crossveins between M and Cu: basal 1m-cu moderately long, only slightly oblique, located near wing base; 2m-cu long, connecting MP and anterior branch of CuA. CuA deeply forked. CuP simple. One long crossvein between CuA, CuP (icu), located far distad 1m-cu. Cu and AA1 fully separate; one short crossvein connecting these located between 1m-cu, 2m-cu. AA1, AA2 fused proximally; their distal (free) parts simple. AA3 short, simple (poorly discernible). One long crossvein between AA1+AA2 and AA3.

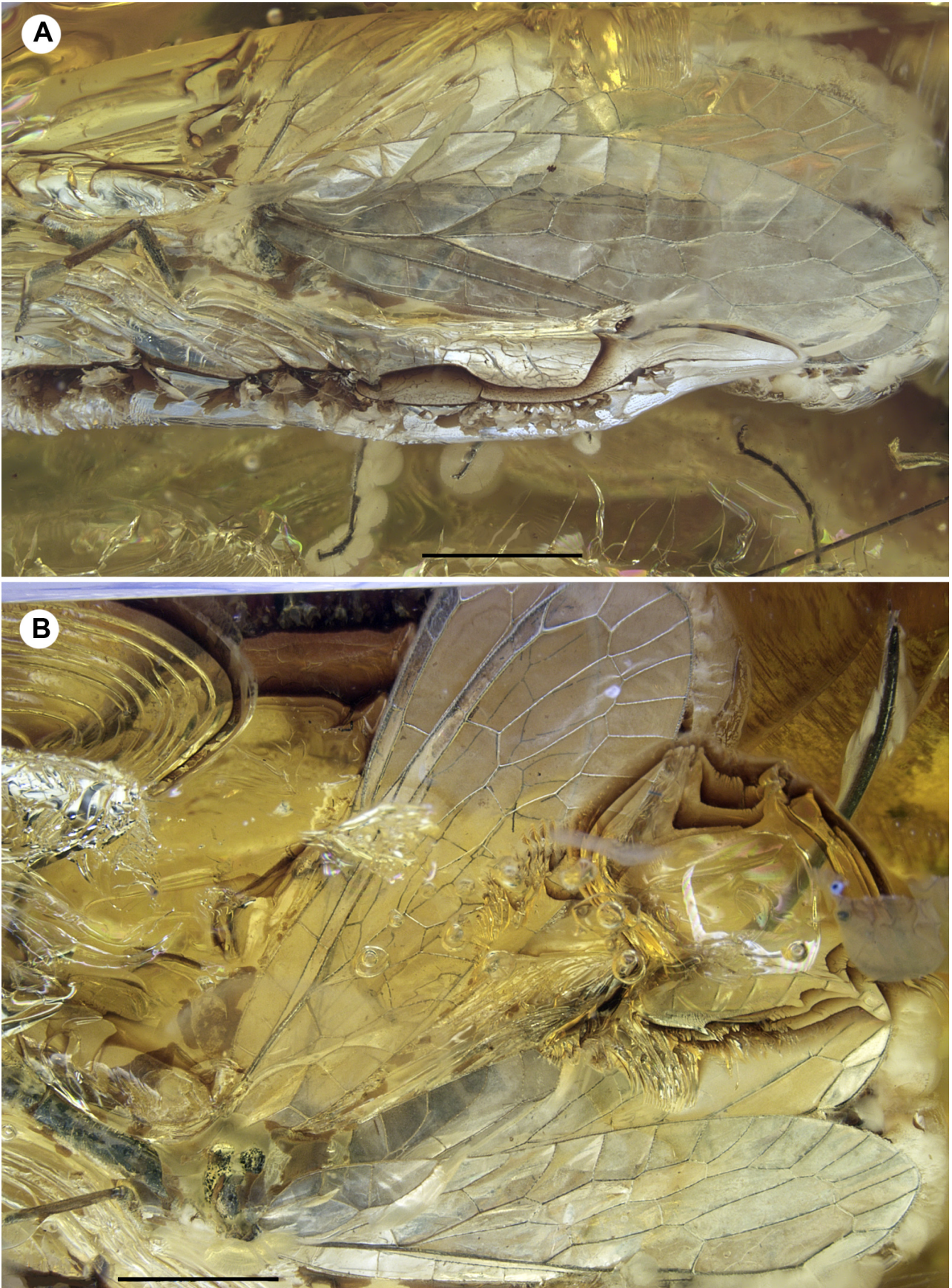


FIGURE 1. *Succinoraphidia radioni* sp. nov., holotype SIZK L-105 as preserved. A, left view; B, dorsal view. Scale bars = 2 mm.

