



## 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

VLADIMIR N. MAKARKIN<sup>1,4</sup>, SONJA WEDMANN<sup>2</sup> & THOMAS WEITERSCHAN<sup>3</sup>

<sup>1</sup>*Institute of Biology and Soil Sciences, Far East Branch of the Russian Academy of Sciences, Vladivostok, 960022, Russia*

<sup>2</sup>*Senckenberg Research Institute, Messel Research Station, Markstr. 35, D-64409 Messel, Germany*

<sup>3</sup>*Forsteler Str.1, 64739 Höchst im Odenwald, Germany*

<sup>4</sup>*Corresponding author. E-mail: vnmakarkin@mail.ru*

### Abstract

A new genus and two new species of Hemerobiidae (Neuroptera) are described from the late Eocene Baltic amber, i.e., *Proneuronema gradatum* **gen. et sp. nov.** and *P. minor* **gen. et sp. nov.** Several Early Eocene species (mostly unnamed) from Europe and North America are also considered to belong to this genus, including *Proneuronema wehri* (Makarkin *et al.*, 2003), **comb. nov.** The new genus is probably most closely related to the extant genus *Neuronema* McLachlan, 1869, and therefore assigned to Drepanopteryginae. A critical review of Cenozoic taxa of the *Megalomus*-like hemerobiids is provided. *Prophlebonema* Krüger, 1923 is considered as a new subjective synonym of *Drepanopteryx* Leach, 1815. *Plesiorobius* Klimaszewski et Kevan, 1986 from the Late Cretaceous is considered as belonging to Hemerobiidae. It is noted that wing venation variability in species of Hemerobiidae (including these fossils) is high. Some of their venational abnormalities (anomalies) may have phylogenetic implications.

**Key words:** Megalominae, Drepanopteryginae, Baltic amber, Eocene

### Introduction

The cosmopolitan family Hemerobiidae is rather speciose, comprising ca. 520 extant valid species (excluding *nomen dubium* and *nomen oblitum*) in 27 genera (Oswald 2015). Interestingly, 25 years ago the family was estimated to include ca. 550 extant species (Monserrat 1990; Oswald, 1993), although since then many new species have been described. This seeming paradox is explained mainly by the synonymization of many old species. Judging from the relative low rate of description of new hemerobiid species, it is unlikely that their total number will exceed 600.

The fossil record of Hemerobiidae is generally rather rich, especially from the Cenozoic. Hitherto however, only three species have been described from the Mesozoic, one from the Late Jurassic of Karatau, Kazakhstan, and two from the Early Cretaceous of England and Mongolia (Panfilov 1980; Ponomarenko 1992; Jepson *et al.* 2012). Additionally, the Late Cretaceous genus *Plesiorobius* Klimaszewski et Kevan, 1986 is now considered to belong to Hemerobiidae (Makarkin 2016; see below for details). Also, two undescribed taxa are known from the earliest Cenomanian Burmese amber and the Turonian New Jersey amber (*pers. obs.*).

Of the Cenozoic hemerobiids, 17 named species have been described from the Eocene to the Miocene: thirteen from Eurasia including Baltic amber (Pictet-Baraban & Hagen 1856; Henriksen 1922; Krüger 1923; Jarzembowski 1980; Makarkin 1991; Makarkin & Wedmann 2009; Jepson *et al.* 2010), and four from the New World (Scudder 1878, 1890; Oswald 2000; Makarkin *et al.* 2003). Many Cenozoic hemerobiids have only been reported, illustrated, or described but not named (e.g., Illies 1941; Larsson 1975; Zherikhin 1978; Nel 1991; Poinar 1992; Ansoerge 1997a; Poinar & Poinar 1999; Rust 1999a,b; Engel & Grimaldi 2007; Obst & Ansoerge 2012; Wang *et al.* 2014).

Hemerobiidae occur quite often in Baltic amber, and five species belonging to four genera and one larva have

been described from there: *Prolachlanius resinatus* Hagen in Pictet et Hagen, 1856, *Prospadobius moestus* Hagen in Pictet et Hagen, 1856, *Prophlebonema resinatum* (Krüger, 1922), *Symphorobius completus* Makarkin et Wedmann, 2009, *S. siriae* Jepson *et al.* 2010, and a larva presumably belonging to *Prolachlanius resinatus* (Makarkin *et al.* 2012). Of these, the genus *Prophlebonema* Krüger, 1923 is here considered as a new subjective synonym of *Drepanepteryx* Leach, 1815, and therefore its single species is now *Drepanepteryx resinata* (Krüger, 1922), **nov. comb.** (see below for details). Many Baltic amber hemerobiids were only illustrated (e.g., Weitschat & Wichard 1998, 2002; Erichson & Weitschat 2000; Kupryjanowicz 2001; Janzen 2002; Scheven 2004; Kobbert 2005; Weitschat 2009).

In this paper, we describe a new genus with two new species from Baltic amber belonging to the subfamily Drepanepteryginae. Also, we critically review Cenozoic taxa of the *Megalomus*-like hemerobiids, and briefly analyze the wing venation variability in the family.

## Material and methods

Five Baltic amber hemerobiid specimens were examined. Of these, one examined amber piece (i.e., GZG.BST.05246) is from the famous amber collection of Geologisch-Päleontologische Institute der Albertus-Universität in Königsberg, a small part of which is now deposited in GZG.

Line drawings were prepared by Thomas Weiterschan and Sonja Wedmann. 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 X64.

The venational terminology in general follows Kukalová-Peck & Lawrence (2004) as interpreted by Yang *et al.* (2012b, 2014). Terminology of wing spaces and details of venation (e.g., veinlets, traces, ‘oblique radial branches’ (“ORB”) concept) follows Oswald (1993). 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; icu, crossvein between CuA and CuP (see details in Makarkin & Wedmann 2009).

Abbreviations: AA1–AA3, first to third anterior anal vein; CuA, anterior cubitus; CuA1, proximal-most branch of CuA; CuP, posterior cubitus; hv, humeral veinlet; hp, humeral plate; jl, jugal lobe; MA and MP, anterior and posterior branches of media; ORB1, ORB2, ORB3, first to third oblique radial branches; RA, anterior radius; RP, posterior sector; ScA, subcosta anterior; ScP, subcosta posterior.

Institutional abbreviations: GZG, Geowissenschaftliches Zentrum der Universität Göttingen [=Geoscience Centre of the University of Göttingen], Germany; SMF, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Frankfurt am Main, Germany.

## Systematic paleontology

### Class Insecta Linnaeus, 1758

### Order Neuroptera Linnaeus, 1758

### Family Hemerobiidae Leach, 1915

### Subfamily Drepanepteryginae Krüger, 1922

### Genus *Proneuronema* gen. nov.

**Type species.** *Proneuronema minor* sp. nov.

**Diagnosis.** May be distinguished from other hemerobiid genera by a combination of the following character states: in forewing, [1] ScP and RA separate distally; [2] at least four subcostal crossveins; [3] additional pre-3ra-rp [=pre-3ir1] crossveins absent; [4] crossveins proximad third gradate series between RP branches absent; [5] two to three ORBs; [6] distal-most ORB strongly pectinate; [7] ORB1 pectinate, with anteriorly-directed branches; [8]

branches of CuA very long; [9] crossveins between branches of CuA continue in outer (fourth) gradate series; in hind wing, [10] basal 1r-m crossvein entering RP slightly distad origin of RP1; [11] two to four crossveins in second gradate series.

**Species included.** *Proneuronema wehri* (Makarkin *et al.*, 2003), **comb. nov.**, from the early Eocene of North America; *P. gradatum* **sp. nov.**, and *P. minor* **sp. nov.** from the late Eocene Baltic amber.

**Etymology.** From the Greek *pro*, before, and *Neuronema*, a genus-group name, in reference to the most closely related extant genus. Gender neuter (ICZN, Article 30.1.2).

**Remarks.** The new genus is most closely related to the extant Asian genus *Neuronema* McLachlan, 1869, based on the similarity of the male and female terminalia and wing venation (see below for details).

The early Eocene '*Cretomerobius*' *wehri* Makarkin *et al.*, 2003 from the North America Okanagan Highlands (Republic locality) probably belongs to this new genus. Its assignment to *Cretomerobius* was erroneous. All the forewing diagnostic character states are present in this species, except character state #4. However, this latter might be intraspecific variability as in one additional specimen of this or a closely related species the crossveins proximad third gradate series between RP branches are also absent (i.e., character state #4 is present) (S.B. Archibald, pers. comm.). Therefore, we assign the species to this genus, as *Proneuronema wehri* (Makarkin *et al.*, 2003), **comb. nov.**, the venation of which is most similar to that of *P. gradatum* **sp. nov.**

Some unnamed hemerobiid specimens reported from the early Eocene of Europe belong to this new genus. The majority of these are from the Mo-clay of Denmark, most are probably from the Fur Formation (Henriksen 1922: Fig. 5; Larsson 1975: Fig. 6; Rust 1999b: Fig. 81, Pl. 24b,c), and one each from Havighorst (Illies 1941: Fig. 4) and Greifswalder Oie Island (Obst & Ansoerge 2012: Fig. 10), both in northern Germany. In general, hemerobiids from the Mo-clay are numerous (perhaps 400–500 specimens: Ansoerge 1997b; Rust 1999a), but only these few have been described or figured. Also, hemerobiids are quite common in the Greifswalder Oie deposits, and these are mainly conspecific with the Danish Mo-clay species (J. Ansoerge, pers. comm.). The venation of all these figured early Eocene members of *Proneuronema* **gen. nov.** is clearly more similar to *P. minor* **sp. nov.** than to *P. gradatum* **sp. nov.**

### ***Proneuronema minor* sp. nov.**

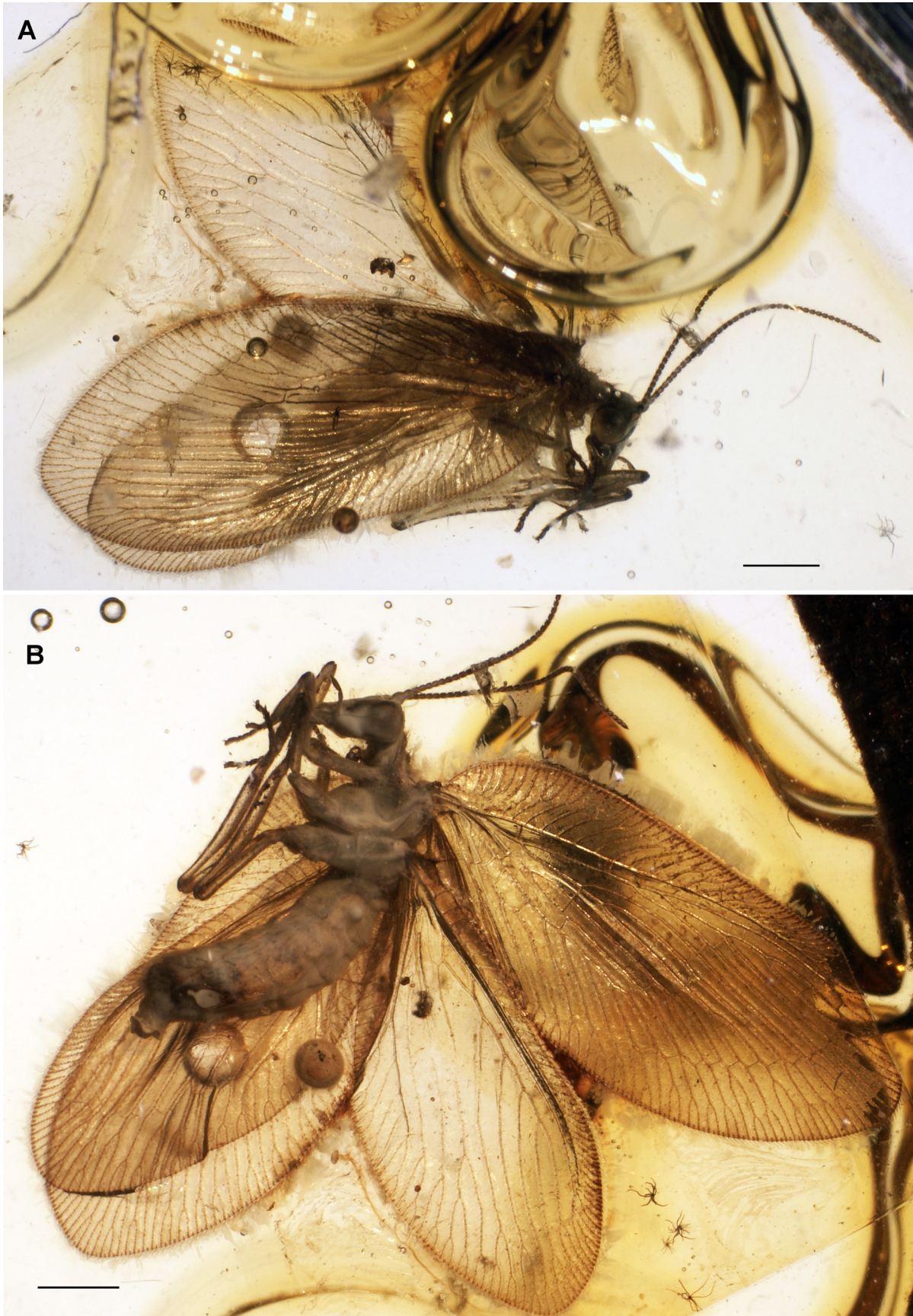
(Figs. 1–6)

**Diagnosis.** May be distinguished from other species by the following characters: crossveins in costal space in forewing absent [at least four costal crossveins in other species]; M only once forked proximad third gradate series [two to three times in other species]; distinct color pattern in forewing absent [present in *P. wehri*; at least a dark band through outer gradate series in *P. gradatum* sp. nov.]; comparatively small size [forewing length 6.3–6.9 mm; 7.9–9.5 mm in *P. gradatum* sp. nov., 9 mm in *P. wehri*].

