

Neotype designation and re-description of *Prolachlanius resinatus* (Hagen) (Neuroptera, Hemerobiidae) from Baltic amber, with the first record of the species from Rovno amber

VLADIMIR N. MAKARKIN^{1,5}, EVGENY E. PERKOVSKY^{2,3} & CARSTEN GRÖHN⁴

¹Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, 690022 Russia

²Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, 15 Bogdan Khmelnytsky Str., Kiev, 01601 Ukraine

³Borissiak Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya Str. 123, 117997, Moscow, Russia

⁴Amber Study Group, c/o Geological-Palaeontological Institute and Museum (Centrum of Natural History) of the University of Hamburg, Bundesstraße 55, 20146, Hamburg, Germany

⁵Corresponding author: E-mail: vnmakarkin@mail.ru

Abstract

Prolachlanius resinatus (Hagen) is re-described, based on five specimens from late Eocene Baltic amber (including the neotype designated herein) and the first recorded specimen from contemporaneous Rovno amber (Klesov locality). This is the most common species of Hemerobiidae in Baltic amber. The forewing venation of *Prolachlanius* is most similar to that of *Symphorobius*, and, therefore, its assignment to Sympherobiinae is confirmed. The genus differs from other Sympherobiinae by the distal branch of RP being not deeply forked, and the presence of crossvein 4r-m in the forewing. The male genitalia of *Prolachlanius* are sufficiently dissimilar from those of other Sympherobiinae to distinguish it as a separate genus, particularly by the structure of the ectoprocts, and the 8th and 9th sternites. The extremely short eighth sternite of *Prolachlanius* is especially noteworthy.

Keywords: Neuroptera, Hemerobiidae, Sympherobiinae, Baltic amber, Rovno amber

Introduction

Brown lacewings (Hemerobiidae) comprise a nearly cosmopolitan family of ca. 520 extant species (Oswald 2018), and 25 fossil species described from the Late Jurassic to the Miocene (pers. data).

They occur rather often in Baltic amber. Seven species in five genera have been described: *Prolachlanius resinatus* (Hagen in Pictet-Baraban et Hagen, 1856), *Prospadobius moestus* (Hagen in Pictet-Baraban et Hagen, 1856), *Drepanopteryx resinata* (Krüger, 1922), *Symphorobius completus* Makarkin et Wedmann, 2009, *S. siriae* Jepson et al., 2010, *Proneuronema minor* Makarkin et al., 2016, and *P. gradatum* Makarkin et al., 2016 (Pictet-Baraban & Hagen 1856; Krüger 1923; Makarkin & Wedmann 2009; Jepson et al. 2010; Makarkin et al. 2016).

Three hemerobiid specimens have been found in late Eocene Rovno amber, which belong to three species of different genera: a species of *Symphorobius* Banks, 1904, an undescribed species of *Proneuronema* Makarkin et al., 2016, and *Prolachlanius resinatus* (pers. obs.). This family was reported from Rovno amber without details by Perkovsky et al. (2010). Previously, only three species of Neuropterida were known from Rovno amber: *Archiconiocompsa prisca* Enderlein, 1910 (Neuroptera: Coniopterygidae), *Rophalis relict*a (Hagen in Pictet-Baraban et Hagen, 1856) (Neuroptera: Nevrothidae), and *Succinoraphidia radioni* Perkovsky et Makarkin, 2019 (Raphidioptera: Raphidiidae) (Kupryjanowicz & Makarkin 2008; Makarkin & Perkovsky 2009; Perkovsky & Makarkin 2019). Of these, *Archiconiocompsa prisca* and *Rophalis relict*a also occur in Baltic and Bitterfeld ambers.

Prolachlanius resinatus was described by Hermann Hagen in Pictet-Baraban & Hagen (1856) as *Hemerobius resinatus* in a work based initially on specimens in the collection of Georg C. Berendt. The first mention of Neuroptera (s.l.) in this collection was published by Berendt (1830), who later asked Francois J. Pictet to describe them in a

forthcoming second volume (second part) of the book *Die im Bernstein befindlichen Organischen Reste der Vorwelt* (1856). By 1845, Pictet had finished the chapter in French. Hagen's translation to German was delayed, and after the death of Berendt in 1850, he continued work on this chapter, now including many specimens from other collections, notably that of Anton Menge from Danzig [now Gdańsk] (Krüger 1923). The taxonomic treatments of some insects had changed over this long period of work by these different people, resulting in the same species bearing different names and attributed to different authors (see below).

Subsequently, Krüger (1923) re-described *Hemerobius resinatus*, based on the holotype, erecting the monotypic genus *Prolachlanius* for it. It is the most common hemerobiid species in Baltic amber. Photographs of it have often been published, usually simply identified as 'Hemerobiidae' (e.g., Weitschat & Wichard 1998: Pl. 56F; Kupryianowicz 2001: Fig. 51; Janzen 2002: Figs 59, 262) and more rarely as *P. resinatus* (e.g., Scheven 2004: Fig. on p. 67). We know of at least 35 specimens in museums and private collections. Nevertheless, the incomplete and obsolete original description and Krüger's (1923) re-description, which lacked illustrations, have remained the main sources of information about this species.

Here, we redescribe *Prolachlanius resinatus* based on five specimens from Baltic amber and one specimen from Rovno amber. A male from Baltic amber with well-preserved terminal segments of the abdomen is here designated as a neotype. The designation of a neotype for this species is necessary as its types are considered lost and as the species is rather variable, there is theoretical possibility of the existence of two or more species within "*Prolachlanius resinatus*" (see ICZN 1999: Article 75).

Material and methods

We re-described the species based on five specimens from Baltic amber and one from Rovno amber, which are deposited in the museums of Germany and Ukraine (see below). Information on Rovno amber and its biota was reported by Perkovsky *et al.* (2010), Sokoloff *et al.* (2018), and Perkovsky & Makarkin (2019, and references therein). The neotype is a male with a well-preserved abdomen. Photographs were taken by CG using a Zeiss stereomicroscope (modified with variable objectives: Nikon MPlan 5x, 10x, 20x, 40x; ZEISS Luminar 18 mm, 25 mm, 40 mm) and an attached Canon EOS 450D digital camera. All line drawings were prepared by VM using Adobe Photoshop CS3.

Venational terminology follows Makarkin *et al.* (2016). The forewing of *Prolachlanius* has three separately originating branches of RP (i.e., three ORBs), and none of these are deeply forked. Therefore, numberings of RP are the same as numberings of ORBs in this genus (i.e., ORB1 = RP1; ORB2 = RP2; ORB3 = RP3). In other Hemerobiidae, the distal ORB (RP proper) is usually pectinately branched, and this ORB (e.g., ORB3 of *Hemerobius* Linnaeus, 1758) possesses several branches homologous with branches of RP (e.g., ORB3 of *Hemerobius* has often three RP branches, i.e., RP3–RP5). Terminology of wing spaces and details of venation (e.g., veinlets, traces) follows Oswald (1993). Crossveins are designated after the longitudinal veins which they connect and are numbered in sequence from the wing base, e.g., 2r-m, second crossvein connecting R/RR and M/MA; icu, crossvein between CuA and CuP.

Abbreviations: AA1–AA3, first to third anterior anal vein; CuA, Anterior Cubitus; CuA1, proximal-most branch of CuA; CuP, Posterior Cubitus; hp, humeral plate; hv, humeral veinlet; MA and MP, anterior and posterior branches of Media; ORB1, ORB2, ORB3, first to third oblique radial branches; RA, Anterior Radius; RP, Posterior Radius; RP1, RP2, RP3, first to third branches of RP; ScP, Subcosta Posterior.

Institutional abbreviations: GPIH, Geologisch-Paläontologisches Institut und Museum der Universität Hamburg (now CeNak, Centrum für Naturkunde), Germany; GZF, Geowissenschaftliches Zentrum der Universität Göttingen, Germany; SIZK, Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine.

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Hemerobiidae Latreille, 1802

Subfamily Sympherobiinae Comstock, 1918

Genus *Prolachlanius* Krüger, 1923

Type species. *Hemerobius resinatus* Hagen in Pictet-Baraban et Hagen, 1856, by original designation.