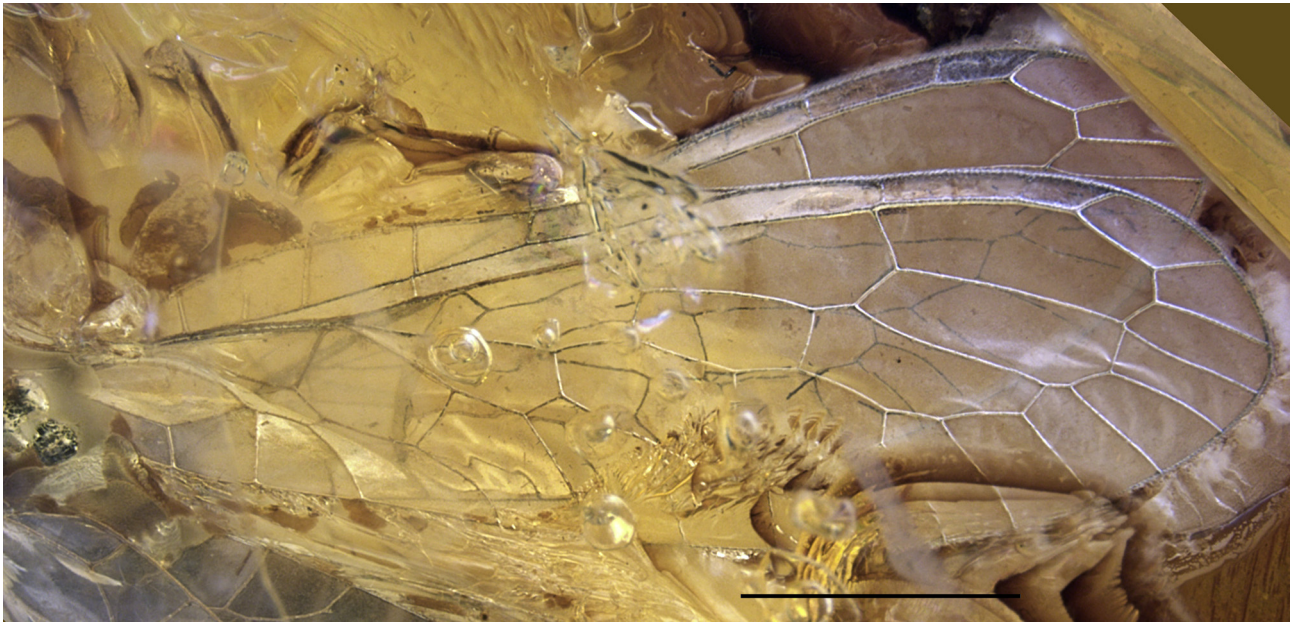


FIGURE 2. *Succinoraphidia radioni* sp. nov., holotype SIZK L-105, right wings. Scale bar = 2 mm.

Etymology. From the first name of Radion F. Khomich, father of the collector of the specimen.

Type material. Holotype: Specimen No. SIZK L-105, collected by Nikolai R. Khomich and currently deposited in his collection, but will be ultimately deposited in SIZK. A poorly-preserved, slightly incomplete female.

Locality and horizon. Rovno amber (Voronki in Vladimirets District of Rovno Region, Ukraine); late Eocene.

Remarks. The new species easily differs from *S. baltica* by the longer ScP. Unfortunately, the venation of *S. exhibens* is incompletely described. However, the photograph of the holotype and the drawing of the basal part of the hind wing (see Aspöck & Aspöck 2004: Figs 1, 5) show that the venation of *S. exhibens* differs from that of the new species by the number of MP branches and the presence of additional long crossvein between MP and CuA in the hind wing, as well as by the coloration of the pterostigma (this is “mainly yellowish, proximally somewhat darker” in *S. exhibens*: Aspöck & Aspöck 2004, p. 12).