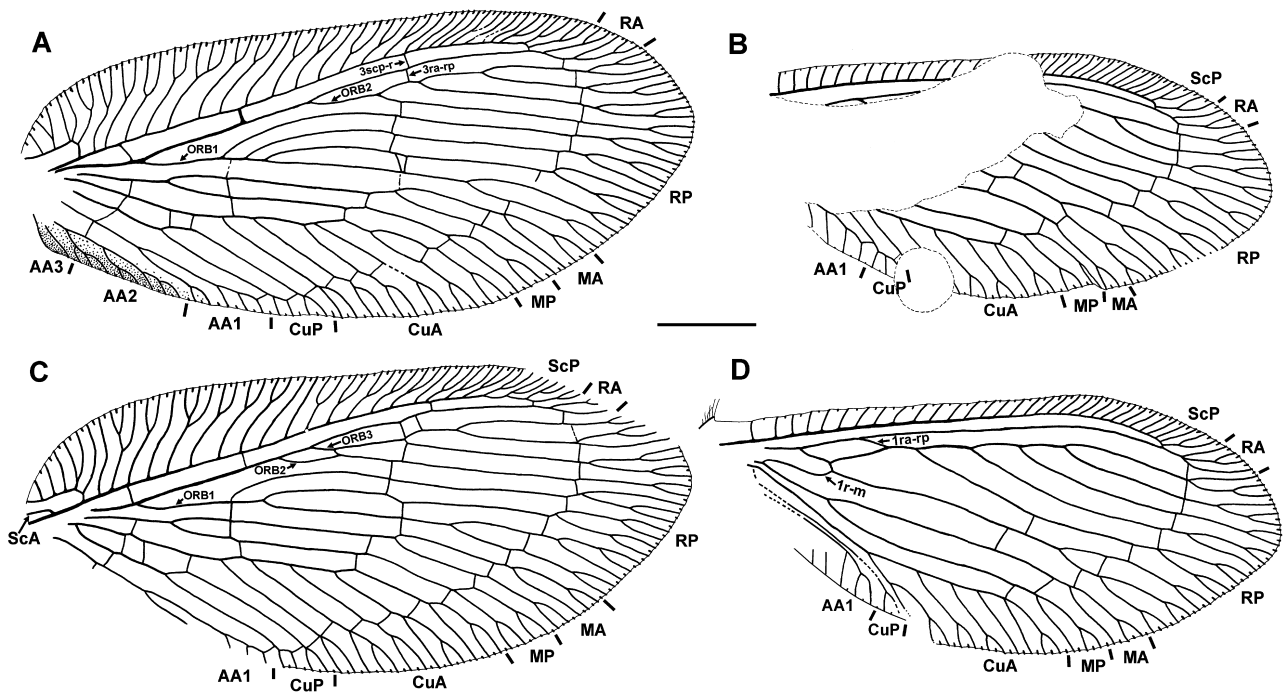
**Description.** *Holotype* GZG.BST.05246 (Figs 1–3). Female. Body length 5.2 mm as preserved. Head cuneiform in lateral view. Eyes relatively large. Vertex slightly elevated. Postocular lobe narrow. Terminal segment of maxillary palps rather broad, without additional subsegment. Antennae: scapus rather large; pedicel markedly larger than proximal flagellomeres; both flagella 40-segmented. Pronotum rather short, covered with dense long setae. Procoxa very long. Metatibia about 1.7 times as long as metafemur, slightly curved and thinner proximally, not especially swollen medially. Two small apical tibial spurs present in each leg.

Abdomen completely visible in left lateral view, but mostly obscured by milky covering. Female terminalia typical for *Megalomus*-like genera, but indistinctly visible: 7th tergite, 7th sternite long, not specialized; 8th tergite probably rather narrow, extending laterally to 7th sternite; 8th sternite not visible (probably transformed to subgenitale); 9th tergite extending laterally to ventral part of abdomen; ventrally it is strongly dilated; gonocoxite 9 almost entirely hidden, but its gonostylus faintly visible; upper part of 9th tergite and ectoproct almost entirely obscured by milky covering and strange flower-like structure (Fig. 3A, '?'); probably, this structure does not belong to the body.

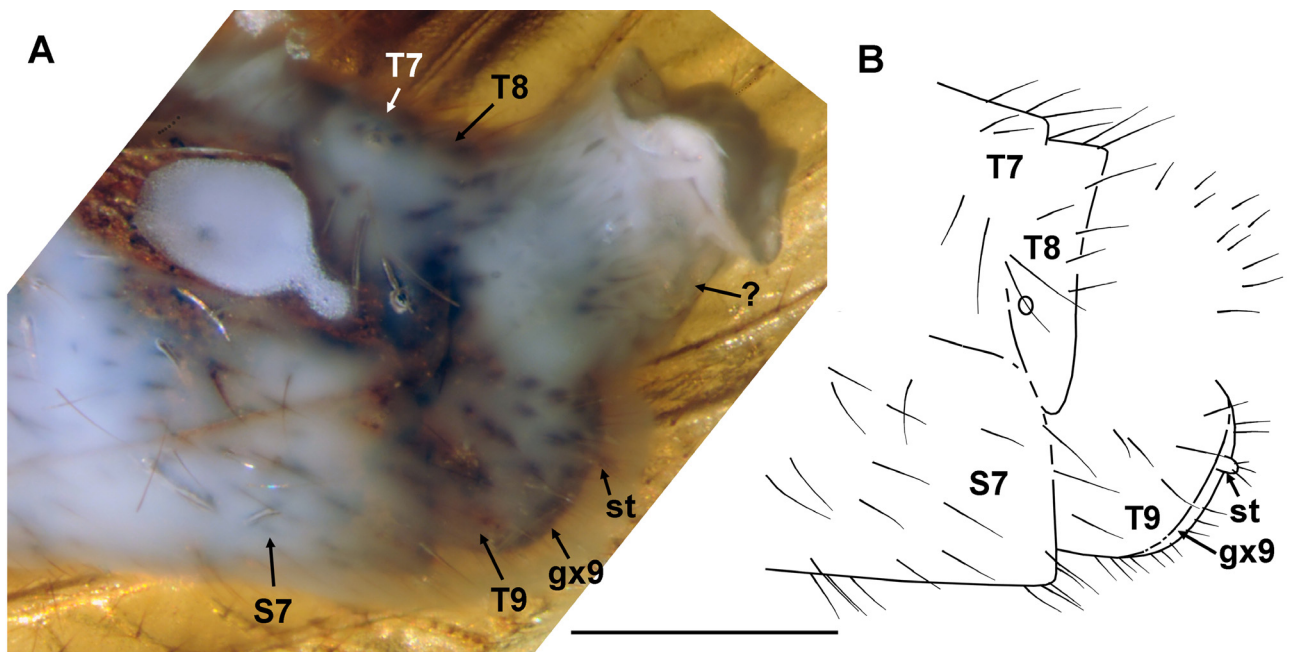
Forewing oval with subacute apex, 6.9 mm long, 3.0 mm wide. Trichosors prominent all around wing margin. Costal space very broad, dilated basally (0.8 mm maximum width). Majority of subcostal veinlets branched once or twice. Humeral veinlet recurrent, pectinately branched, with five branches (one to two forked). Presumable ScA distinct. No true crossveins in costal space. Subcostal space moderately wide for entire length, with four crossveins (basal 1scp-r, intermediate 2scp-r, 3scp-r, distal 4scp-r). Posterior trace of RA forked apically, with two distal



**FIGURE 1.** *Proneuronema minor* gen. et sp. nov., holotype GZGBST.05246, lateral view. A, right side. B, left side. Scale bars = 1 mm.



**FIGURE 2.** *Proneuronema minor* gen. et sp. nov., wing venation of the holotype GZG.BST.05246. A, right forewing. B, right hind wing. C, left forewing. D, left hind wing (C, D converted to standard right dorsal view). Scale bar = 1 mm (all to scale).



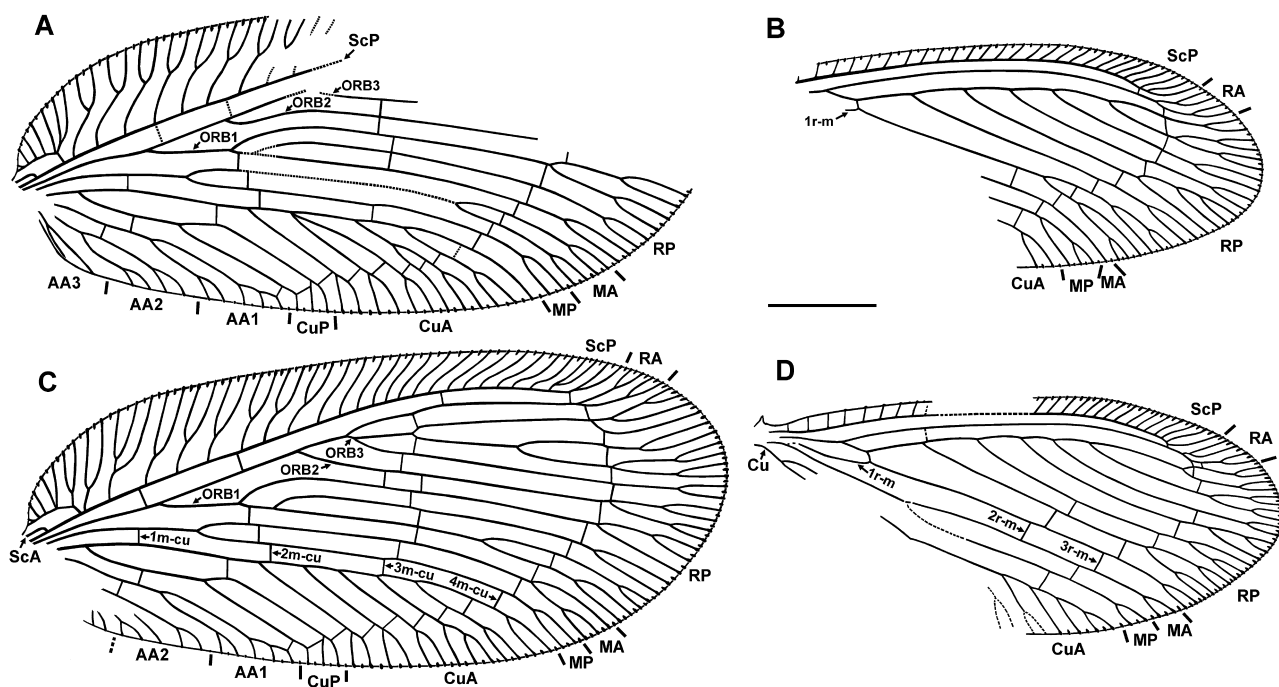
**FIGURE 3.** *Proneuronema minor* gen. et sp. nov., holotype GZG.BST.05246, apex of female abdomen. A, photograph. B, line drawing. gx9, gonocoxite 9; S7, 7th sternite; st, gonostylus of gonocoxite 9; T7, T8, T9, 7th to 9th tergites. Scale bar = 0.5 mm.