Diagnosis. May be easily distinguished from other genera of the subfamily by male genitalia (e.g., elongated ectoprocts with strong setae and spines apically; extremely short 8th sternite), and distal branch of RP being not deeply forked and presence of crossveins 4r-m in the forewing.

Species composition. The type species, known from Baltic and Rovno ambers, and probably one undescribed species from Baltic amber.

Remarks. One specimen deposited in the private collection of Thomas Weiterschan probably represents a new species of the genus. It differs from *Prolachlanius resinatus* by forewing characters, e.g., the widely-spaced subcostal veinlets, the one-branched CuA, and its narrower, paler wing almost lacking maculation.

Prolachlanius resinatus (Hagen in Pictet-Baraban et Hagen, 1856)

Figs 1–6

Type material. Neotype (by present designation) GPIH Typ. Kat. Nr. 4994 (collection of Carsten Gröhn, no. 7322), deposited in GPIH (CeNak). A complete male specimen.

Type locality and horizon. Baltic amber (Yantarnyi [formerly Palmnicken], Kaliningrad Region, Russia). Late Eocene.

Other material. Four specimens from Baltic amber (probably collected near present-day Kaliningrad): GZG.BST. 05240-5858 (possibly a male, but not clearly visible), GZG.BST. 05241-5868 (female), GZG.BST. 05242-5870 (apparently female); GZG.BST. 05238-5914 (apparently female). All are from the famous amber collection of Geologisch-Paläontologische Institute der Albertus-Universität in Königsberg, a small part of which is deposited in GZG.

Specimen SIZK K-6835 (sex unknown) from the Klesov locality (Pugach quarry) in the Rovno Region, Ukraine (Rovno amber); late Eocene, deposited in SIZK. Syninclusion: Coleoptera (Corylophidae?).

Re-description. Head cuneiform in lateral view. Eyes relatively large. Vertex slightly elevated covered with long scarce setae. Terminal segment of maxillary and labial palpi relatively thick, apically abruptly narrowed to form elongate acute portion (forming additional sub-segment?) (Fig. 3B). Antennae 35–39-segmented; scape distinctly enlarged and elongated.

Pronotum relatively short, transverse, covered with long, rather scarce setae (Fig. 3A). Structure of meso- and metanotum usual for Hemerobiidae.

Foreleg shorter than mid-, hind legs. Femora markedly narrower than tibiae, which are swollen: protibia shorter, less swollen than mesotibia; mesotibia shorter, less swollen than metatibia, which are longest, strongly swollen. Tibial spurs in all legs very short. Tarsi of all legs similarly constructed, with short tarsomeres (basitarsi longest). All legs covered with fine short relatively scarce setae.

Forewing oval, 4.2–5.6 mm long, 1.9–2.6 mm wide (length/width ratio 2.15–2.26). Trichosors prominent along entire wing margin. Costal space broad, strongly dilated proximally. Majority of pre-pterostigmal subcostal veinlets forked once or twice; pterostigmal subcostal veinlets mostly simple, some poorly discernible near ScP. Humeral veinlet (i.e., basal-most subcostal veinlet) recurrent, pectinately branched, with four (rarely three, including neotype) branches (usually proximal three simple, distal one forked). True crossveins in costal space absent. Subcostal space moderately wide for entire length, with two crossveins: basal, distal (in Klesov specimen two to three distal crossveins). Posterior trace of RA forked apically, with two to four branches, mostly once forked. Three separate branches of RP originated from R (formally from RA). RP1 relatively profusely, in general pectinately branched, with two to three branches. RP2, RP3 dichotomously branched distad fourth gradate series. M forked slightly distad origin of RP1. MA, MP normally similarly dichotomously forked: deep fork at fourth gradate series, both branches once to twice shallowly forked (Figs 1A, F, 6C, D); rarer, these veins have other mode of branching, e.g., MA with more number of branches (Fig. 5B), MP more deeply forked at third gradate series (Fig. 5E). Anterior trace of CuA forked apically once to twice; pectinately branched, with two to three long branches, most of which once (rarely

twice) forked. CuP with only one marginal fork. AA1 shallowly forked once or twice. AA2 deeply forked; anterior branch pectinate, with two to four short simple branches; posterior branch probably pectinate, with one to two very short branches (not clearly discernible in most specimens due to recurved anal region). AA3 simple. Four gradate series of crossveins (series 1 to 4 of Oswald, 1993) posterior to RA. First series consists of four crossveins: 1m-cu, 1cu-aa1, 1aa1-aa2, aa2-aa3, arranged similarly as in *Symphorobius*; all relatively pale. Second series includes three crossveins: 2r-m, 2m-cu, 2icu; of these, latter two dark brown. Third ('inner') series with six crossveins (from 3ra-rp to 3m-cu); 3rp1-rp2 usually shifted distally relative to next crossveins in series; all brown to dark brown. Fourth ('outer') series normally complete, with six crossveins (from 4ra-rp to 4m-cu); of these three posterior darker (brown) than anterior three, which are relatively pale. Crossveins absent between branches of CuA. Wing membrane brownish, rarely pale; some crossveins (especially 3ra-rp, 3rp2-rp3, 3rp1-rp2, 2m-cu, 2icu) margined with dark brown, narrowly (e.g., Figs 1A, 4C, 6A, B) to more broadly (e.g., Figs 4A, D); posterior part of pterostigma with dark brown shading, more or less broad (e.g., Fig. 4B) to narrow (e.g., Figs 1, 4C, D, 6A, B).

Hind wing (Figs 5D, G, 6E) ca. 3.3–3.4 mm long, 1.4 mm wide (neotype). Humeral plate well developed. Trichosors prominent along entire margin. Costal space narrow, dilated in pterostigmal area (in neotype and GZG.BST.05240-5858 strongly dilated). Subcostal veinlets simple, these in pterostigmal area poorly discernibly near ScP. Subcostal space narrow, with one distal crossvein (in Klesov specimen two distal crossveins). RA with two to three distal veinlets. Crossvein 1ra-rp relatively short to moderately long, perpendicular to RP. RP with two branches. Anterior trace of RP and RP2 dichotomously branched, with two to three forks each. RP1 pectinately branched, with two to three branches. Basal crossveins 1r-m sinuous, connecting M with RP1. Two crossveins in inner gradate series, none in other. M forked distad origin of most proximal branch of CuA and of RP2. Anterior trace of CuA forked distally, with four to five pectinate branches (of these, two to three branches forked once or twice (rarely), other simple) (based on neotype and specimen GZG.BST.05240-5858). CuP present, forked terminally. Anal veins not clearly discernible in any specimens, as region hidden by forewings or poorly preserved. All veins pale brownish; wing membrane pale brownish to nearly hyaline; pterostigmal area more fuscous, partially blackish in neotype (Fig. 1B).

Abdominal details poorly discernible in most specimens, especially their terminal segments.

Male (neotype). Sixth, seventh tergites, sternites not specialized (tergites little extended laterally, sternites more strongly so). Eighth tergite relatively short, stronger extending laterally than previous tergites. Eighth sternite very narrow, extending laterally like seventh sternite. Ninth tergite narrow, strong extending laterally, ventrally with acute apices (clearly visibly on right side (Fig. 2B), but this portion on left side poorly preserved (Fig. 3D)). Ninth sternite relatively small, short, shifted far proximally; surface distad it smooth, lacking any trichiation, even microtrichia (this is possibly visible apical part of parabaculum (=gonocoxites + gonapophyses 10 of Aspöck & Aspöck 2008)). Ectoprocts elongate, directed ventrally; its dorsal part dilated narrowing ventrad; apically distinctly dilated, inwardly curved, furnished with ten spines and strong setae (Fig. 3C). Callus cerci rounded (oval), number of trichobothria hard to count (probably >20). All segment covered with macro- and microtrichiae; setae especially long, dense ventrally on sixth to eighth sternites. Presumable mediuncus (=gonostyli 9 of Aspöck & Aspöck 2008) well developed extending far from ectoprocts; appears unpaired oval structure (in lateral view) with acute apex, which is bent ventrally.

Female. Nine tergite strongly dilated ventrally. Ectoproct large, more or less rounded. Gonostylus 9 rather long. Other details not clearly discernible.