***Succinoraphidia baltica* (Carpenter, 1957), comb. nov.**

Fig. 5

Raphidia baltica Carpenter, 1957: 78, Fig. 1; Larsson 1978: 162; Keilbach 1982: 283; Oswald 1990: 160; Spahr 1992: 69; Weitschat & Wichard 1998: 144; Aspöck & Aspöck 2004: 11, 13; Engel & Grimaldi 2007: 5; Engel & Grimaldi 2008: 86. “*Raphidia*” *baltica*: Aspöck *et al.* 1991: 540, 665, Fig. 3055; Engel 2002: 21.

Type material. Holotype: Specimen No. 5122, deposited in MCZ. A nearly complete female. Verbatim label data: [hand written] “Neuroptera / 17941”; [typed and hand written] “Mus. Comp. Zool. / no. 5122 / *Raphidia* / *baltica* / Carpenter / 272 Baltic amber”.

Type locality. Baltic amber (precise collecting locality is unknown).

Comments. The pterostigma of this species is not shorter than in other species of the genus (Fig. 5). The venation of the holotype is correctly figured by Carpenter (1957) and fully concordant with the diagnosis of *Succinoraphidia*. At least, the species cannot be assigned to *Raphidia* Linnaeus, 1758 or any other genus of the extant and fossil Raphidiidae as some character states of *S. baltica* are absent in these (see below).

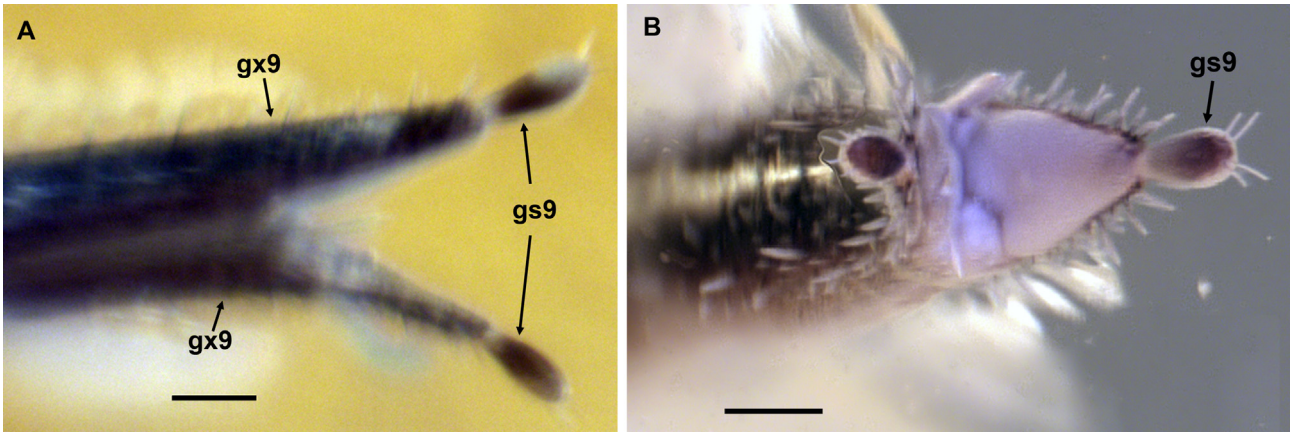


FIGURE 3. *Succinoraphidia radioni* sp. nov., holotype SIZK L-105, apex of ovipositor. A, ventral view; B, latero-caudal view. gs9, gonistyli of 9th segment; gx9, gonocoxites of 9th segment. Scale bars = 0.1 mm.