branches, one of them forked once, the other simple. RA space as wide as subcostal space basally. RP with two (left forewing) or three (right forewing) ORBs. ORB1 with two (right wing) or three (left wing) branches directed anteriorly, originating proximad third gradate series of crossveins. ORB2 (left forewing) simple. ORB3 (left forewing) or ORB2 (right forewing) (RP proper) possesses two (left wing) or three (right wing) branches, originating proximad fourth gradate series. M appears not fused basally with R. M forked proximal to second gradate series; MA, MP parallel before terminal branching. Cu dividing into CuA, CuP close to wing base. CuA pectinately branched, with five branches, all of which have marginal forks. CuP deeply forked, each branch with

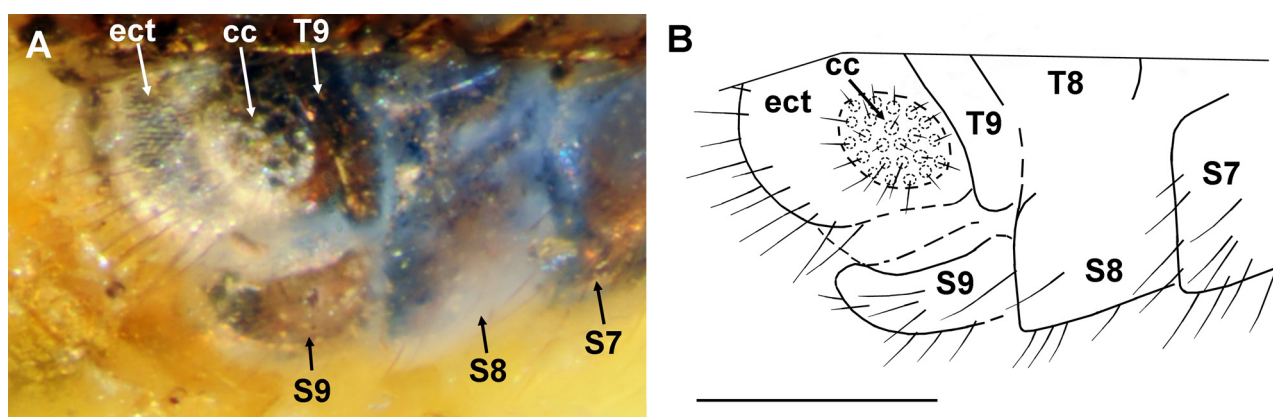
marginal fork. 1AA deeply forked, anterior branch with two short simple pectinate branches; posterior branch only with marginal fork. 2AA pectinately branched. 3AA probably simple (not clearly visible). Four gradate series of crossveins (series 1–4 of Oswald 1993) posterior to RA. First series consists of four crossveins: 1m-cu, 1cu-a1, 1a1-a2; an additional (aberrant) crossvein located distad 1cu (present in right forewing only). Second series includes four crossveins: 2r-m, 2im, 2m-cu, 2icu; an additional (aberrant) crossvein located basad 2icu (present in left forewing only). Third ('inner') series with eight crossveins, from 3ra-rp to 3m-cu; 3ra-rp (left forewing) and 2irp (right forewing) aberrantly doubled. Fourth ('outer') series complete, with 21 (right forewing) and 19 (left forewing) crossveins, from 4ra-rp to 4cu-a1. All longitudinal veins relatively pale. Membrane slightly fuscous, no pattern.



**FIGURE 4.** *Proneuronema minor* gen. et sp. nov., specimen SMF Be 2535 as preserved. A, right side. B, left side. Scale bar = 3 mm (both to scale).



**FIGURE 5.** *Proneuronema minor* gen. et sp. nov., wing venation of the specimen SMF Be 2535. A, right forewing. B, right hind wing. C, left forewing. D, left hind wing (C, D converted to standard right dorsal view). Scale bar = 1 mm (all to scale).



**FIGURE 6.** *Proneuronema minor* gen. et sp. nov., apex of abdomen of the male specimen SMF Be 2535 (lateral view). A, photograph. B, line drawing. cc, callus cerci; ect, ectoproct; S7, S8, S9, 7th to 9th sternites; T8, T9, 8th and 9th tergites. Scale bar = 0.3 mm.

Hind wing 5.9 mm long as preserved (estimated length 6.1 mm), 2.6 mm wide. Trichosors prominent all around wing margin. Costal space narrow, slightly dilated distally, 31 simple veinlets, one distal-most forked. Humeral lobe triangular. Humeral plate bears long, dense bristles. Only distal subcostal crossvein detected. RA distally with three veinlets (one-two forked). RA space proximally only slightly dilated, narrowest at crossvein 1r1-rs, which is strongly oblique. RP with five (left wing) to six (right wing) branches before outer gradate series, one of them originating before 1ra-rp. Basal sinuous crossvein 1r-m connecting RP1 and M. M forked distad origin of RP1; MA, MP nearly parallel before outer gradate series, then both forked. CuA pectinate, with five branches; proximal-most branch of CuA forked twice; most of other branches with marginal fork. CuP thin, with two short branches (right wing). AA1 pectinate. Second (inner) gradate series includes two crossveins (between RP2, MA); third (outer) series with 10 crossveins (from RA to CuA). One marginal crossvein between CuA, CuP, and one between CuP, AA1. All longitudinal veins relatively pale. Membrane paler than in forewing; no pattern.

*Specimen* SMF Be 2535 (Figs 4–6). Male. Head cuneiform in lateral view. Eyes relatively large. Postocular lobe narrow. Terminal segment of maxillary palps rather broad, without additional subsegment. Scapus rather large.

Metatibia about 1.5 times as long as metafemur, slightly curved and thinner proximally, markedly swollen medially. Apical tibial spurs small. Male abdominal terminalia: 8th sternite long, unspecialized; 9th tergite narrow, extending laterally almost to 9th sternite; 9th sternite long and rather narrow (boat-like), extending caudally to level of outer margin of ectoproct; ectoproct in general rounded, appears slightly concave ventrally (poorly visible), with long setae and large rounded callus cerci (Fig. 6); outer, ventral margins of ectoproct without visible processes.

Forewing oval with rounded apex, 6.3 mm long, 2.9 mm wide. Trichosors prominent all around wing margin. Costal space very broad, dilated basally. Eight proximal and one distal-most subcostal veinlets forked; 14 distal subcostal veinlets simple. Humeral veinlet recurrent, pectinately branched, with six branches (of these one forked). Presumable ScA short. No crossveins in costal space. Subcostal space moderately broad for entire length, with four crossveins (basal 1scp-r, intermediate 2scp-r, 3scp-r, distal 4scp-r). RA forked apically; its two branches once forked. RA space as wide as subcostal space basally. RP consists of three ORBs. ORB1 twice deeply forked, originating far proximad third gradate series, with branches directed anteriorly. ORB2 simple for most length, distally dichotomously branched. ORB3 (RP proper) originating relatively far from wing base, with three branches originating proximad fourth gradate series in left forewing; second branch rather deeply dichotomously branched. M basally not fused with R, forked distad origin of ORB1. MA, MP parallel before terminal branching. Cu dividing into CuA, CuP close to wing base. CuA pectinately branched, with five forked branches; in right wing, two branches touching each other at their origin, and one other branch deeply forked. CuP rather deeply forked; anterior branch with marginal fork, posterior branch simple. AA1 rather deeply forked; anterior branch with two short simple pectinate branches; posterior branch with marginal fork. AA2 rather deeply forked; each branch with marginal fork (right wing). AA3 short, deeply forked; each branch simple (right wing). Four gradate series of crossveins posterior to RA. First (basal) series consists of three crossveins: 1m-cu, 1cu-aa1, 1aa1-aa2. Second series consists of four crossveins: 2r-m, 2im, 2m-cu, 2icu. Third ('inner') series consists of nine crossveins (left wing), from RA to CuA; 3rp1-rp2 aberrantly doubled. Fourth ('outer') series complete, with 20 crossveins (left wing), from RA to AA1. No color pattern.

Hind wing 5.0 mm long, 2.2 mm wide as preserved (left wing). Trichosors prominent along all preserved wing margin. Costal space narrow, somewhat dilated distally, with all subcostal veinlets simple. Only one (distal) subcostal crossvein detected. RA distally dichotomously branched. RA space slightly wider than subcostal space; crossvein 1ra-rp not detected in right wing, indistinct in left. Six (right wing) to seven (left wing) branches of RP before outer gradate series. Basal sinuous crossvein 1r-m long, connecting RP1 and M. M forked probably much distad origin of RP1; MA, MP nearly parallel for most length; MA simple (right wing) and with terminal fork (left wing); MP once (left wing) and twice (right wing) forked distally. Cu dividing into CuA, CuP near wing base. CuA pectinate, with four distal branches preserved. CuP, anal veins poorly visible. Second ('inner') gradate series consists of three crossveins (from RP3 to MA) in left wing; poorly preserved in right wing (only one clearly visible). Third ('outer') with 11 preserved crossveins (from RA to CuA) in right wing, 10 crossveins in left wing (4ra-rp abnormally doubled).

**Material.** Holotype GZG.BST.05246, deposited in GZG. Old labels: "B[ernstein] S[ammlung] d[er] Univers[it]at Koenigsberg i[n] Pr[eu]ssen."; N 19"; "5238" "5864". A complete female specimen (but apical tip of one of the forewings is missing); left body side is obscured by a milky covering.

Specimen No. SMF Be 2535, deposited in SMF (formerly in the private collection of Thomas Weitzsch, coll. No. 1655). An almost complete male specimen (distal part of right forewing is missing); the body is partially obscured by a milky covering.

**Type locality and horizon.** Baltic amber (the holotype was probably collected near present-day Kaliningrad; precise collecting site of specimen SMF Be 2535 is unknown); late Eocene.

**Etymology.** From the Latin *parvus* [-a, -um] (comparative *minor*), small (smaller), in reference to its smaller size compared to other species of the genus.

**Remarks.** These two specimens have a very similar venation (considering its variability) but differ in particular by the shape and relative length of the metatibia. The absence of the crossvein 1ra-rp in the hind wing as found in SMF Be 2535 occurs as an anomaly also in a specimen of *M. flinti* (see Monserrat 1997: Fig. 104).

The venation of a specimen of Hemerobiidae from Baltic amber (the forewing is about 6 mm long) reported by Erichson & Weitzsch (2000: Fig. 45) is similar to that of *Proneuronema minor* **sp. nov.** However, its forewing appears darker, and third and fourth gradate series of crossveins appear to be margined with dark brown.