Remarks. *Prolachlanus resinatus* was described from five specimens (see Pictet-Baraban & Hagen 1856), but Krüger (1923) found that only one belongs to this species, which he designated as 'Arttype' (i.e., species' type, or the holotype). Five other specimens labeled "*resinatus*" belong to other orders (one Lepidoptera and four Trichoptera), these are probably not from the type series. He assumed that the other four specimens of the type series belong to *Proberotha prisca* Krüger, 1923, because one of these was labelled "*Hemerobius*". It is interesting to note that Pictet-Baraban & Hagen (1856) and Krüger (1923) possibly examined two different specimens of *Prolachlanus resinatus*. Hagen wrote that there are six crossveins in the fourth gradate series, and the figure verifies it (Pictet-Baraban & Hagen 1856: Pl. 8, fig. 17). In contrast, Krüger mentioned only five of these crossveins, similar to the condition seen in the neotype and specimen GZG.BST.05241/5868 (Fig. 5B, C).

The holotype has not been located in German or Polish museums, and appears to be lost. Here, we designate a male with a well-preserved abdomen with clearly visible terminal segments as its neotype to avoid probable future taxonomic misunderstandings. The neotype and the lost holotype have very similar forewing venation; they are undoubtedly conspecific.

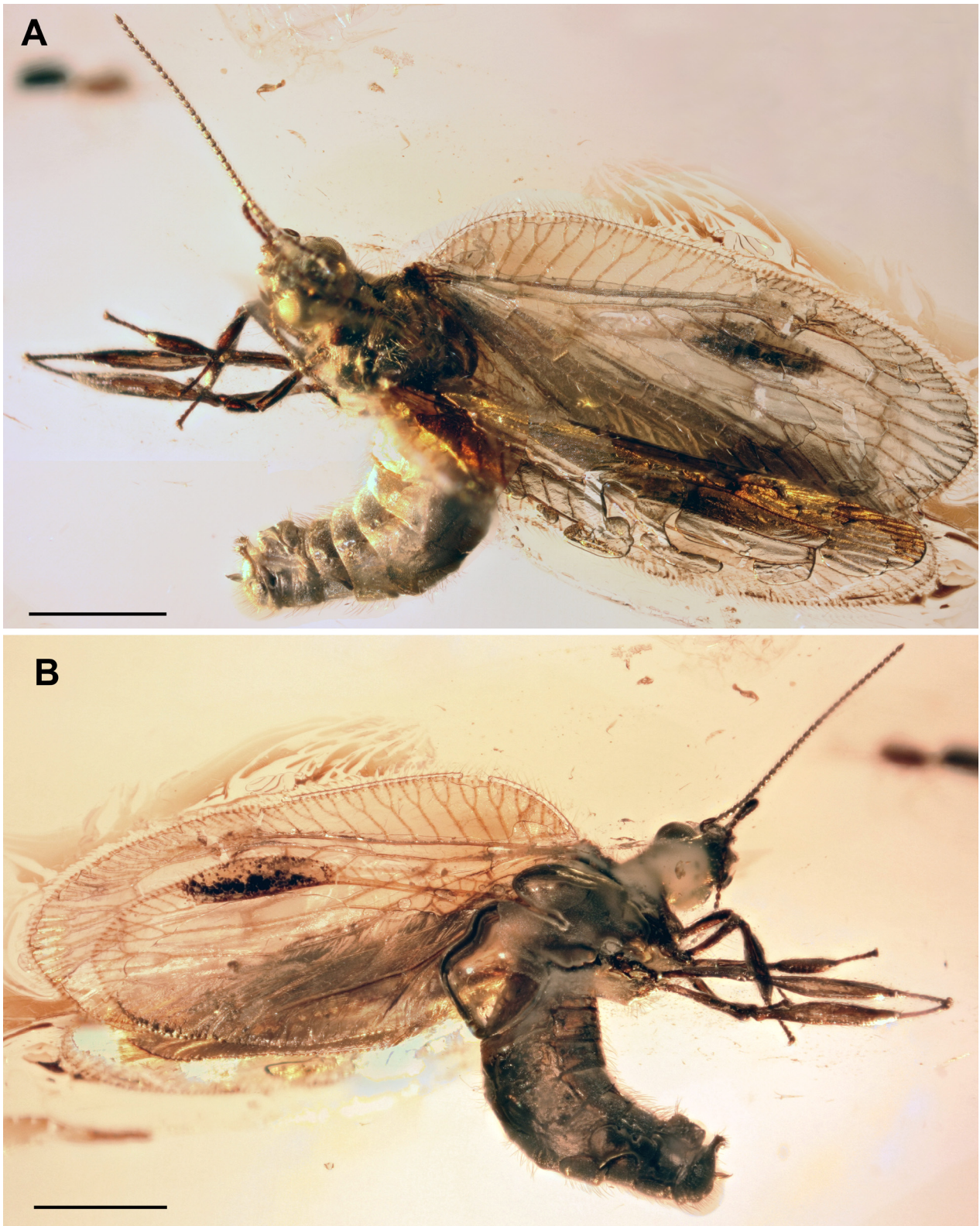


FIGURE 1. *Prolachlanius resinatus* (Hagen in Pictet-Baraban et Hagen, 1856), neotype GPIH, no 4994 (coll. Gröhn, no. 7322). A, dorso-lateral view; B, ventro-lateral view. Scale bars = 1 mm.

This species is apparently sexually dimorphic in the structure of the hind wing pterostigmal area. At least, this is evidently dilated and strongly fuscous in the male (neotype) so that the costal margin in pterostigmal area is convex (Fig. 5D), while this area in the female (at least in GZG.BST. 05241-5868: Fig. 4D) is not dilated and only slightly fuscous, and the margin is not convex. If this hypothesis is correct, the Rovno amber specimen is a female.