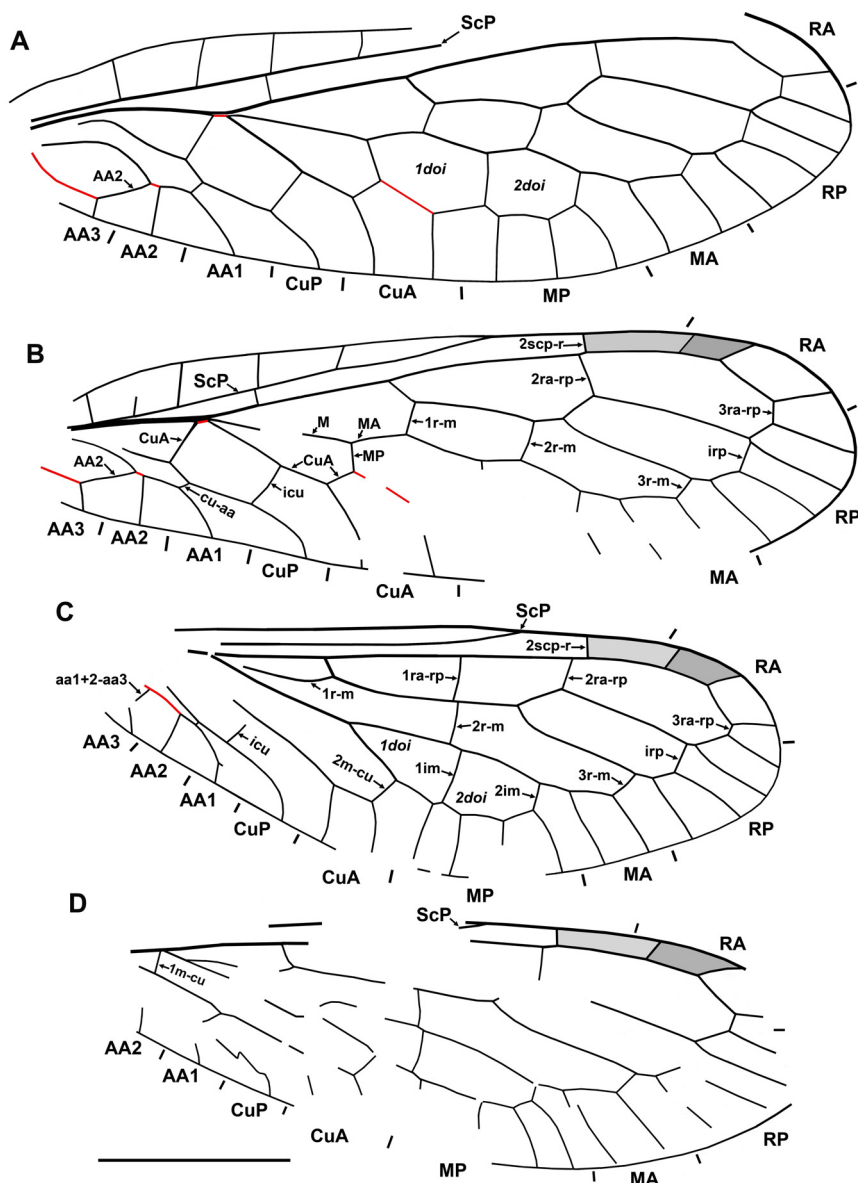


FIGURE 4. Wing venation of *Succinoraphidia radioni* sp. nov., holotype SIZK L-105. A, left forewing; B, right forewing; C, left hind wing; D, right hind wing (A and C converted to standard view, with apex to the right). Fused veins are shown by red lines. Scale bar = 2 mm (all to scale).

Venation characteristics of *Succinoraphidia*

The genus *Succinoraphidia* strongly differs from all other genera of Raphidiidae, and the separation of it into the monophyletic subfamily Succinoraphidiinae by Aspöck & Aspöck (2004) based on male genitalia is reasonable. The genus differs also from all extant genera by the venation, main characteristics of which enumerate in the generic diagnosis. These are analysed below.