***Proneuronema gradatum* sp. nov.**

(Figs 7–12)

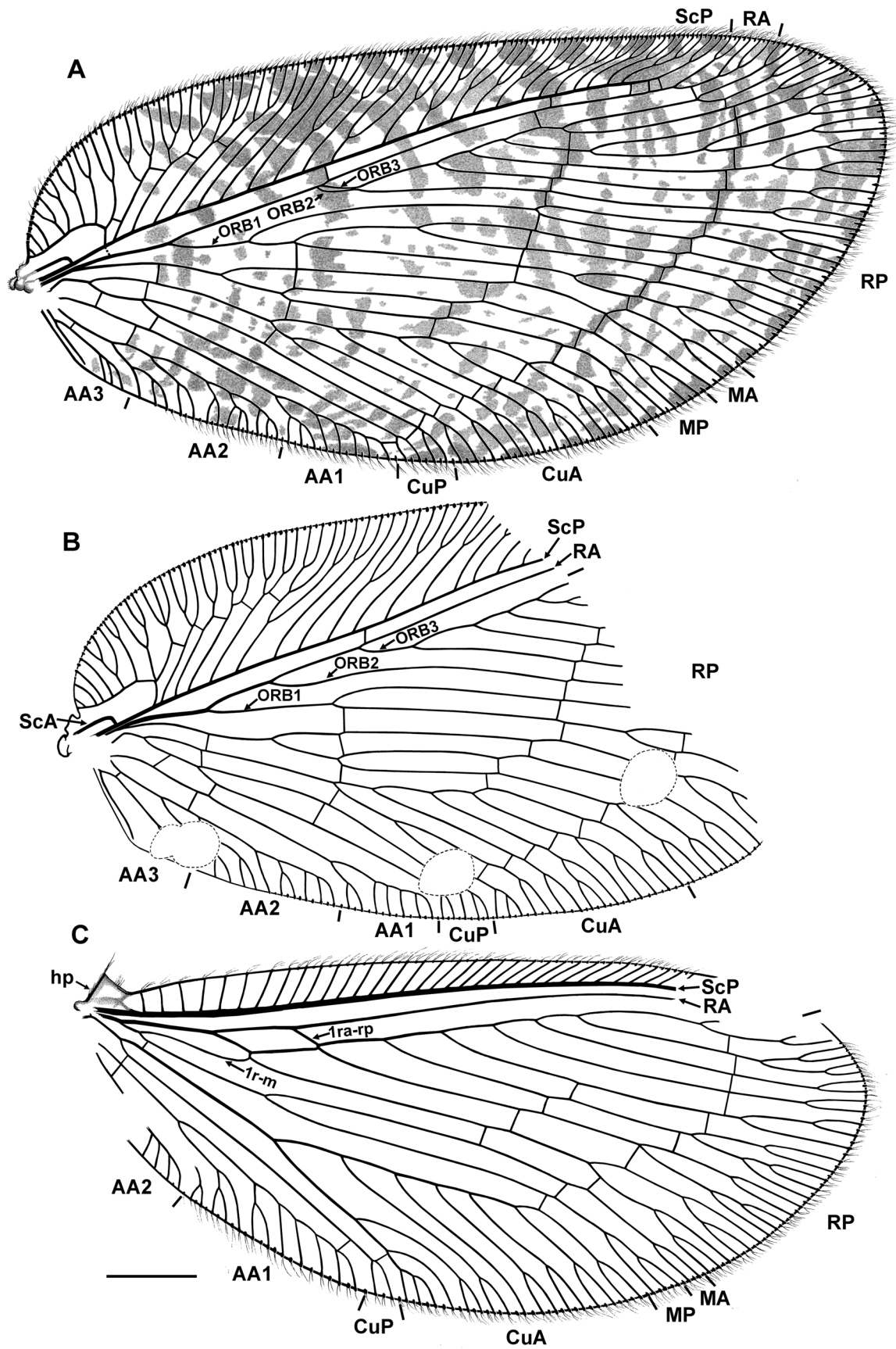
**Diagnosis.** May be distinguished from other species by the following characters: crossveins in costal space in forewing present [absent in *P. minor* sp. nov.]; M two to three times forked proximad third gradate series [once in *P. minor* sp. nov.]; dark pigmentation through outer gradate series present [absent in other species]; comparatively big size [its forewing 7.9–9.5 mm; 6.3–6.9 mm in *P. minor* sp. nov.].



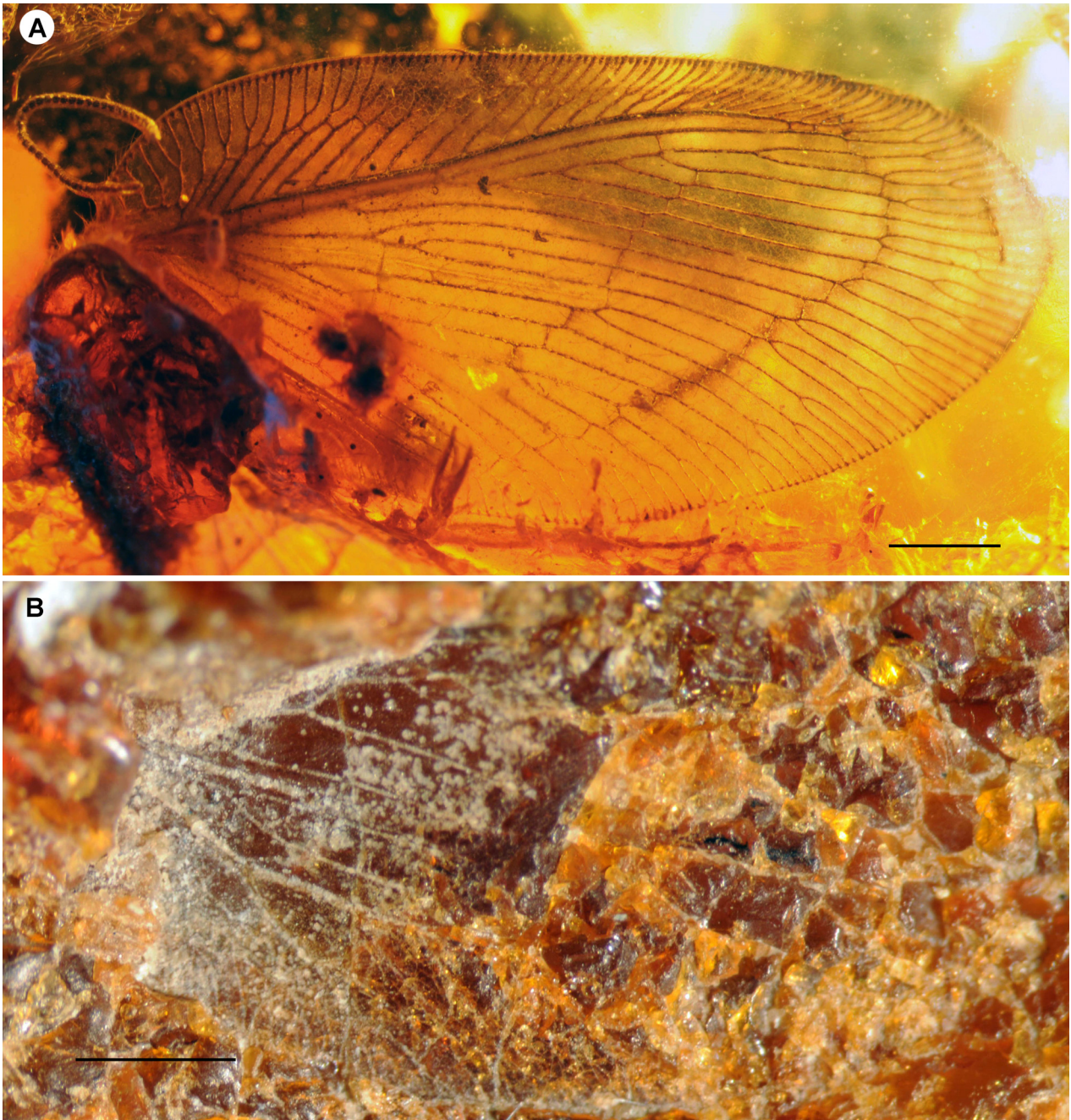
**FIGURE 7.** *Proneuronema gradatum* gen. et sp. nov., holotype SMF Be 2534 as preserved (dorsal view). Scale bar = 1 mm.

**Description.** *Holotype* SMF Be 2534 (Figs 7, 8). Head capsule completely missing, but large part of one antenna with about 50 flagellomeres preserved. Meso- and metathorax poorly preserved. Rest of body missing.

Forewing broadly oval, 9.5 mm long, 4.6 mm wide. Trichosors prominent all around wing margin. Costal space very broad, dilated proximally. Subcostal veinlets 22 in number, two of them simple, others once to three times forked. Humeral veinlet (basal-most subcostal veinlet) recurrent, pectinately branched, with eight branches (of these, five branches once forked in right wing; four branches once to twice forked in left wing). Four (right wing), five (left wing) crossveins form gradate series in proximal part of costal space. Presumable ScA distinct. Subcostal space moderately broad for entire length, with six crossveins in right wing: basal 1scp-r (located opposite to origin of humeral veinlet, poorly visible in right wing; not detected in left wing); two crossveins in middle of wing (2scp-r, 3scp-r); three in distal part. RA forked apically, with two branches each forked once or twice. RA space (between RA, RP) nearly as wide as subcostal space in its basal part. Three ORBs in both forewings. ORB1 once (left wing) or twice (right wing) deeply forked proximad third gradate series of crossveins, with branches directed anteriorly; of these, distal branch deeply forked proximad third gradate series in right wing. ORB2 in right wing simple before fourth gradate series, once forked after; its origin located near origin of ORB3, touching near their origins for short distance. ORB2 in left wing originating far from origin of ORB3. ORB3 (RP proper)



**FIGURE 8.** *Proneuronema gradatum* gen. et sp. nov., wing venation of the holotype SMF Be 2534. A, right forewing. B, left forewing (color pattern is omitted; converted to standard right dorsal view). C, right hind wing. Scale bar = 1 mm.

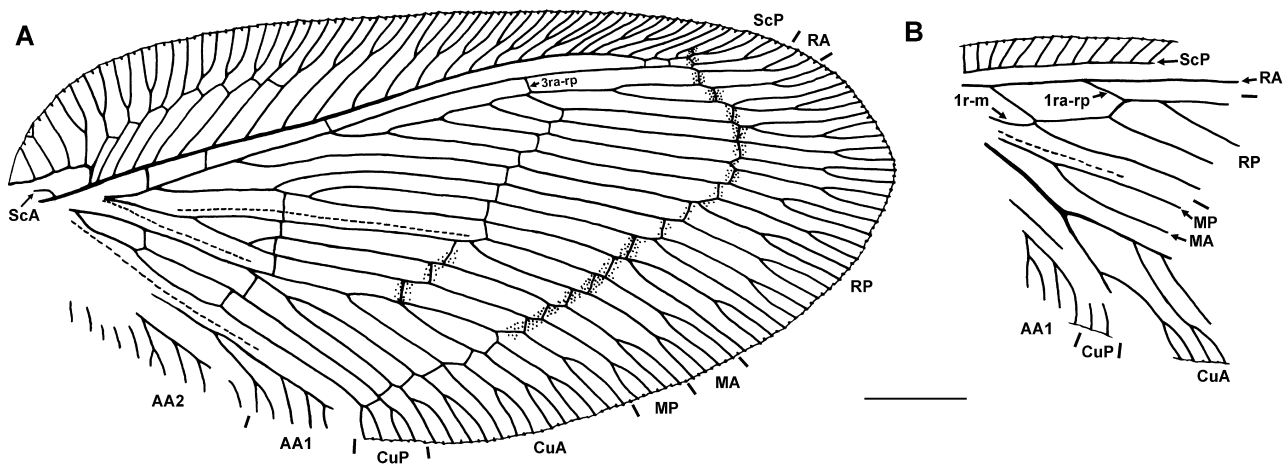


**FIGURE 9.** *Proneuronema gradatum* gen. et sp. nov., paratype SMF Be 376a as preserved. A, right forewing, fragment of antenna. B, fragment of right hind wing. Scale bars = 1 mm.

originating slightly proximad 2scp-r in both wings, pectinate, with five branches originating proximad fourth gradate series in right wing (third branch of ORB3 twice forked between third, fourth gradate series). M appears not fused basally with R, forked proximad second gradate series. MA forked at fourth gradate series; anterior branch with marginal fork, posterior branch simple. MP deeply forked shortly proximad second gradate series; both branches not forked before marginal branching. Cu dividing into CuA, CuP close to wing base. CuA pectinately branched, with four (left wing) or five (right wing) branches, proximal-most branch deeply forked; all branches forked rather shallowly once or twice. CuP deeply forked, each branch with marginal fork (anterior branch in left wing twice forked). AA1 nearly straight, pectinately branched distally, with proximal-most branch forked once (left wing) or twice (right wing), and four simple short branches. AA2 pectinately branched, with six branches; of these, three (left wing) and four (right wing) branches forked (in right wing, two branches twice forked). AA3 very deeply forked; anterior branch shallowly forked, posterior branch simple. Four gradate series of

crossveins (series 1–4 of Oswald 1993) posterior to RA. First (basal) gradate series consists of five crossveins (1m-cu, 1icu, 1cu-aa, 1aa1-aa2, 1aa2-aa3); 1aa2-aa3 strongly shifted towards wing base than other crossveins; one additional crossvein between CuP, AA1 located proximad first series. Second gradate series consists of four (right wing) and five (left wing) crossveins (2r-m, 2im, 2m-cu, 2icu, 2icup (only in left wing)). Third (‘inner’) gradate series consisting of 13 crossveins (in right wing), from RA to CuA. Fourth (‘outer’) gradate series complete, with 26 crossveins, from RA to AA1. Membrane with distinct color pattern consisting of dark brown spots near margins (except for humeral, anal areas), dark brown band through crossveins of fourth gradate series (from anterior branches of RP to CuA), and lighter spots all over wing.