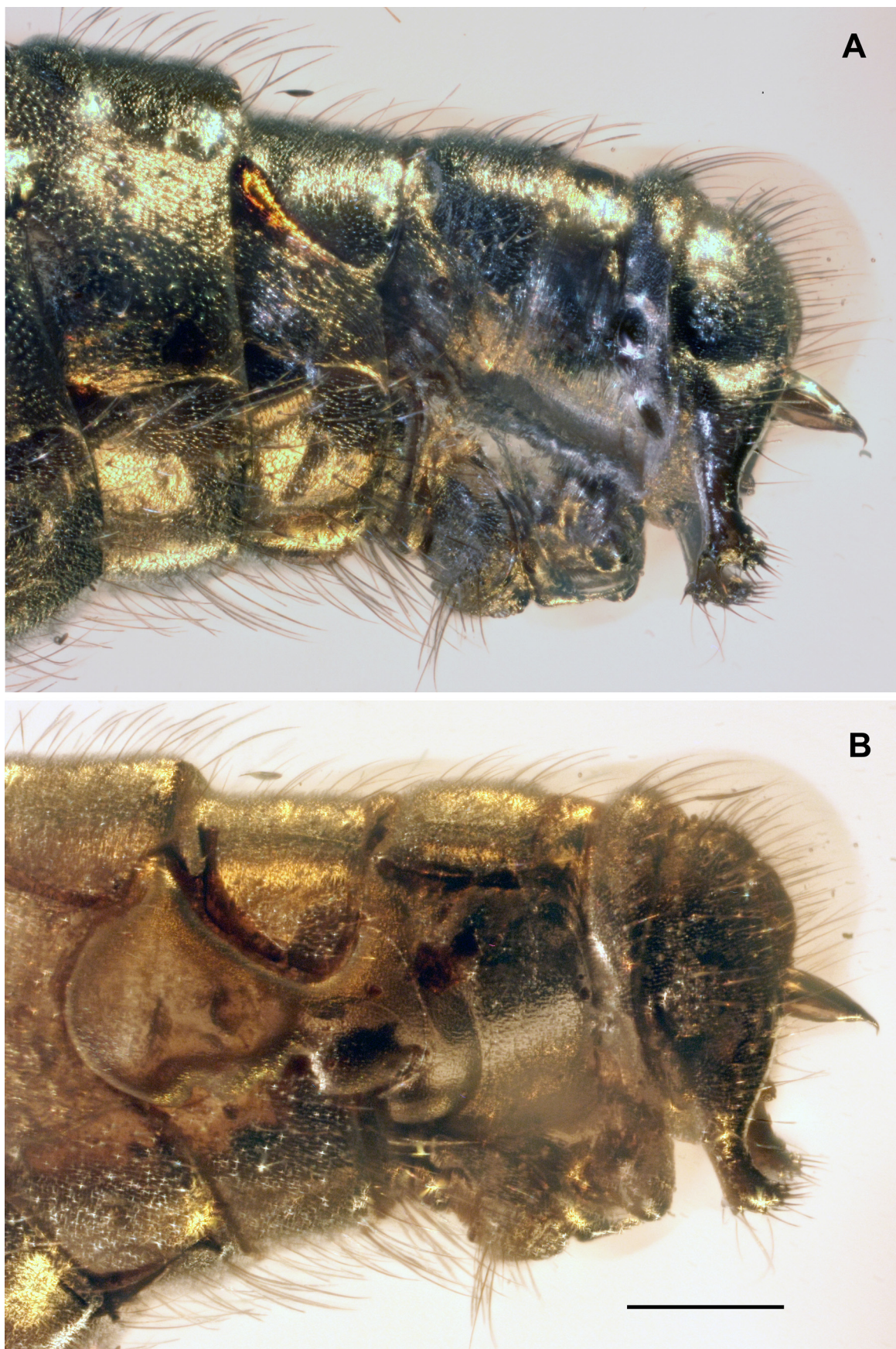


FIGURE 2. Apex of abdomen of *Prolachlanius resinatus* (Hagen in Pictet-Baraban et Hagen, 1856), neotype GPIH, no 4994 (coll. Gröhn, no. 7322). A, left lateral view; B, right lateral view (converted to left view). Scale bar = 0.2 mm (both to same scale).

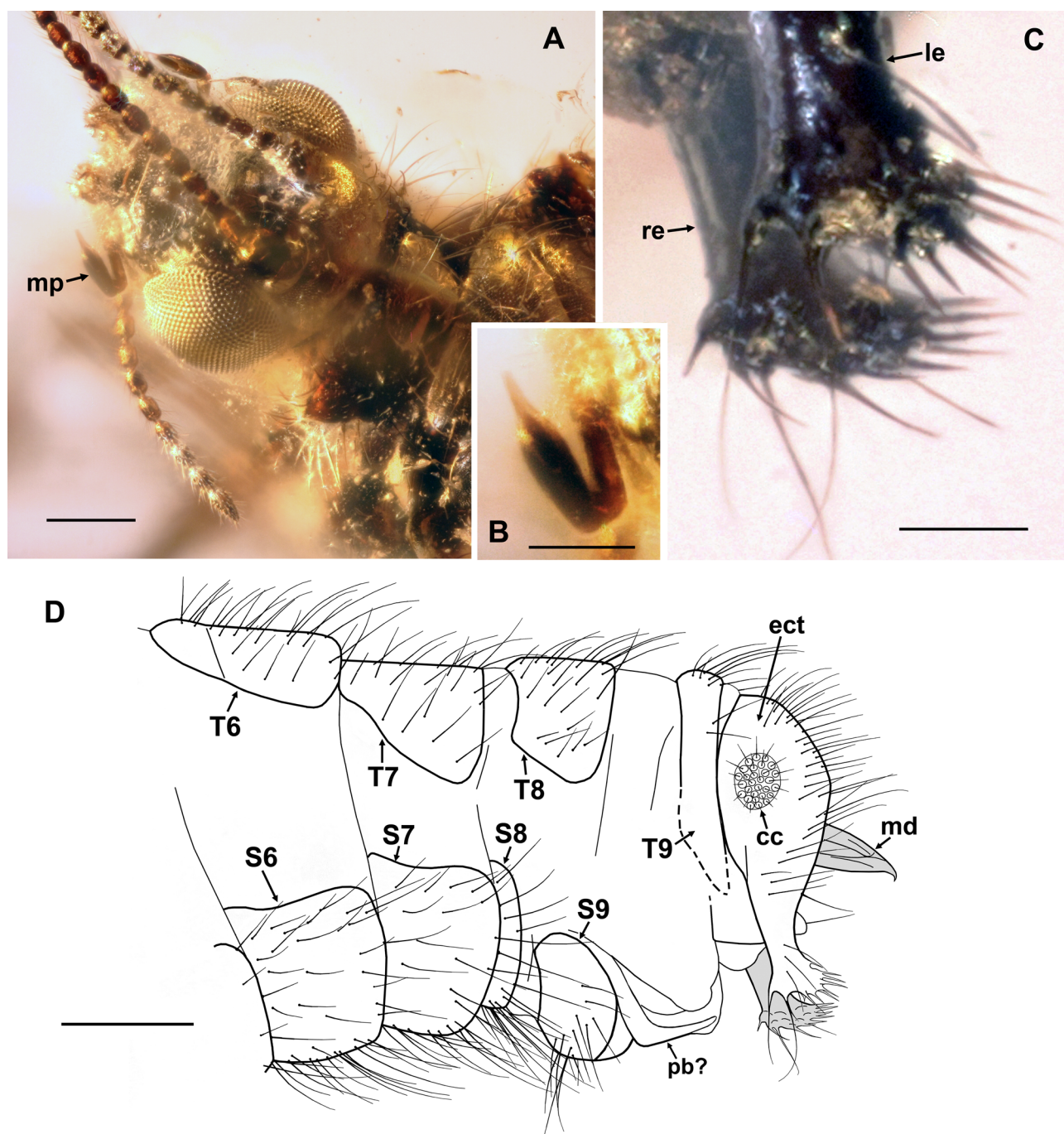


FIGURE 3. Details of *Prolachlanius resinatus* (Hagen in Pictet-Baraban et Hagen, 1856), neotype GPIH, no 4994 (coll. Gröhn, no. 7322). A, head and pronotum, dorsal view; B, left maxillary palpus; C, apices of ectoprocts, lateral view. D, line drawing of abdominal apex, lateral view. cc, callus cerci; ect, ectoproct; le, left ectoproct; md, mediuncus; mp, maxillary palpus; pb, parabaculum; re, right ectoproct; S6–S9, sixth to ninth sternites; T6–T9, sixth to ninth tergites. Scale bars = 0.2 mm (A, D), 0.1 mm (B), 0.05 mm (C).

Also, the difference in relative widths of the forewing of this species is probably at least partly explained by sexual dimorphism. In some species of other genera of Hemerobiidae, the forewing in the female is significantly narrower than that of males (Makarkin & Kholin 1995).

Wing venation and maculation are variable in *Prolachlanius resinatus*. Specimen GZG.BST.05240/5858 has notably atypical maculation for the species (see Fig. 4A). Some specimens have almost hyaline wings, although with distinct maculation, but a few have a darker, nearly single-colored membrane lacking distinct maculation (Fig. 7). Of these, specimen T079 is noteworthy by the absence of crossveins 4r-m, 4im and 4m-cu in the left forewing,

i.e., a condition characteristic of the genus *Symphorobius* (also see below). Its forewing is 4.6 mm long, i.e., slightly shorter than in more typical specimens. It is hard to decide if specimen T079 represents an atypical *Prolachlanius resinatus* or a new species.

Some venational aberrations should be mentioned. In one specimen from a private collection with typical maculation and otherwise typical venation, CuA has only one branch. In specimen GZG.BST.05238/5914 there are a number of anomalies, including MP being deeply forked at the third gradate series (Figs 4B, 5E).