- [1] **The elongate pterostigma, with one incorporated branch (veinlet) of RA.** The pterostigma in most extant Raphidiidae is shorter than in *Succinoraphidia*, but the presence of one incorporated branch of RA within the pterostigma is typical for the family. However, this branch is not or poorly discernible in some Eocene Raphidiidae from North American localities (i.e., Florissant and Okanagan Highlands) (see e.g., Makarkin & Archibald 2014: Fig. 9). Unlike *Succinoraphidia*, the pterostigma in all Eocene Raphidiidae from North America is unicoloured.
- [2–3] **RA distad the pterostigma and RP distad the crossvein 3ra-rp.** The non-forked RA distad the pterostigma occurs relatively rarely in Raphidiidae. In particular, this condition is found in the Eocene genera *Archiraphidia* and *Florissantoraphidia*, and some extant species of the genera *Mongoloraphidia* Aspöck & Aspöck, 1968, *Ohmella* Aspöck & Aspöck, 1968, *Subilla* Navás, 1916, *Turcoraphidia* Aspöck & Aspöck, 1968, *Ulrike* Aspöck, 1968 and *Venustoraphidia* Aspöck & Aspöck, 1968 (see e.g., Steinmann 1964: Fig. 52; Aspöck & Aspöck 1965: Fig. 22; Aspöck *et al.* 1982: Fig. 2; Monserrat & Papenberg 2012: Fig. 2). But 3ra-rp is located far from the wing margin in all these species and RP distad it is forked at least two times. In *Xanthostigma xanthostigma*, the non-forked RA occurs as an aberration, i.e., in one specimen of 85 (Zeleny 1969: Fig. 36).
The anterior trace of RP distad the crossvein 3ra-rp is not forked in *Succinoraphidia*. This vein is branched or at least once forked in all other Eocene and extant species of Raphidiidae, except only for *Mongoloraphidia tshimganica* (Aspöck *et al.*, 1968), in which it is not forked (Aspöck *et al.* 1969: Fig. 94). But in other numerous species of this genus, RP distad 3ra-rp is branched or once forked. Therefore, the branched/forked RP distad 3ra-rp is characteristic of all other genera of Raphidiidae.
In contrast to Raphidiidae, the non-forked RP distad 3ra-rp and the non-forked RA distad the pterostigma often occur in ‘Mesoraphidiidae’, but the crossvein 3ra-rp in the vast majority of these species is located within the pterostigma, not distad. Therefore, both conditions (the terminally non-forked RP and RA) may be plesiomorphic in Raphidiidae.
- [4] **The location of the distal crossvein 3ra-rp.** This crossvein is located distad the pterostigma in *Succinoraphidia*, a condition that is characteristic also of most extant genera of the family. In contrast, the crossvein 3ra-rp is located within the pterostigma in all Eocene Raphidiidae from North America (including undescribed species from the early Eocene) (see Makarkin & Archibald 2014: Figs 5–8, 11, 13, 22).
- [5] **The crossvein 1r-m long and longitudinal in the hind wing.** This character state is plesiomorphic, and occurs in the vast majority of Raphidiomorpha. The crossvein 1r-m is in an apomorphic state in many genera of Raphidiidae, i.e., it is short and crossvein-like (for more detail see Makarkin & Archibald 2014, p. 408).
- [6] **The fully separate hind wing CuP and AA1.** These veins are clearly separate in *Succinoraphidia*, all Inocelliidae and all ‘Mesoraphidiidae’ from Cretaceous ambers when this part of the hind wing is well preserved (e.g., Spanish (El Soplao), Burmese and New Jersey ambers). This condition is obviously plesiomorphic. Unfortunately, the relationship between CuP and AA1 is poorly discernible in most fossil impression raphidiids, but their partial fusion may be present at least in the late Eocene *Florissantoraphidia* from Florissant judging from the preserved venation (see e.g., Makarkin & Archibald 2014: Fig. 22). These veins are certainly partially fused in *Megaraphidia* from Florissant (Makarkin & Archibald 2014: Fig. 8), and in all extant genera of Raphidiidae.
- [7] **The crossvein between AA1+2 and AA3 in the hind wing.** This crossvein is absent in all extant Raphidiidae, but present in *Succinoraphidia* and the Mesozoic ‘Mesoraphidiidae’ when the basal part of the hind wing is well preserved. One anal crossvein is also present in all Inocelliidae, extant and fossil, but it connects AA1 and AA2+3. It is unclear if these crossveins are homologous or not. If so, the presence of the anal crossvein is plesiomorphic in Raphidiomorpha.

Of these, character states of *Succinoraphidia* [3], [6] and [7] are unique in Raphidiidae. However, some or most of its diagnostic features are plesiomorphic in the family, i.e., [5] – [7], and possibly [2] – [4]. No apomorphic character states in the venation of *Succinoraphidia* are found that is however characteristic of most basal groups.

Succinoraphidia and ‘Mesoraphidiidae’