Hind wing broad, 8.4 mm long, 3.8 mm wide. Costal space narrow, slightly dilated proximally, with all preserved veinlets simple. Humeral plate long, straight; covered with numerous fine setae, and few longer and stronger setae at top. ScP stout. No subcostal crossvein detected. RA space nearly equal in width for most length; crossvein 1ra-rp strongly oblique; other crossveins not detected. RP with eight pectinate branches, two of them originating before/at 1ra-rp; RP1 to RP3 dichotomously branched at or slightly proximad outer gradate series; other branches once to three times forked distad outer gradate series. Basal sinuous crossvein 1r-m very long, connecting RP, M slightly distad origin of RP1. M forked distad origin of RP1. MA, MP simple before marginal branching. Cu dividing into CuA, CuP very close to wing base. CuA nearly straight proximad CuA1, then markedly bent anteriorly; pectinately branched with six long branches; posterior trace of CuA with three pectinate branches directed anteriorly (two of these shallowly forked); other branches of CuA with shallow (marginal) forks. CuP thin, straight, with marginal fork. AA1 pectinate, probably with six branches; proximal-most branch heavily branched. AA2 incompletely preserved, pectinate, with short simple branches. AA3 not preserved. Three gradate series of crossveins posterior to RA. First (basal) series consists of five crossveins (1ra-rp, 1r-m, 1m-cu, 1cu-aa, 1aa1-aa2). Second (‘inner’) series consists of four crossveins, from RP4 to MA. Third (‘outer’) series consists of 12 crossveins running from RP to CuA, and two crossveins between CuA1 and AA2. Membrane hyaline with badly preserved color pattern.



**FIGURE 10.** *Proneuronema gradatum* gen. et sp. nov., wing venation of the paratype SMF Be 376a. A, right forewing. B, right hind wing. Scale bar = 1 mm (both to scale).

*Specimen SMF Be 376a* (Figs 9, 10). Forewing oval with nearly rounded apex, 8.8 mm long, 4.3 mm wide. Trichosors prominent all wing margin round. Costal space very broad, dilated proximally. Vast majority of subcostal veinlets once or twice forked. Humeral veinlet (basal-most subcostal veinlet) recurrent, pectinately branched, with four branches (one deeply forked). Seven crossveins form gradate series in proximal part of costal space. Subcostal space moderately wide for entire length, with six crossveins (one basal, two intermediate, three distal). RA forked apically, with two branched, each forked once. RA space (between RA and RP) nearly as wide as subcostal space basally. Three ORBs. ORB1 (RP1) with two branches directed anteriorly proximal to third gradate series; ORB2 simple before fourth gradate series, then forked. ORB3 (RP proper) possesses five branches, originating proximal to fourth gradate series. M appears not fused basally with R. M dividing into MA, MP proximal to second gradate series; MA deeply forked at third gradate series; MP deeply forked just proximad second gradate series; all branches of M not forked before terminal branching. Cu dividing into CuA, CuP close to

wing base. CuA pectinately branched, with four branches, CuA1 deeply forked. All branches of RP, M, and CuA have marginal forks. CuP deeply forked, each branch with marginal fork. AA1 rather deeply forked, anterior branch with three short simple pectinate branches; posterior branch only with marginal fork. AA2 probably pectinately branched (poorly preserved). AA3 not preserved. Four gradate series of crossveins (series 1–4 of Oswald 1993) posterior to RA. First series consists of one crossvein preserved (1cu), others not preserved. Second series includes six crossveins: 2r-m, 2im, 2imp, 2m-cu, 2icu, 1cu-a1. Third ('inner') series with twelve crossveins, from 3r1-rs to 3m-cu. Fourth ('outer') series complete, with 21 crossveins, from 4r1-rs to 4icup. Membrane hyaline; most crossveins in fourth series, and three posterior crossveins in third series margined with darker pigmentation; no other distinct maculation.

Hind wing fragmentary, 2.7 mm long, 3.2 mm wide (probably represents actual wing width). Costal space narrow, with all preserved veinlets simple. No subcostal crossvein detected. RA space proximally dilated (before RP2); crossvein 1r1-rs strongly oblique. Three branches of RP preserved, two of them originated before 1r1-rs. Basal sinuate crossvein r-m connects RP at origin of RP1, M. M forked distad origin of RP1. CuA stout proximad its branching; proximal-most branch of CuA forked twice; other branches apparently with marginal fork (two preserved). CuP thin, with marginal fork. AA1 probably pectinate.

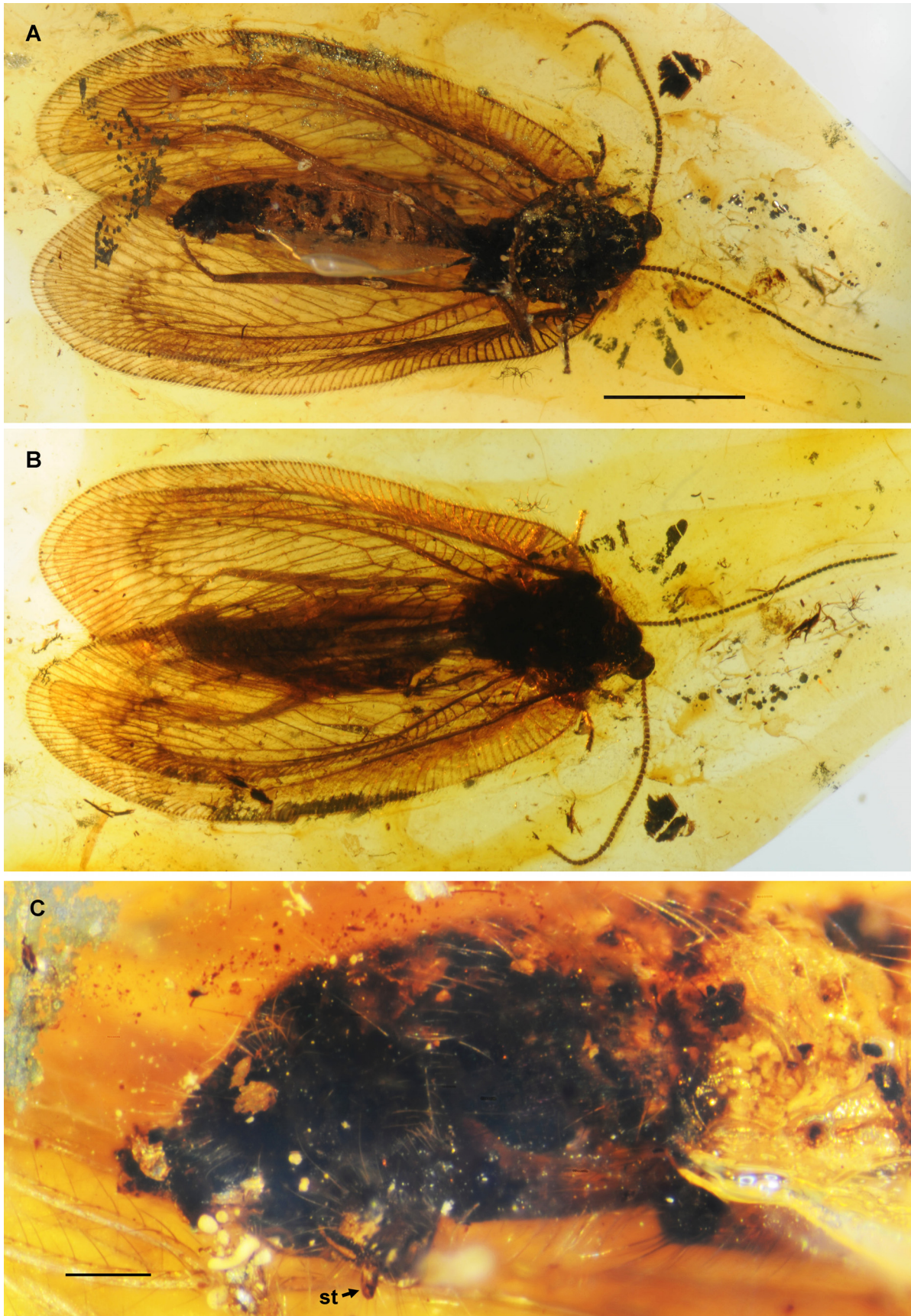
*Specimen No. 1545* (Figs 11, 12). Female. Body completely preserved, but most details poorly discernible. Antennae completely preserved; visible part of flagellum consists of 43 (left) and 46 (right) segments. Four distal segments of left maxillary palpus visible. Abdominal terminalia very crumpled, and segmentation not clear; gonostylus of gonocoxite 9 prominent, covered with scarce long setae (Fig. 11C).

Mesofemur, mesotibia visible, but their length cannot be measured. Metafemur ca. 1.1 mm. Left metatibia relatively long (2.1 mm), only slightly swollen medially, with two short apical spurs (visible on left metatibia); right metatibia in its basal third slender, then broadens abruptly to at least twice basal thickness; and apically becoming again gradually more slender (right metatibia possibly abnormal). Four tarsomeres of metatarsus visible; basimetatarsus more than twice as long as each other visible tarsomere.

Forewing 7.9 mm long, width not measurable, slightly distorted. Trichosors distinct along entire wing margin. Costal space broad, dilated proximally; 19 subcostal veinlets present, but a few distal not discernible; most of them once to twice forked. Humeral veinlet strongly recurrent, pectinately branched, with two of five branches once forked (left wing). Gradate series of crossveins present in proximal part of costal space, with five discernible crossveins. ScA not discernible. Subcostal space only visible in distal part of wing, with one (distal) crossvein. In RA space, abnormally doubled crossvein 3ra-rp well discernible in left wing. RP with three ORBs. ORB1 twice deeply forked near crossvein 2r-m, with branches directed anteriorly and not forked before fourth gradate series; posterior trace of ORB1 forked proximad fourth gradate series. ORB2 shallowly forked distad fourth gradate series. ORB3 (RP proper) pectinate, with five branches, two of which forked proximad fourth gradate series. M forked proximad second gradate series. MA deeply forked at second gradate series, its anterior branch forked at level of third gradate series; distal part not visible. MP forked at level of third gradate series; distal part not visible. Proximal part of CuA and CuP not visible. CuA pectinately branched, probably with four long branches, but other details not visible. CuP fragmentarily discernible. Anal space not visible. Only three gradate series of crossveins visible, first series not visible. Of second gradate series, only crossveins 2r-m, 2icu visible. Of third ('inner') gradate series, 11 crossveins visible, from RA to CuA. Of fourth ('outer') gradate series, 16 anterior crossveins visible, from RA to posterior trace of M. Outer gradate series distinctly margined with brownish-colored membrane.

Hind wing ca. 6.9 mm long, width not measurable. Trichosors distinct along entire wing margin. All subcostal veinlets simple. RA space dilated proximally; crossvein 1ra-rp strongly oblique; other crossveins not detected. RP with seven (left wing), eight (right wing) pectinate branches, two of them originating before 1ra-rp; branches not forked proximad outer gradate series. Basal sinuous crossvein 1r-m very long, connecting RP1 and M slightly distad origin of RP1. Three gradate series of crossveins posterior to RA. Of first (basal) series, two crossveins (1ra-rp and 1r-m) discernible. Three crossveins discernible in second ('inner') series, from RP5 to RP2; other two to three crossveins possible. Crossveins of third ('outer') series not well discernible due to preservation. Membrane hyaline, no distinct color pattern.

**Material.** Holotype SMF Be 2534, deposited in SMF (formerly in the private collection of Thomas Weatherschan, former coll. No.1620). An incomplete specimen: mesothorax; one fragmentary antenna; completely preserved right fore- and hind wings; distal parts of left fore- and hind wings are missing.



**FIGURE 11.** *Proneuronema gradatum* gen. et sp. nov., female specimen No. 1545 (Hoffeins' collection). A, ventral view. B, dorsal view. C, apex of abdomen. st, gonostylus of gonocoxite 9. Scale bars = 2 mm (A, B to scale), 0.2 mm (C).