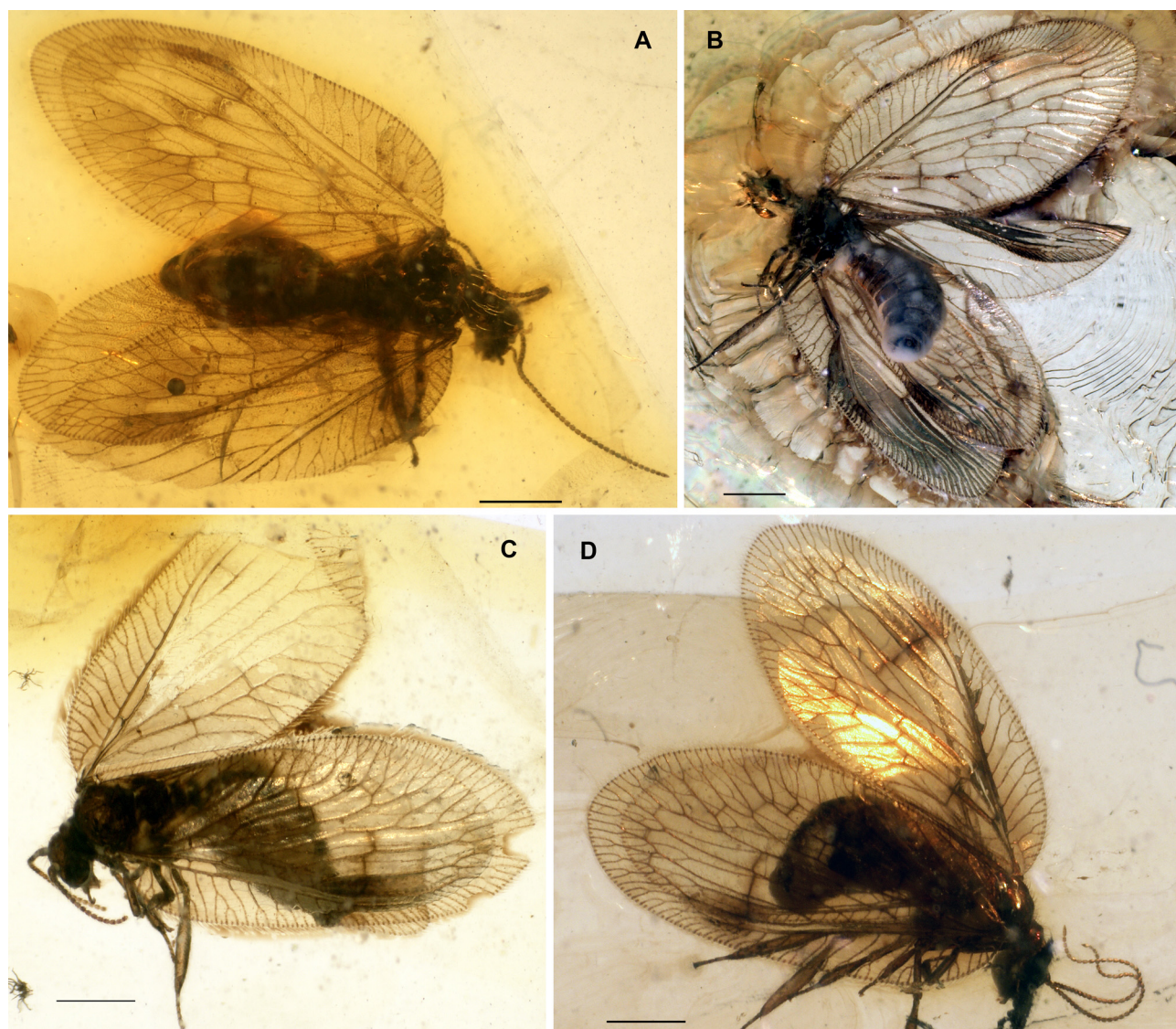


FIGURE 4. *Prolachlanius resinatus* (Hagen in Pictet-Baraban et Hagen, 1856) from Baltic amber. A, specimen GZG.BST.05240-5858, with atypical maculation; B, specimen GZG.BST.05241-5868 with anomalous deeply-forked forewing MP and additional crossveins; C, specimen GZG.BST.05238-5914; D, specimen GZG.BST.05242-5870. Scale bars = 1 mm.

The forewings of the Klesov specimen (Rovno amber) have generally very similar venation to those of most specimens from Baltic amber, but differ from these by [1] more reduced dark bordering of crossveins 3ra-rp, 3rp2-rp3 and 3rp1-rp2, [2] the loss of crossvein 4rp1-rp2, and [2] a greater number of distal subcostal crossveins (Fig. 6).

[1] The Klesov specimen is probably more similar to the holotype than it is to some other Baltic amber specimens by this character state; at least, Pictet-Baraban and Hagen (1856) and Krüger (1923) do not mention the crossveins having dark borders. Hagen wrote only that “wings are hyaline and some gradate crossveins are dark, in [the] pterostigma [there is a] brown-shaded spot” [Die Flügel sind wasserklar und einzelne Stufenadern dunkel, im Pterostigma ein brauner Schattenfleck] (p. 88), i.e., the holotype maculation is very similar to that of the Klesov specimen, but the membrane of both fore- and hind wings in the Klesov specimen and most Baltic amber specimens (including the neotype) are clearly slightly brownish.

[2] The loss of crossvein 4rp1-rp2 is most probably an anomaly as the loss of almost any crossvein may occur in individual extant hemerobiids.

[3] The presence of two to three distal subcostal crossveins in the Klesov specimen is noteworthy, although this is not a specific character state in this family. The number of these crossveins vary strongly within species of extant Hemerobiidae, e.g., there are one to six distal crossveins in *Micromus angulatus* (Stephens, 1836); two to eight in *Micromus dissimilis* (Nakahara, 1915); and two to three in *Hemerobius tristriatus* Kuwayama, 1954 (VM, pers. obs.). However, only one distal subcostal crossvein is present in all extant Sympherobiinae. At least, the presence of two or more is unknown to occur in any extant specimens of *Sympherobius*, even as an anomaly.

Therefore, character state [3] may have some taxonomic value. However, to evaluate how much value, it is necessary to study more specimens from Rovno amber.