It is now clear that the Mesozoic ‘Mesoraphidiidae’ is a paraphyletic group, which includes in particular the stem lineages leading to extant Raphidiidae and Inocelliidae (Makarkin & Archibald 2014). The venation of *Succinoraphidia* is more similar to that of some ‘Mesoraphidiidae’ than the venation of any genus of Raphidiidae. Moreover, there are a few mesoraphidiids in which all diagnostic character states of *Succinoraphidia* are found (except for the structure of the pterostigma). It is characteristic of some minute species from the early Late Cretaceous, e.g., *Grimaldiraphidia luzzii* (Grimaldi, 2000) from the Turonian New Jersey amber; *Nanoraphidia electroburmica* Engel, 2002 and *Burmoraphidia reni* Liu *et al.*, 2016 from the early Cenomanian Burmese amber. These genera are considered to belong to the tribe Nanoraphidiini (Bechly & Wolf-Schwenninger 2011; Liu *et al.* 2016). But the structure of their pterostigma differs from that of *Succinoraphidia*. It lacks the crossvein 2scp-r at the proximal end of the pterostigma (*B. reni*) or incorporated branches of RA within pterostigma (*G. luzzii* and *N. electroburmica*). However, the pterostigma of some other ‘Mesoraphidiidae’ from Burmese amber (e.g., *Dolichoraphidia engeli* Liu *et al.*, 2016) is very similar to that of Raphidiidae with a long pterostigma, including *Succinoraphidia*, i.e., it possesses the crossvein 2scp-r at the proximal end of the pterostigma and the incorporated branch of RA within the pterostigma (see Liu *et al.* 2016: Fig. 4). The venation of *Dolichoraphidia engeli* differs from that of Raphidiidae only by the number of discoidal cells: one in *D. engeli* and normally two in all Raphidiidae, except some species, which have one discoidal cell in the hind wings, e.g., those of *Harraphidia* Steinmann, 1963 (see Monserrat & Papenberg 2006: Figs 1–4).

Judging from great similarity of the venation of Nanoraphidiini (and similar genera of the Late Cretaceous ‘Mesoraphidiidae’) and *Succinoraphidia*, among the former may be present a stem group leading to Raphidiidae.

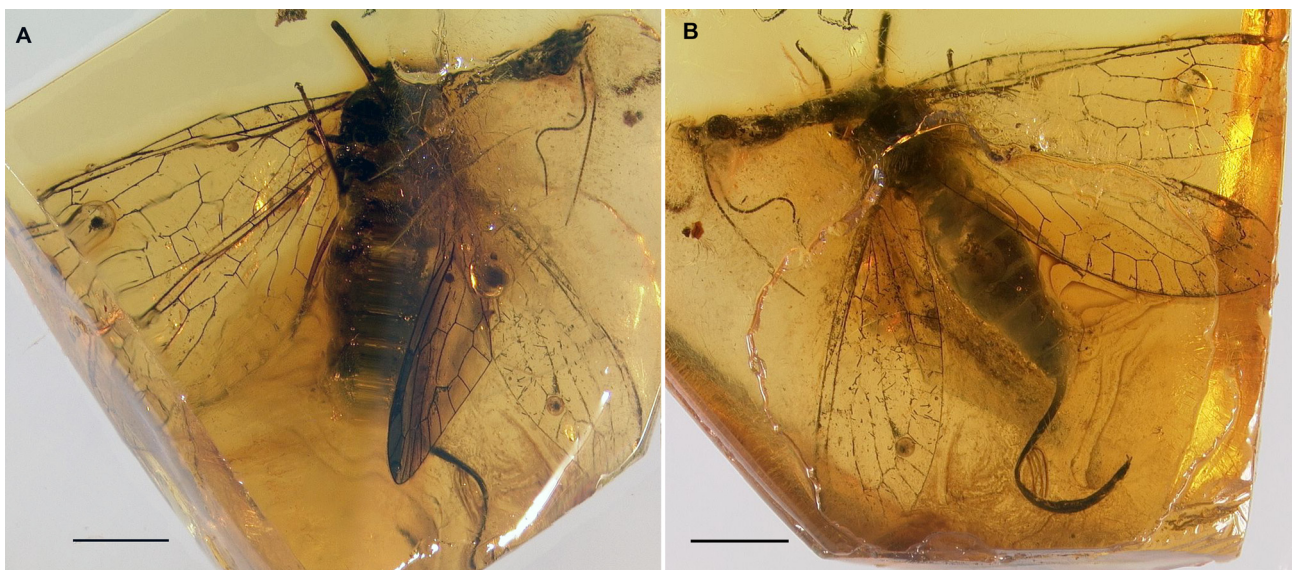


FIGURE 5. *Succinoraphidia baltica* (Carpenter, 1957), holotype MCZ 5122. A, ventral view; B, dorsal view. Scale bars = 2 mm.

Conclusions

The late Eocene genus *Succinoraphidia* is certainly most primitive within Raphidiidae, and the monophyletic subfamily Succinoraphidiinae represents a basal group within the family or possibly even a potential stem group of Raphidiidae. The discovery of the new species of this genus in Rovno amber, which is not yet recorded in Baltic

amber, agrees with an opinion that their biotas differ significantly. This is the southern-most record of Raphidiidae in the Eurasian Eocene.

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