Specimen SMF Be 376a, deposited in SMF (formerly in the private collection of Thomas Weiterschan, former coll. No. 1390). A fragmentary specimen (nearly complete right forewing, one fragmentary antenna, and fragmentary hind wing).

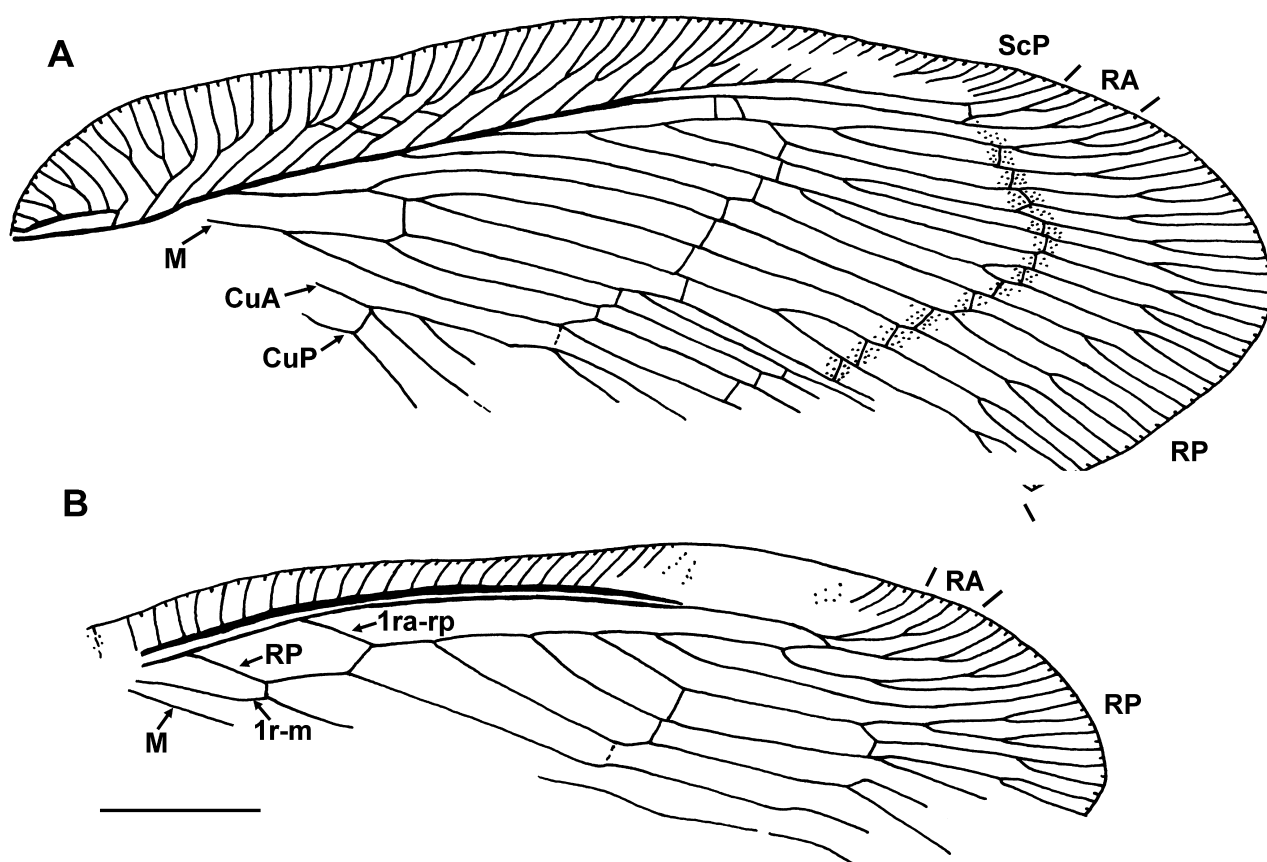
Specimen No. 1545, deposited in the private collection of Christel and Hans-Werner Hoffeins (Hamburg, Germany). A complete female specimen, with crumpled abdomen. Wings are completely preserved, but strongly overlapping and partly deformed, so only parts of the wing venation of the right wing pair can be clearly seen; the wing venation of the left wing pair is for the most part not visible.

**Type locality and horizon.** Baltic amber (precise collecting site unknown); late Eocene.

**Etymology.** From the Latin *gradatus*, gradate, in reference to the presence of the gradate series of crossveins in the forewing costal space.

**Remarks.** All these specimens are considered to belong to the same species as they have a similar size and their venation clearly differs from that of *Proneuronema minor* **sp. nov.** However, the holotype and other two specimens strongly differ from each other in their wing color pattern. These differences may not be sufficient reason for dividing the species into two, as many extant hemerobiid species have great intraspecific variability in wing color pattern. Some species have even stronger color pattern variability than in this new species, e.g., *Megalomus stangei* Gonzalez Olazo, 1981 (Gonzalez Olazo 1981: Fig. 4; Monserrat 2003: Figs 38, 39), *M. moestus* Banks, 1895 (Monserrat 1997: Figs 99, 100), *Drepanopteryx punctata* (Okamoto, 1905), and *Micromus sjostedti* van der Weele, 1910 (Tjeder 1961: Figs 530–533). Nonetheless, the holotype on the one hand and other two specimens on the other may theoretically represent two distinct species. This problem will be resolved by the discovery of more complete specimens whose genitalia segments are easily discernible.

A specimen from Baltic amber that was previously erroneously referred to as “Chrysopidae” by Weitschat & Wichard (1998: Pl. 56c) and later as “second undescribed *Megalomus*-like species” by Makarkin *et al.* (2012) surely belongs to *Proneuronema gradatum* **sp. nov.** This specimen is deposited in a private collection, and currently inaccessible for study. Examination of the photograph in Weitschat & Wichard (1998) shows that the venation and color pattern are most similar to the specimen SMF Be 376a.



**FIGURE 12.** *Proneuronema gradatum* **gen. et sp. nov.**, wing venation of the specimen No. 1545 (Hoffeins' collection). A, left forewing, slightly distorted. B, left hind wing (both converted to standard right dorsal view). Scale bar = 1 mm (both to scale).

## Confirmation of the validity of *Proneuronema*, its comparison with other genera and subfamily affinity

**Fossil genera.** Up to date, eight fossil hemerobiid genera have been described: *Promegalomus* Panfilov, 1980 (Late Jurassic of Kazakhstan); *Purbemerobius* Jepson *et al.*, 2012 (Early Cretaceous of England); *Cretomerobius* Ponomarenko, 1992 (Early Cretaceous of Mongolia); *Plesiorobius* (Late Cretaceous of North America and Asia); *Prophlebonema* Krüger, 1923, *Prospadobius* Krüger, 1923, *Prolachlanius* Krüger, 1923 (all from the Eocene Baltic amber), and *Bothromicromus* Scudder, 1878 (Early Oligocene of Quesnel, Canada). All these genera are monotypic, except *Plesiorobius*. The venation of all known fossil genera differ quite significantly to that of *Proneuronema* **gen. nov.**

Of these, the venation of *Cretomerobius* and *Promegalomus* is similar to that of *Proneuronema* **gen. nov.** in having a fan-shaped configuration of ORB1. In *Cretomerobius*, however, ScP and RA are fused distally, and crossveins between the branches of RP proximad the third gradate series are present (see Makarkin *et al.* 2003: Fig. 5). The structure of the distal ORB in *Promegalomus* is so peculiar that it is unknown in all other hemerobiids (see Panfilov 1980: Fig. 91). These character states are different to those of the new genus.

The genus *Purbemerobius* is known from a single slightly incomplete hind wing. The structure of its M is most similar to that of the South American *Gayomyia* Banks, 1913: M in both of these genera is deeply forked three times proximad the second gradate series, this is once forked in all other hemerobiids, including the new genus. However, the fragmentary nature of *Purbemerobius* does not allow further, more detailed comparison.

*Prophlebonema* is a synonym of *Drepanepteryx* (see below).

*Bothromicromus* is a poorly known genus, but available data indicate that this genus is either closely related to *Megalomus* or its synonym (see below for details). In this genus, numerous ORBs are present, and ORB1 is shallowly forked contrary to those of *Proneuronema* **gen. nov.**

The genera *Prolachlanius* and *Prospadobius* belong to Sympherobiinae (the former with certainty, and the latter presumably), and therefore these are very distantly related to the new genus.

The genus *Plesiorobius* is known from two or three Late Cretaceous species: *P. sibiricus* Makarkin, 1994 from the Santonian/Coniacian Ola Formation (northeastern Siberia), *P. aff. canadensis* Klimaszewski *et* Kevan, 1986 (the Santonian Taimyr amber, northern Siberia; Makarkin, 1994), and *P. canadensis* from the Campanian Canadian amber. This genus was recently transferred from Berothidae to Hemerobiidae, based on the examination of high resolution photographs of its type species (*P. canadensis*) (Makarkin 2016). The type species possesses all characters of Hemerobiidae including the configuration of the hind wing CuA and swollen metatibia. The venation of this genus is most similar to that of the extant Adelphohemerobiinae and an undescribed species from Burmese amber in having a single RP in the forewing, and the distally fused/touching ScP and RA.

**Extant genera.** The venation of *Proneuronema* **gen. nov.** is most similar to that of seven extant genera classified by Oswald (1993) as members of three different subfamilies: Drepanacrinae (*Drepanacra* Tillyard, 1916, *Austromegalomus* Esben-Petersen, 1935, and *Conchopterella* Handschin, 1955), Drepanepteryginae (*Drepanepteryx*, *Gayomyia*, and *Neuronema*), and Megalomiinae (*Megalomus*). We apply to this group an informal group name 'the *Megalomus*-like genera'. In particular, this group is characterized by a rather dense venation, the deeply forked CuP in the forewing, and the fully-developed CuP in the hind wing (except *Austromegalomus*). In all other hemerobiids, CuP in the forewing is shallowly forked (except *Notiobiella* Banks, 1909, *Notherobius* New, 1988, and *Noius* Navás, 1929), and CuP in the hind wing is reduced (except *Adelphohemerobius* Oswald, 1994).

*Drepanepteryx* and *Gayomyia* are most distantly similar to the new genus in this group. Both these genera have numerous ORBs, a shallowly forked ORB1, and numerous crossveins in the second gradate series in the hind wing. Also, the gonostylus of gonocoxites 9 in the females of *Drepanepteryx* is lost, and M of *Gayomyia* is deeply forked three times proximal to the second gradate series.

*Proneuronema* **gen. nov.** is characterized by ORB1 being deeply forked two or more times, with its posterior trace nearly straight and its branches directed anteriorly (i.e., fan-shaped configuration). This character state is also characteristic of *Promegalomus* and *Cretomerobius* among fossil taxa, and some *Megalomus*-like genera among extant hemerobiids: all the species of Drepanacrinae (*Drepanacra*, *Austromegalomus*, and *Conchopterella*: Oswald 1988: Fig. 1; Oswald 1993: Figs 132, 140, 149), many species of *Megalomus* from the New World, i.e., *M. angulatus* Carpenter, 1940, *M. moestus*, *M. pictus* Hagen, 1861, *M. darwini* Banks, 1924, *M. flinti* (Nakahara, 1965), *M. democraticus* Monserrat, 1997, and *M. australis* (Gonzalez Olazo, 1992) (Nakahara, 1965: Fig. 7; Monserrat 1997: Figs 96–100, 114, 115), and a few species of *Neuronema*, i.e., *N. decisum* (Walker, 1860) (Oswald 1993: Fig. 166).

The ORB1 branching in these species exhibits intraspecific variation in the number of branches. For example, both *Megalomus moestus* and *M. flinti* each have one (Monserrat 1997: Figs 99, 104) or two deep branches of ORB1 (Nakahara 1965: Fig. 7; Monserrat 1997: Fig. 105). The number of these branches in both species of *Proneuronema* **gen. nov.** differs in the right and left forewings of the same specimens (see Figs 2A, B, 8A, C).

The venation of *Proneuronema* **gen. nov.** is distinguished from those species of *Megalomus* whose ORB1 is fan-shaped, in that the latter has at least four ORBs, and 3scp-r is normally absent in all the species except *M. pictus*. Most species of *Megalomus* have many ORBs and ORB1 is shallowly forked (Fig. 13A). Also, their male 9th sternite is non-specialized (short and not boat-like), and the ectoproct is armed with some processes or elongated.