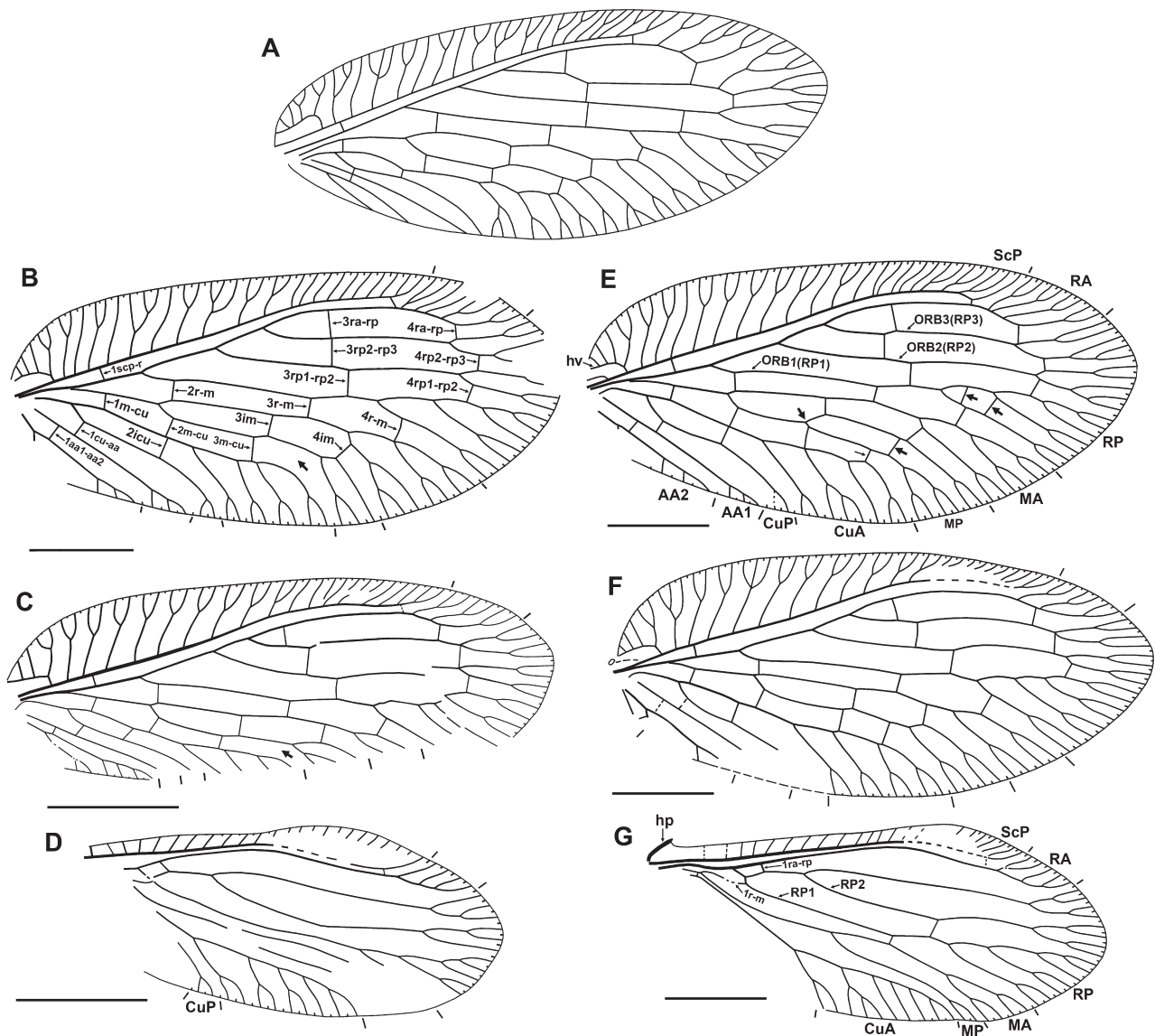


FIGURE 5. The forewing (A–C, E–F) and hind wing (D, G) venation of *Prolachlanius resinatus* (Hagen in Pictet-Baraban et Hagen, 1856). A, holotype, re-drawn from Pictet-Baraban and Hagen (1856) with corrections of Krüger (1923); B, specimen GZG.BST.05241-5868, left forewing, with venation most similar to that of the holotype; C, neotype GPIH, no 4994 (coll. Gröhn, no. 7322), right forewing; D, same, right hind wing; E, specimen GZG.BST.05238-5914; F, specimen GZG.BST.05240-5858, left forewing; G, same, left hind wing. Venational anomalies are shown by thicker arrows. All wings are shown in standard right view. Scale bars = 1 mm.

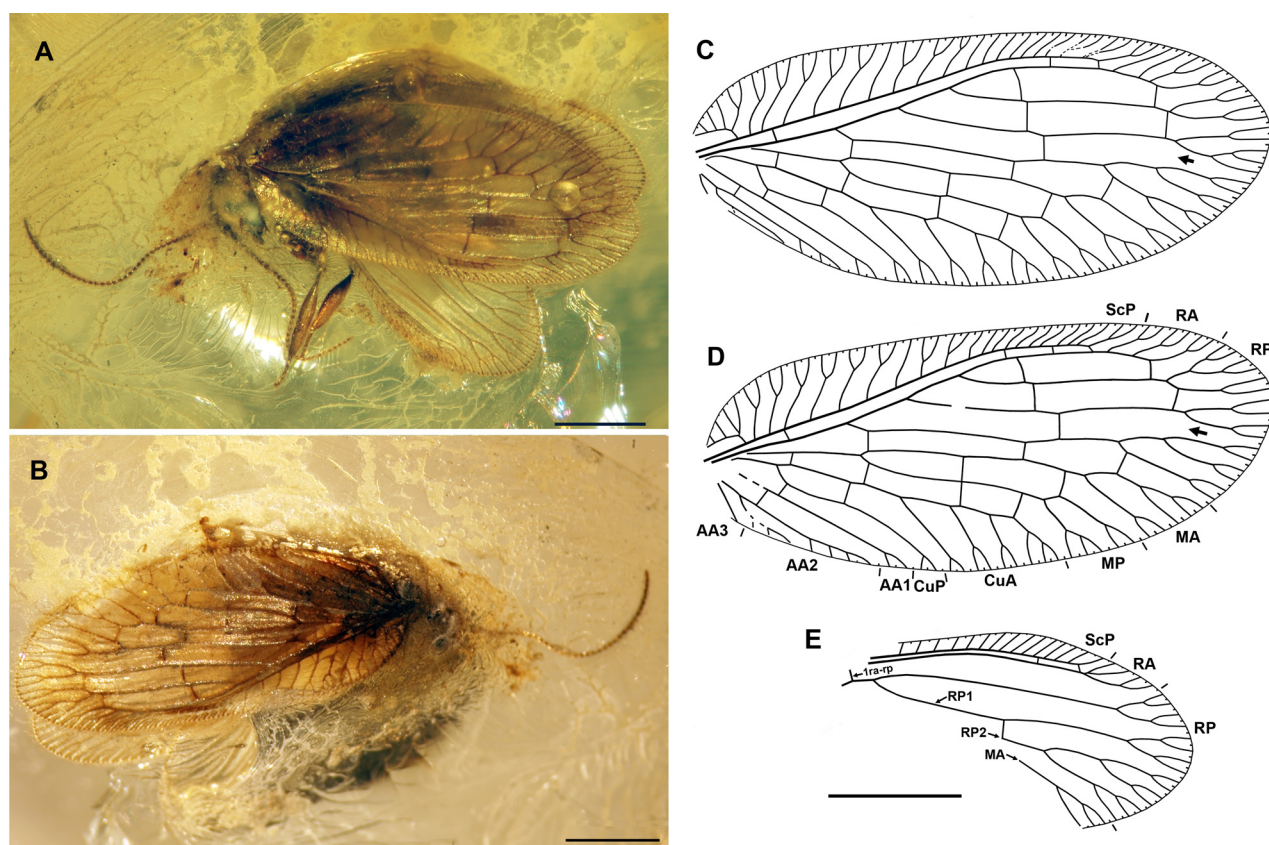


FIGURE 6. *Prolachlanius resinatus* (Hagen in Pictet-Baraban et Hagen, 1856), specimen SIZK K-6835 from Rovno amber. A, lateral left view; B, lateral right view; C, venation of the left forewing; D, venation of the right forewing; E, venation of the left hind wing. Venational anomalies are shown by thicker arrows. All wings are shown in standard right view. Scale bars = 1 mm (C–E to same scale).

The systematic position and validity of the genus *Prolachlanius*

Krüger (1923) assigned *Prolachlanius* to Sympherobiinae, which was confirmed by Makarkin *et al.* (2012). This subfamily comprises three extant genera (i.e., *Sympherobius* Banks, 1904, *Nomerobius* Navás, 1915 and *Neosympherobius* Kimmins, 1929), of which the former is also known from Baltic amber and Miocene Dominican amber (Oswald 1993; Engel & Grimaldi 2007; Makarkin & Wedmann 2009). Of the four synapomorphies of Sympherobiinae identified by Oswald (1993), two might be detected in fossil specimens, i.e., “forewing radiomedial crossvein 4r-m absent”, and “posteroventral angle of male 9th tergite produced as a narrow, membrane margined lobe” (p. 222). However, in the vast majority of known specimens of *Prolachlanius* (except one, see below) crossvein 4r-m is present, and the posteroventral lobe in the male ninth tergite is not developed, although the tergite is narrowed ventrally. Nevertheless, detailed examination of the venation of this genus indicate that it clearly belongs to the Sympherobiinae.

The outer series of gradate crossveins in the hind wing is lost in *Prolachlanius*. Such a condition occurs only in three subfamilies, Sympherobiinae, Notiobiellinae and Zachobiellinae according to Garzón-Orduña *et al.* (2016). In the notiobielline and zachobielline forewing, however, the intermediate subcostal crossvein is present and the outer series of gradate crossveins is absent, character states not found in any specimens of *Prolachlanius*. In general, the venation of *Prolachlanius* differs strongly from that of Notiobiellinae and Zachobiellinae by many other characters.

The genus *Prolachlanius* is most similar to *Sympherobius* with three ORBs (i.e., the *fuscescens* species group) in its size, wing venation, and in other characters such as its swollen hind tibiae. It is especially important that both genera occur in Baltic and Rovno ambers. Two species of the Baltic amber *Sympherobius* are typical representatives of the genus differing from extant species only by a different location of crossveins (see the diagnosis of

Sympherobius completus in Makarkin & Wedmann 2009). Two character states of the forewing distinguish these two genera: the presence of crossveins 4r-m, 4im and 4m-cu, and the ORB3 without branches in *Prolachlanius*. In *Sympherobius*, these crossveins are absent and ORB3 possess one long branch. However, these crossveins are absent in at least in one specimen of the putative *Prolachlanius resinatus* (Fig. 7). A photograph of this specimen was published by Kobbert (2005: Fig. on p. 105). It was considered by Makarkin *et al.* (2012) as an undescribed species of *Sympherobius*, probably of the *fuscescens* species group. We find now that the specimen actually belongs to *Prolachlanius*. It is unclear yet if the loss of these crossveins is an aberration (anomaly) or its common condition. If the latter, the only character state that distinguishes *Prolachlanius* from *Sympherobius* is the lack of branching of ORB3 in the forewing. However, this character state occurs very rarely in the extant *Sympherobius fuscescens* (Wallengren, 1863) as an anomaly (see Makarkin & Wedmann 2009: Fig. 5). Given that the genus *Sympherobius* is speciose, this anomaly in one species is not significant. Therefore, the normal forewing venation of *Prolachlanius* differs from that of *Sympherobius* by the presence of three crossveins (4r-m, 4im and 4m-cu), and the non-branched distal branch of RP (i.e., ORB3).



FIGURE 7. A specimen of the putative *Prolachlanius resinatus* (Hagen in Pictet-Baraban et Hagen, 1856) from Baltic amber, in which posterior crossveins in the outer gradate series of the left forewing are lost (private collection of Max J. Kobbert, no. T079). Scale bar = 1 mm.

The forewing venation of *Nomerobius* is in general similar to that of *Sympherobius* with two ORBs (both are deeply forked), but the crossvein 4m-cu is present (see Oswald 1990: Fig. 31; Oswald 1993: Fig. 66).

The forewing venation of *Neosympherobius* strongly differs from that of *Prolachlanius*, e.g., in the absence of gradate series of crossveins in the radial space and the pectinately branched distal ORB.

The hind venation of all these genera is essentially identical.

The male terminalia of *Prolachlanius* are strongly dissimilar to those of three genera of extant Sympherobiinae, especially by the structure of ectoproct, and the 8th and 9th sternites. Its ectoproct most resembles those of some *Megalomus* Rambur, 1842 from the other subfamily Megalominiinae in its shape and the presence of strong bristles or

spines at the apex, e.g., *M. tineoides* Rambur, 1842, *M. marginatus* Banks, 1910, *M. ricoi* Monserrat, 1997 (Makarkin 1986: Fig. 33; Monserrat 1997: Figs 60, 66).

The 9th sternite is long to very long in extant Sympherobiinae (Oswald 1993: Figs 69, 79, 86), whereas it is short in *Prolachlanius* and shifted proximally to a place that occupies the 8th sternite in other Sympherobiinae. The extremely short 8th sternite of *Prolachlanius* is noteworthy. Even if we assumed that some of its portion is hidden by the 7th sternite, this is the shortest 8th sternite known among Hemerobiidae.

The well-developed presumed mediuncus of *Prolachlanius* (=gonostyli 9 of Aspöck & Aspöck 2008) is somewhat similar to that of *Nomerobius* in lateral view (see Oswald 1990: Fig. 1). But the mediuncus of *Prolachlanius* appears to be unpaired, whereas that of *Nomerobius* is paired (however, this fossil does not allow observing the mediuncus from either dorsal or ventral views, so the possibility exists that it is paired). The mediuncus is lost in *Symphorobius* and *Neosymphorobius* (Oswald 1993). In these genera, there are no structures in the genitalia that might be interpreted to be this presumed mediuncus as in *Prolachlanius*.

The caudal part of the parabaculum is located near the ventral abdominal surface caudad the 9th sternite in *Nomerobius* (Oswald 1990: Fig. 1). We may reasonably assume that this is the same in *Prolachlanius* (Fig. 3D, pb?). In summary, *Prolachlanius* is certainly a distinct genus. Its venation is most similar to that of genera of the Sympherobiinae, differing from these by the presence of crossveins 4r-m and RP3 (ORB3) without branches. However, the genus is dissimilar to other genera of Sympherobiinae in the structure of genitalia, although these slightly resembles those of *Nomerobius*.

Nomenclature remarks

Initially, Pictet (1854) used the name “*Macropalpus* [sic] *elegans* Pict. et Ber.” for this species. The genus name should be considered an obvious lapsus calami, because the name *Mucropalpus* was previously used for this genus (Pictet 1846; without specific name) and again subsequently (Pictet-Baraban & Hagen, 1856). The name *Mucropalpus elegans* Pictet, 1854 is available, as it was accompanied by the short diagnosis: the genus and species is “characterized by the last article of the tarsus [should be ‘palpi’, probably a lapsus calami] being large and very sharp” (“caractérisé par le dernier article des tarses, gros et très pointu”, p. 378). Later, when describing *Hemerobius resinatus*, Hagen treated *Mucropalpus elegans* as its synonym (a name attributed to Berendt: “*Mucropalpus elegans*. Berendt”). Formally, the name *Mucropalpus elegans* Hagen in Pictet-Baraban et Hagen, 1856 is also available as it is accompanied by its own drawing (Pl. 7, Fig. 24), probably of Erichson (“stammt wohl von Erichson”: Krüger 1923, p. 89), with the caption “*Mucropalpus elegans*”. However, both available names (i.e., *Mucropalpus elegans* Pictet, 1854 and *Mucropalpus elegans* Hagen in Pictet-Baraban et Hagen, 1856) are invalid as these were preoccupied by the extant *Hemerobius* (= *Mucropalpus*) *elegans* Stephens, 1836.

It is now not possible to ascertain if these three species are based on the same specimen or not. At least, judging from the figure 24 in plate 7, *Mucropalpus elegans* Hagen in Pictet-Baraban et Hagen, 1856 is the same species as *Hemerobius resinatus*, and was even possibly based on the same specimen as the holotype of *Hemerobius resinatus* Hagen in Pictet-Baraban et Hagen, 1856.

Acknowledgments

We thank Mike Reich (Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany) and Max J. Kobbert (Münster, Germany) for providing photographs of Baltic amber hemerobiids and helpful information; Anatoly P. Vlaskin (SIZK) for cutting and polishing the Rovno piece; Christian Neumann (Museum für Naturkunde, Berlin, Germany) for information on the holotype of *Prolachlanius resinatus*; Jonas Damzen (Vilnius, Lithuania) for information on collecting locality of the neotype; S. Bruce Archibald (Simon Fraser University, Burnaby, Canada) for editing the English; Roy Bechemeyer (University of Kansas, Lawrence, USA), David Bowles (Missouri State University, USA), and an anonymous reviewer for providing valuable comments and recommendations.