The venation of Drepanacrinae (*Drepanacra*, *Austromegalomus*, and *Conchopterella*) is generally similar to that of *Megalomus*. Of these genera, *Proneuronema* **gen. nov.** is most similar to *Drepanacra*, but the latter lacks 3scr-r, and the fork of M is shifted distally. Also, the male of *Drepanacra* has the short and non-specialized 9th sternite, and the elongated ectoproct. The male terminalia of *Austromegalomus* and *Conchopterella* are similarly constructed, and their ORBs are numerous (at least five).

The male terminalia of *Proneuronema* **gen. nov.** is certainly most similar to that of the genus *Neuronema*. In particular, these two genera share the long boat-like 9th sternite. Also, the ectoproct in some (few) species has a more or less similar shape and does not bear any processes (e.g., *Neuronema ypsilum* Zhao *et al.*, 2013: Fig. 3). The female terminalia is also similar to that of *Neuronema*, along with most *Megalomus*-like genera. The venation of *Proneuronema* **gen. nov.** is generally similar to that of a few species of that genus which have a fan-shaped ORB1. Oswald (1993) identified one venational synapomorphy of the genus, i.e., the forewing additional pre-3ra-rp [=pre-3ir1] crossveins are present, whereas these are absent in *Proneuronema* **gen. nov.** Sometimes however, these crossveins are also absent in *Neuronema* (see Fig. 13C). All examined species of *Neuronema* have at least one (usually more) crossvein between the branches of RP proximad the third gradate series; normally, only two-three (see Fig. 13C) subcostal crossveins in the forewing; five or more crossveins in the second (inner) gradate series in the hind wing (a crossvein between CuA and CuP in this series is always present); and the basal 1r-m crossvein enters RP far distad the origin of RP1 (see e.g., Nakahara 1960: Pl. 15, Fig. 31; Yang 1964: Figs 1, 17; Nakahara 1971: Fig. 26; Zhao *et al.* 2013: Figs 1, 2). Also, ORB1 is usually shallowly forked (Fig. 13C). The character states of the venation of the new genus differ strongly from these.

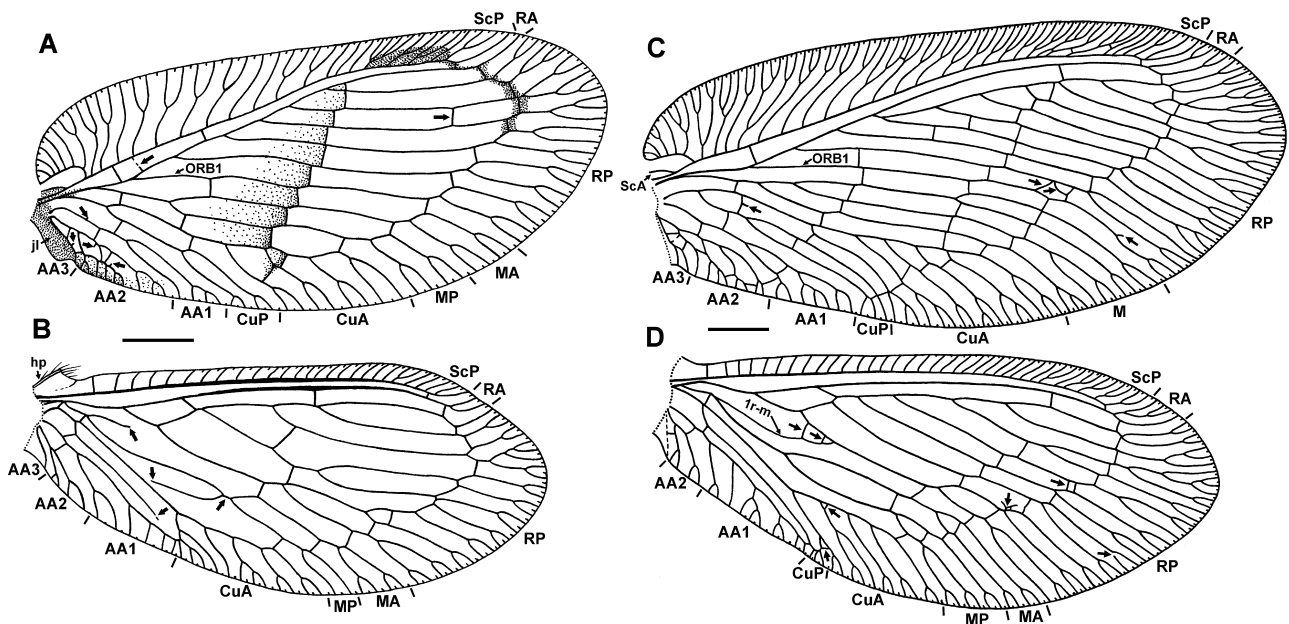
In summary, the two new species cannot be assigned to any existing genus, both fossil and extant, although we could not identify any autapomorphies of *Proneuronema* **gen. nov.**

**Subfamily affinity of *Proneuronema*.** Ten subfamilies are currently recognized in the family Hemerobiidae: Adelphohemerobiinae, Carobiinae, Hemerobiinae, Sympherobiinae, Notiobiellinae, Psychobiellinae, Drepanacrinae, Megalominae, Drepanopteryginae, and Microminae (Oswald 1993, 1994). Of the fossil genera, *Prolachlanius* likely belongs to Sympherobiinae, *Bothromicromus* possibly to Megalominae, and the subfamily affinities of the other five genera are still unclear.

As mentioned above, *Proneuronema* **gen. nov.** belongs to the informal *Megalomus*-like genus-group of the family, which includes genera of Drepanacrinae, Megalominae, Drepanopteryginae, and probably Psychobiellinae. A few forewing venation character states were proposed by Oswald (1993) as synapomorphies of these subfamilies (except Megalominae which has no venational synapomorphies): the presence of the intramedial crossvein 2im, and the intercubital crossvein 1cua-cup (synapomorphies of Drepanopteryginae); AA1 is deeply forked, with the most proximal fork being located in the proximal half of the posterior AA1 trace (a synapomorphy of Drepanacrinae); and three ORBs with ORB1 being deeply forked (a synapomorphy of Psychobiellinae). However, all these character states are homoplasious within the family. These subfamilies actually have no clear venational synapomorphies, and can be diagnosed only by a combination of wing venation character states and genitalia. The venation of the *Megalomus*-like genera possesses many plesiomorphic features at the family level (e.g., CuP is present in the hind wing; the fan-shaped ORB1 (presumably), the complete fourth gradate series (from RA to CuA), and CuP is deeply forked in the forewing). As a result, there is some difficulty in the subfamily assignment of fossil (and even extant) genera in this group. For example, Oswald (1993) considered the extant *Megalomus stangei* Gonzalez Olazo, 1981 to be in the genus *Conchopterella*, i.e., in Drepanacrinae, whereas Monserrat (1997) placed it in Megalominae.

The comparison of the venation and the male and female genital segments of *Proneuronema* **gen. nov.** with those of other *Megalomus*-like genera (see above) reveals that this genus is most closely related to the genus

*Neuronema* (Drepanepteryginae). Based on this, we assign this genus also to this subfamily, although its type genus (i.e., *Drepanepteryx*) strongly differs from the new genus, both by the venation and the female genital segments.



**FIGURE 13.** Wing venation of extant *Megalomus setosulus* (Walker, 1860) (India: Himachal Pradesh) (A, B), and *Neuronema kuwayamai* Nakahara, 1960 (Japan: Hokkaido) (C, D). A, C, forewings. B, D, hind wings. Venational anomalies are shown by stouter arrows. Scale bars = 1 mm (A, B and C, D to scale).

### Fossil representatives of the extant genera *Megalomus*, *Neuronema*, and *Drepanepteryx*

The Cenozoic hemerobiids whose venation is more or less similar to that of the new genus are usually assigned to the extant genera *Megalomus*, *Neuronema* and *Drepanepteryx*, but often they actually do not belong to any of these genera. Below, we critically review the fossil *Megalomus*-like species, except those species which belong to *Proneuronema* **gen. nov.**

***Megalomus*.** This genus includes about 30 extant species distributed in Europe, northern Africa, Middle East, south-eastern Asia (India, Nepal, China, Philippines), and the Americas, from southern Canada to Chile (Oswald 2015). Some South American species, however, are so different in the genitalia and venation that they may be separated into at least one additional genus. It applies especially to *Megalomus australis* (see Monserrat 1997) which was originally described as the type species of the genus *Navasius* Gonzalez Olazo, 1992 (*nomen praeoccupatum*).

The actual generic affinity of a large species (the forewing is 18 mm long) from the early Eocene Mo-clay described as *Megalomus densistriatus* is unclear (Henriksen 1922: Fig. 4). There is another undescribed specimen of this species from the same locality in the Natural History Museum (London). It is represented by a proximal portion of a forewing (estimated complete length is 14–15 mm). Examination of drawings of these specimens (a draft drawing of the London specimen was done by S. Bruce Archibald) allows us to conclude that they might belong to a new genus. This is supported by the great size; numerous ORBs (but it needs a confirmation); the strongly fan-shaped ORB1 with five deep branches; the multi-branched M (probably with six deep branches); and the few-branched CuA with very oblique branches. Unfortunately, both specimens appear to be poorly preserved. Therefore, it is necessary to re-examine them (and possible other specimens) to establish a new genus or refer them to some valid genus.

*Hemerobius tinctus* Jarzembowski, 1980 was described from the latest Eocene of the Bembridge Marls (England) based on a small nearly complete (5 mm long) forewing (Jarzembowski, 1980: Fig. 31). The assignment of this species to *Hemerobius* Linnaeus, 1758 is erroneous. Makarkin (1991) referred it to the genus *Megalomus*. Indeed, a combination of its character states (i.e., the strongly recurrent and branched humeral veinlet; the deeply-

forked CuP; the complete fourth gradate series of crossveins running from RA to AA1) is present only in the *Megalomus*-like genera, and of these, *Megalomus* is the most likely generic affinity; its forewing with three ORBs (not four or more) is probably a result of its minute size. Oswald (1993) did not exclude “its possible relationship with [the Australian genus] *Psychobiella*” (p. 261). However, in the latter genus, CuP and AA1 are shallowly forked (see Tillyard 1916: Fig. 21; Nakahara 1960: Pl. 15, Fig. 30; Oswald 1993: Fig. 90), whereas these are deeply forked in *M. tinctus*.

On the other hand, this species may theoretically belong to *Proneuronema* **gen. nov.** It differs from *P. minor* **sp. nov.** only in the absence of 3scp-r, and by ORB1 which is once deeply forked, not two to three times. The former character might be poorly preserved in the specimen, and the latter is variable (see above) or a result of the small size of the specimen. Therefore, we consider the assignment of this species to *Megalomus* only preliminary.

*Bothromicromus lachlani* Scudder, 1878 was described from the early Oligocene locality near Quesnel on Fraser River, British Columbia, Canada (the age according to Wilson 1978); its forewing length is 9.5 mm. It was reexamined by Scudder (1890: Pl. 2, Figs 7–10), but further reexamination is necessary. A part (No. 36), deposited in the Geological Survey of Canada (Ottawa) the photograph of which we studied, is poorly preserved and largely destroyed. The current depository of the counterpart whose forewing venation is better preserved is unknown. The analysis of all available data shows that this genus is closely related to *Megalomus*. It possesses numerous (eight) ORBs; simple ORB1; crossveins of the second gradate series are absent between RP branches. A set of these character states is present in many *Megalomus* species, and absent in all other extant *Megalomus*-like genera and *Proneuronema* **gen. nov.** Therefore, we cannot exclude that this species belongs to *Megalomus*, but it needs a confirmation by the examination of the holotype.

Two species from the middle Miocene (Tchokrakian/ Karagonian) of Vishnevaya Balka in the vicinity of Stavropol (Russia) can be assigned to the genus with relative certainty: *Megalomus maculosus* Makarkin, 1991 and *M. caucasicus* Makarkin, 1991.

*Megalomus caucasicus* is represented by a complete forewing, 7.5 mm long. Its venation is quite typical for the genus, except its CuA with only two oblique branches is not characteristic of extant species of the genus. Its RP consists of six ORBs, ORB1 is deeply forked, and the distal-most ORB lacks branches. In general, this configuration is most similar to that of the extant *M. moestus* or *M. flinti* (see Monserrat 1997: Figs 99, 104).