References

- Aspöck, U. & Aspöck, H. (2008) Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). *Systematic Entomology*, 33, 97–127.
<https://doi.org/10.1111/j.1365-3113.2007.00396.x>
- Banks, N. (1904) A list of neuropteroid insects, exclusive of Odonata, from the vicinity of Washington, D.C. *Proceedings of the Entomological Society of Washington*, 6, 201–217.
- Banks, N. (1910) New South American neuropteroid insects. *Proceedings of the Entomological Society of Washington*, 12, 146–160.
- Berendt, G.C. (1830) *Die Insekten im Bernstein. Ein Beitrag zur Thiergeschichte der Vorwelt. Erstes Heft*. Auf Kosten des Verfassers, Nicolai in Commission, Danzig, 38 pp.
- Comstock, J.H. (1918) *The wings of insects: An exposition of the uniform terminology of the wing-veins of insects and a discussion of the more general characteristics of the wings of the several orders of insects*. Comstock Publishing Company, Ithaca, New York, ix + 430 pp.
<https://doi.org/10.5962/bhl.title.54605>
- Enderlein, G. (1910) Über die Beziehungen der fossilen Coniopterygiden zu den recenten und über *Archiconiocompsa prisca* nov. gen. nov. spec. *Zoologischer Anzeiger*, 35, 673–677.
- Engel, M.S. & Grimaldi, D. (2007) The Neuropterid fauna of Dominican and Mexican amber (Neuropterida: Megaloptera, Neuroptera). *American Museum Novitates*, 3587, 1–58.
[https://doi.org/10.1206/0003-0082\(2007\)3587\[1:TNFODA\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2007)3587[1:TNFODA]2.0.CO;2)
- Garzón-Orduña, I.J., Menchaca-Armenta, I., Contreras-Ramos, A., Liu, X.Y. & Winterton, S.L. (2016) The phylogeny of brown lacewings (Neuroptera: Hemeroibiidae) reveals multiple reductions in wing venation. *BMC Evolutionary Biology*, 16, 192.
<https://doi.org/10.1186/s12862-016-0746-5>
- ICZN (1999) *International Code of Zoological Nomenclature*. 4th edition. International Trust for Zoological Nomenclature, London, xxix + 305 pp.
- Janzen, J.-W. (2002) *Arthropods in Baltic amber*. Ampyx Verlag, Halle, 167 pp.
- Jepson, J.E., Penney, D. & Green, D.I. (2010) A new species of brown lacewing (Neuroptera: Hemeroibiidae) from Eocene Baltic amber. *Zootaxa*, 2692 (1)f, 61–68.
<https://doi.org/10.11646/zootaxa.2692.1.4>
- Kimmins, D.E. (1929) Some new and little known Argentine Neuroptera. *Revista de la Sociedad Entomológica Argentina*, 2, 187–192.
- Kobbert, M.J. (2005) *Bernstein—Fenster in die Urzeit*. Planet Poster Press, Göttingen, 224 pp.
- Krüger, L. (1922) Hemeroibiidae. Beiträge zu einer Monographie der Neuropteren-Familie der Hemeroibiiden. *Stettiner Entomologische Zeitung*, 83, 138–172.
- Krüger, L. (1923) Neuroptera succinica baltica. Die im baltischen Bernstein eingeschlossenen Neuroptera des Westpreussischen Provinzial-Museums (heute Museum für Naturkunde und Vorgeschichte) in Danzig. *Stettiner Entomologische Zeitung*, 84, 68–92.
- Kupryjanowicz, J. (2001) Arthropods in Baltic amber and their photographic record. In: Kosmowska-Ceranowicz, B. (Ed.), *The amber treasure trove. Part I. The Tadeusz Giecwicz's collection at the Museum of the Earth*. Polish Academy of Sciences, Warsaw, Warsaw, pp. 19–72.
- Kupryjanowicz, J. & Makarkin, V.N. (2008) *Archiconiocompsa prisca* Enderlein (Neuroptera: Coniopterygidae): The first neuropteran fossil in Rovno amber (Ukraine). *Entomologica Fennica*, 19, 25–31.
<https://doi.org/10.33338/ef.84410>
- Kuwayama, S. (1954) Neuroptera-Planipennia from the Daisetsuzan National Park, Hokkaido, Japan. *Insecta Matsumurana*, 18, 94–102.
- Latreille, P.A. (1802) *Histoire naturelle, générale et particulière des crustacés et des insectes*. Vol. 3. Dufart, Paris, 467 pp.
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tenth edition. Vol. 1. Holmiae, Salvii, 824 pp.
<https://doi.org/10.5962/bhl.title.542>
- Makarkin, V.N. (1986) Review of the lacewings of the family Hemeroibiidae (Neuroptera) of the fauna of the USSR. II. The genera *Wesmaelius* Krüger, *Symphorobius* Banks, *Psectra* Hagen, *Megalomus* Ramb., *Neuronema* MacLach. and *Drepanopteryx* Leach. *Entomologicheskoe Obozrenie*, 65 (3), 604–617. [in Russian]
- Makarkin, V.N. & Kholin, S.K. (1995) Sexual differences in relative length of forewing in Hemeroibiidae (Neuroptera). *Beiträge zur Entomologie*, 45, 421–425.
- Makarkin, V.N. & Perkovsky, E.E. (2009) *Rophalis relict*a Hagen (Neuroptera, Nevrothidae) in the Late Eocene Rovno amber, with a discussion of the taxonomic status of the genus. *Denisia*, 26, 137–144.
- Makarkin, V.N. & Wedmann, S. (2009) First record of the genus *Symphorobius* (Neuroptera: Hemeroibiidae) from Baltic amber. *Zootaxa*, 2078 (1), 55–62.
<https://doi.org/10.11646/zootaxa.2078.1.3>
- Makarkin, V.N., Wedmann, S. & Weiterschan, T. (2012) First record of a fossil larva of Hemeroibiidae (Neuroptera) from Baltic amber. *Zootaxa*, 3417 (1), 53–63.

<https://doi.org/10.11646/zootaxa.3417.1.3>

- Makarkin, V.N., Wedmann, S. & Weiterschan, T. (2016) A new genus of Hemerobiidae (Neuroptera) from Baltic amber, with a critical review of the Cenozoic *Megalomus*-like taxa and remarks on the wing venation variability of the family. *Zootaxa*, 4179 (3), 345–370.
<https://doi.org/10.11646/zootaxa.4179.3.2>
- Monserat, V.J. (1997) Revisión del género *Megalomus* de Latinoamérica (Neuroptera, Hemerobiidae). *Fragmenta Entomologica*, 29, 123–206.
- Nakahara, W. (1915) On the Hemerobiinae of Japan. *Annotationes Zoologicae Japonenses*, 9, 11–48.
- Navás, L. (1915) Neurópteros nuevos o poco conocidos (Sexta serie). *Memorias de la Real Academia de Ciencias y Artes de Barcelona*, Series 3, 12, 119–136.
- Oswald, J.D. (1990) Revision of the Neotropical brown lacewing genus *Nomerobius* (Neuroptera: Hemerobiidae). *Annals of the Entomological Society of America*, 83, 18–29.
<https://doi.org/10.1093/aesa/83.1.18>
- 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.
- Oswald, J.D. (2018) Neuropterida Species of the World. Available from: <http://lacewing.tamu.edu/SpeciesCatalog/Main> (accessed 28 April 2019)
- Perkovsky, E.E. & Makarkin, V.N. (2019) A new species of *Succinoraphidia* Aspöck & Aspöck, 2004 (Raphidioptera: Raphidiidae) from the late Eocene Rovno amber, with venation characteristics of the genus. *Zootaxa*, 4576 (3), 570–580.
<https://doi.org/10.11646/zootaxa.4576.3.9>
- Perkovsky, E.E., Zosimovich, V.Yu. & Vlaskin, A.P. (2010) Rovno amber. In: Penney, D. (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, pp. 116–136.
- Pictet, F.J. (1846) *Traité de Paléontologie ou histoire naturelle des animaux fossiles considérés dans leurs rapports zoologiques et géologiques. Vol. 4.* Langlois et Leclercq, Paris, xv + 458 pp.
- Pictet, F.J. (1854) *Traité de Paléontologie ou histoire naturelle des animaux fossiles considérés dans leurs rapports zoologiques et géologiques. 2nd Edition. Vol. 2.* J.-B. Baillière, Paris, 727 pp.
<https://doi.org/10.5962/bhl.title.13903>
- Pictet-Baraban, F.J. & Hagen, H.A. (1856) Die im Bernstein befindlichen Neuropteren der Vorwelt. In: *Die im Bernstein befindlichen organischen Reste der Vorwelt gesammelt, in Verbindung mit Mehreren bearbeitet und herausgegeben von Dr. Georg Carl Berendt. Bd 2. Abt. 2.* Nicolaische Buchhandlung, Berlin, pp. 41–125.
- Rambur, J.P. (1842) *Histoire Naturelle des Insectes, Névroptères*. Fain et Thunot, Paris, [xviii] + 534 pp.
- Scheven, J. (2004) *Bernstein-Einschlüsse: Eine untergegangene Welt bezeugt die Schöpfung. Erinnerungen an die Welt vor der Sintflut*. Kuratorium Lebendige Vorwelt, Hofheim a.T., 160 pp.
- Sokoloff, D.D., Ignatov, M.S., Remizowa, M.V., Nuraliev, M.S., Blagoderov, V., Garbout, A. & Perkovsky, E.E. (2018) A male flower of *Prunus* s.l. (Rosaceae) from Eocene Rovno amber (Ukraine). *Journal of Plant Research*, 131, 925–943.
<https://doi.org/10.1007/s10265-018-1057-2>
- Stephens, J.F. (1836) *Illustrations of British entomology; or, a synopsis of indigenous insects: containing their generic and specific distinctions; with an account of their metamorphoses, times of appearance, localities, food, economyMandibulata. Vol. 6.* Baldwin and Cradock, London, 240 pp.
- Wallengren, H.D.J. (1863) Bidrag till kännedomen af Sveriges Neuroptera. *Öfversigt af Kongl. Vetenskaps-Akademiens Forhandlingar*, 20, 15–26.
- Weitschat, W. & Wichard, W. (1998) *Atlas der Pflanzen und Tiere im Baltischen Bernstein*. Dr. Friedrich Pfeil Verlag, München, 256 pp.