*Megalomus maculosus* is represented by an anterior proximal part of a forewing (5.1 mm long as preserved; estimated complete length 7–8 mm). Its venation is most similar to that of *M. darwini* from the Galápagos Islands by possessing four ORBs and a similar configuration of ORB1 with its two deep branches (cf. Klimaszewski *et al.* 1987: Fig. 14; Monserrat 1997: Fig. 96).

A distal portion of a forewing (8.8 mm long as preserved; estimated complete length ca. 12 mm) from the late Miocene (late Messinian) of the Sainte-Reine locality (near Murat, France) was identified by Nel (1991: Fig. 15) as *Drepanopteryx* sp. However, its ORB1 is twice deeply forked, which is definitely not characteristic of *Drepanopteryx*. This species is similar to *Megalomus maculosus* by this feature and similar maculation, and also possibly belongs to *Megalomus* due to the possession of many (eight) ORBs. This determination is preliminary as the specimen is very incomplete.

In summary, four European fossil species may be assigned to *Megalomus*: the latest Eocene *M. tinctus* (preliminary), and three Miocene species, i.e., the middle Miocene *M. caucasicus* and *M. maculosus*, and the late Miocene (Messinian) *Megalomus* sp. from the Sainte-Reine locality (preliminary). The *Megalomus* affinity of the earlier Oligocene ‘*Bothromicromus lachlani*’ from North America needs confirmation.

**Neuronema.** The genus comprises ca. 30 large extant species distributed in eastern Asia, from Pakistan and Tajikistan through India, Nepal and China to Korea, southern Far East of Russia and Japan (Zhao *et al.* 2013; Oswald 2015).

Two fragmentary specimens were preliminary assigned to this genus, «?*Neuronema* species A» and «?*Neuronema* species B» from the latest Eocene of Bembridge Marls, England (Jarzembowski 1980: Figs. 39, 40). We agree with Oswald (1993) in that the visible characters of these fragments “appear consistent with this generic determination” (p. 261). However, these specimens may well also belong to *Proneuronema* **gen. nov.** Unfortunately, their fragmentary and poor preservation prevents further determination.

**Drepanopteryx.** The genus comprises five large extant Palearctic species (Oswald 2015). Interestingly, the distribution of the genus in China is restricted by the occurrence of *D. phalaenoides* (Linnaeus, 1758) in the north of the country, whereas three species are known from Japan (Makarkin 1993).

Hagen (1852) reported '*Drepanopteryx*' (an incorrect subsequent spelling of *Drepanopteryx* Leach, 1815) from Baltic amber, but it was never described or even mentioned in his subsequent papers (Hagen 1854; Pictet-Baraban & Hagen 1856; Hagen 1866). It is very probably that this specimen is the same as the holotype of *Prophlebonema resinatum* (Krüger, 1922) (see Tjeder 1963), which is now probably lost, and which belongs to the genus *Drepanopteryx* judging from the description of Krüger (1923). Moreover, it was considered as *Drepanopteryx resinata* in a list by Monserrat (1990), but without any explanation and as *nomen dubium*.

This species was briefly described as '*Phlebonema resinata*' by Krüger (1922). Krüger (1923) described it in detail as a new species ('*Prophlebonema resinata*') based on the same specimen, but did not figure it. He noted that the venation of this species is very similar to that of *Drepanopteryx algida* (Erichson, 1851). The forewing of *P. resinatum* possesses in particular seven crossveins in the costal spaces; eight ORBs; numerous crossveins in the second gradate series ['Gabelreihe'] (seven crossveins in its anterior part are preserved); M is divided into MA and MP near the wing base ['früh'], and both shortly forked again; CuP is heavily branched ["stark verästelt"]. Such a combination of character states is present only in *Drepanopteryx*, and indeed it may occur in *Drepanopteryx algida* or closely related species. Therefore, we may rather confidently consider *Prophlebonema* as a synonym of *Drepanopteryx* (**syn. nov.**), and treat this species as *Drepanopteryx resinata*. Unfortunately, we do not know of any undescribed hemerobiid from Baltic amber whose features would be concordant with those of *D. resinata*.

*Drepanopteryx oedobia* Makarkin, 1991 was described from the late Eocene/early Oligocene locality near the mouth of Tikhii Stream (Russia: Primorskii Krai: Ternei District: vicinity of Velikaya Kema Village) based on an incomplete hind wing. Its venation is typical for the genus, including the basal crossvein 1r-m joining RP proximad the origin of RP1. All species of *Drepanopteryx* possess this character state (see e.g., Nakahara 1960: Pl. 16, Fig. 33; Tjeder 1963: Figs 1, 2; Nakahara 1971: Fig. 25), while 1r-m joins RP1 in all other *Megalomus*-like genera.

*Drepanopteryx ramosa* Makarkin, 1991 was described from the middle Miocene (Tchokrakian/ Karagonian) of Vishnevaya Balka in the vicinity of Stavropol (Russia) based on an incomplete forewing. Its venation is typical for the genus, including numerous ORBs, the simple ORB1, and the multi-branched M.

In summary, we consider three fossil Eurasiatic species as belonging to *Drepanopteryx*: the late Eocene *D. resinata*, the late Eocene/early Oligocene *D. oedobia*, and the Miocene *D. ramosa*.

### Remarks on wing venation variability in Hemerobiidae, especially their venational abnormalities (anomalies)

The wing venation variability as found in these new species of *Proneuronema* **gen. nov.** is usual for the family. It is no exaggeration to say that there are no identical wings in Hemerobiidae, especially in *Megalomus*-like genera, like in many other insects with complicated venation (e.g., Odonata, Ephemeroptera). This variability is known as normal ('continuous') phenotypic variation. For example, the number of RP branches in *Drepanopteryx phalaenoides* varies from 8 to 14 and the number of crossveins in the fourth gradate series in that species varies from 20 to 25, but all these conditions are normal for this species. However, a wing has occasionally some abnormalities in its venation, which are beyond the norm for a species (or a higher taxon), e.g., the reduction and fusion of veins that are normally present and not fused, respectively; and the appearance of some additional crossveins (see Fig. 13).

One type of normal phenotypic variation is fluctuating asymmetry. Fluctuating asymmetry is non-directional deviation from bilateral symmetry (Palmer & Strobeck 1986). This phenomenon has attracted special attention for more than fifty years, since the work of VanValen (1962). Neuropteran wings could be a good object to study this phenomenon, but little has been done in this respect. Examples are the works of Clarke (1993) and New (1998) for single species of *Chrysopa* Schneider (Chrysopidae) and *Eumantispa* Okamoto (Mantispidae), respectively.

It is thought that the degree of fluctuating asymmetry is connected with the stability of development. The greater the index of fluctuating asymmetry is, the more unstable the development was (e.g., Palmer 1994; Palmer & Strobeck 1992, 2003; Leung *et al.* 2000). However, one, or even several specimens are not very useful to study this, here a population study would be needed. We may assume only that the developmental conditions of the specimen GZG.BST.05246 of *Proneuronema minor* has deviated from the normal for this species because of the high amount of aberrations.

It is assumed that the instability of development may cause abnormalities of the venation (Muzlanov 2002). A

possible reason for the highly aberrant wing venation of one species of Apochrysinæ (Chrysopidae) is assumed to be a developmental malformation (Winterton 2006). Makarkin (1985, 1990) studied the distribution and frequency of 18 anomalies in the forewing of the East Asian green lacewing *Chrysopa intima* McLachlan, and found that the sum frequency of all anomalies per population was higher in the northern-most populations whose developmental conditions are less favorable for the species.

We studied the sum frequency of venational anomalies (A) in the forewings (FW) of different species in the genus *Hemerobius* Linnaeus, 1758 (Table 1). The A/FW ratio varies rather widely but reveals some regularity. *H. humulinus* Linnaeus, 1758 and *H. simulans* Walker, 1853 are widely distributed in the Holarctic, and their A/FW ratio is low. This wide distribution may be linked with the assumption that these species are quite possibly among the youngest species within the genus, and therefore more adapted to the current climatic factors than the other species of the genus (i.e., their development is stable). *H. tristriatus* Kuwayama, 1954 and *H. subfalcatus* Nakahara, 1960 are distributed only in an area of the Sea of Japan, and their A/FW ratio is highest. Their characters reveal that these species appear to be more ancient; their high A/FW ratio may be linked with current unfavorable climate conditions throughout their areas, or only in the Russian Far East (the northern limit of their areas).

**TABLE 1.** Relative number of venation anomalies in the forewings of extant species of *Hemerobius*. All species are from the Asian part of Russia, except *Hemerobius micans* which is from the Ukraine.

Species	Number of anomalies (A)	Number of forewings examined (FW)	A/FW ratio
<i>H. tristriatus</i> Kuwayama	175	171	1.02
<i>H. subfalcatus</i> Nakahara	10	15	0.67
<i>H. atrifrons</i> McLachlan	70	140	0.50
<i>H. stigma</i> Stephens	57	150	0.38
<i>H. marginatus</i> Stephens	133	386	0.35
<i>H. poppii</i> Esben-Petersen	16	51	0.33
<i>H. fujimotoi</i> Nakahara	19	58	0.33
<i>H. exoterus</i> Navás	26	88	0.30
<i>H. humulinus</i> Linnaeus	120	486	0.25
<i>H. marginatus lapponicus</i> Meinander	5	22	0.23
<i>H. simulans</i> Walker	51	324	0.18
<i>H. japonicus</i> Nakahara	5	51	0.10
<i>H. micans</i> Olivier	0	50	0.00

An abnormal (anomalous) venation often occurs in fossil and extant species of Hemerobiidae (as well as Neuroptera in general). Some authors drew special attention to such a venation in Hemerobiidae (e.g., Killington 1932; Verdcourt 1949; Makarkin 1995, 1996a, b). *Hemerobius convexus* Monserrat, 2004 was described from Kenya based on a single female specimen with strongly anomalous venation (Monserrat 2004: Fig. 1a). Similar strongly abnormal venation is present in *Megalomus* sp. (Monserrat 1997: Fig. 112). Generally, such anomalous venation is more characteristic of the *Megalomus*-like genera which have more multi-veined venation than other hemerobiids (see e.g., Fig. 13). Therefore, it is quite ‘normal’ that the venation of all specimens of *Proneuronema* **gen. nov.** strongly differs in their left and right wings, and among specimens. In addition, we found in these specimens some venational anomalies, i.e., the duplication of five crossveins in both specimens of *Proneuronema minor* **sp. nov.**

There are some hypotheses suggesting phylogenetic implications of the occurrence of a particular wing venation anomaly. The ‘atavistic phenotype’ hypothesis is one of most well known. This hypothesis says that “the wing vein prepatterning mechanism can be conserved in highly derived species” (Palsson & Gibson 2000, p. 617). It was applied mainly for Diptera with simplified venation, like Drosophilidae and their relatives. Earlier, a similar hypothesis was proposed by Kozlov (1987) and applied for Lepidoptera: “the appearance of additional veins probably expresses the characteristics of wing structures of ancestral forms”. (p. 243).

A related hypothesis is the ‘phyletic phenocopies paradigm’ (Basille & Stebbins 1986). It is assumed that

“mutant phenotypes of a particular character observed in a model organism often mimic phenotypes of these same characters found in other organisms” (Stark *et al.* 1999, p. 118).

Unfortunately, we cannot know the genetic basis of anomalies in Hemeroibiidae: which anomaly is heritable (i.e., ‘mutation’) and which anomaly appears during the development of an individual organism (i.e., a nonheritable anomaly). The presence of the crossvein 3rs3-rs2 as an anomaly in some species of *Symphorobius* Banks, 1904 in which it is normally absent may be a good example of an ‘atavistic phenotype’ (see Makarkin & Wedmann 2009). Another example of an ‘atavistic phenotype’ is found in the Mesozoic Mesochrysopidae, where CuP in the hind wing is reduced. However, in one of the hind wings of *Kareninoides lii* Yang *et al.*, 2012 CuP is fully developed and absent in the other one (see Yang *et al.* 2012a: Fig. 7). But most other anomalies appear to have no great phylogenetic implications as similar anomalies occur in various taxa (e.g., the duplication of crossveins in gradate series may occur in any species of Hemeroibiidae or Chrysopidae). In any case, the study of venation variation in Hemeroibiidae, and Neuroptera in general, appears to be promising.

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