



New fossil species of Nymphidae (Neuroptera) from the Eocene of North America and Europe

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Abstract

Two new fossil species of Nymphidae (Neuroptera) are described: *Nymphes georgei* **sp. nov.** from the Early Eocene locality at Republic, Washington, U.S.A., and *Pronymphes hoffeinsorum* **sp. nov.** from Late Eocene Baltic amber. The assignment of the new Republic species to *Nymphes* Leach maintains some doubt. This is the first fossil record of the genus (or one very closely related), today restricted to the Australian region, and its biogeographical implications are briefly discussed. The genus *Pronymphes* Krüger is considered to be valid and a diagnosis is provided, as is an amended diagnosis for the wings of *Nymphes*.

Key words: Nymphidae, Eocene, Okanagan Highlands, Baltic amber

Introduction

Today, the Nymphidae is a small family of Neuroptera with 35 known species in 7 genera, restricted to Australia, New Guinea and adjacent islands (New 1982, 1985, 1986, 1988, 1991; Oswald 1997, 1998). A further species was described from the Philippines (Navás 1921), but its single known specimen is apparently lost, and thus it is impossible to confirm the occurrence of the family in that area with certainty (New 1982). Nymphids are of particular phylogenetic interest, as they exhibit numerous plesiomorphic characteristics for the clade of extant myrmeleontid families Nymphidae + Nemopteridae + Myrmeleontidae + Ascalaphidae (Henry 1982; Oswald 1998), with the oldest fossil record among these. Fossil occurrences include eleven species belonging to eight genera recorded from the Late Jurassic to Eocene of Europe, Asia and South America (Krüger 1923; Carpenter 1929; Panfilov 1980; Ponomarenko 1992; Martins-Neto 2005; Menon *et al.* 2005; Ren & Engel 2007; Engel & Grimaldi 2008). Hitherto, Cenozoic nymphids were known only from Late Eocene (Priabonian) Baltic amber, *i.e.*, the genus *Pronymphes* Krüger, represented by an adult (Pictet-Baraban & Hagen 1856; Krüger 1923) and a larva tentatively assigned to this genus (MacLeod 1971). Here we describe two new species of Nymphidae, from the Early Eocene (Ypresian) of the North America, tentatively assigned to the genus *Nymphes* Leach, and from Priabonian Baltic amber, tentatively assigned to the genus *Pronymphes*.

Material and methods

One specimen described here is from exposures of the Tom Thumb Tuff Member of the Klondike Mountain Formation in town of Republic, Ferry County, in northeastern Washington (USA), assigned a date of 49.42 ±

0.54 Ma, *i.e.*, Ypresian (Greenwood *et al.* 2005; Moss *et al.* 2005). The other is from Baltic amber collected in the Jantarny [=Palmnicken] amber mine, Kaliningradskaya Oblast', Russia. The amber is embedded in epoxy resin; amber + resin size is 19 x 17 x 9 mm.

Although an early Middle Eocene (Lutetian) age has been estimated for the Baltic amber-bearing sediments by K-Ar dating (Ritzkowski 1997), marine microfossil biostratigraphy supports a younger, Priabonian determination (Kosmowska-Ceranowicz & Müller 1985; Kosmowska-Ceranowicz 1987). For this, and other stratigraphic reasons discussed by Perkovsky *et al.* (2007), here, we follow the Priabonian estimation.

We use the traditional (*sensu* Wootton 2003) venational terminology of Comstock (1918) in the recent interpretation of Oswald (1993), Makarkin & Menon (2005), Archibald & Makarkin (2006), and Wedmann & Makarkin (2007). Venation abbreviations: 1A–3A, anal veins; C, costa; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media (M); R1, first branch of radius (R); Rs, radial sector; Rs1, most proximal branch of Rs; Sc, subcosta. All wings are figured with the apex to the right.

Institutional abbreviations: SRIC, Stonerose Interpretive Center, Republic, Washington (U.S.A.); SDEI, Senckenberg Deutsches Entomologisches Institut, Müncheberg (Germany).

Systematic paleontology

Insecta Linnaeus, 1758

Neuroptera Linnaeus, 1758

Nymphidae Rambur, 1842

Genus *Nymphes* Leach, 1814

Type species. *Nymphes myrmeleonoides* Leach, 1814, by monotypy.

Amended diagnosis for characters of the wing (based on New 1982). Separated from other nymphid genera by the following combination of character states of its wing venation [comparative character states of other genera in brackets]: M simple or forked distad origin of Rs1 in forewing [shared by *Austronymphe* Esben-Petersen, 1914, but forked much proximad origin of Rs1 in other genera]; large enclosed cell between 2A, 3A in forewing absent [present in *Austronymphe*]; CuA space in forewing, MP space in hind wing large, of characteristic 'myrmeleontid' triangular shape, enclosed by distal portion of MP, basalmost branch of MP [shared by *Austronymphe*, but absent or reduced in all fossil genera]; crossveins between branches of CuP in forewing, CuA in hind wing present (except *N. nigrescens*) [this combination absent in other genera].

Included species. *Nymphes georgei* sp. nov. from the Ypresian of North America (Republic, Washington, U.S.A.); five extant species from Australia and Tasmania: *N. myrmeleonoides*, *N. modesta* Gerstaecker, 1885b; *N. paramyrmeleonoides* New, 1982; *N. nigrescens* New, 1982; *N. aperta* New, 1982.

Comments. The diagnosis provided here augments that of New (1982), which distinguishes general characters of the insect; here, we revise this with regards to wing characters.

Nymphes georgei sp. nov.

Fig. 1A–B

Etymology. The specific epithet is formed from the surname of Steven George, collector of the holotype, in recognition of his generous contribution to science in the donation of this specimen.

Holotype. Specimen SR09-07-08 (part only), collected by Steven George, and deposited in SRIC. A well-preserved, incomplete hind wing.

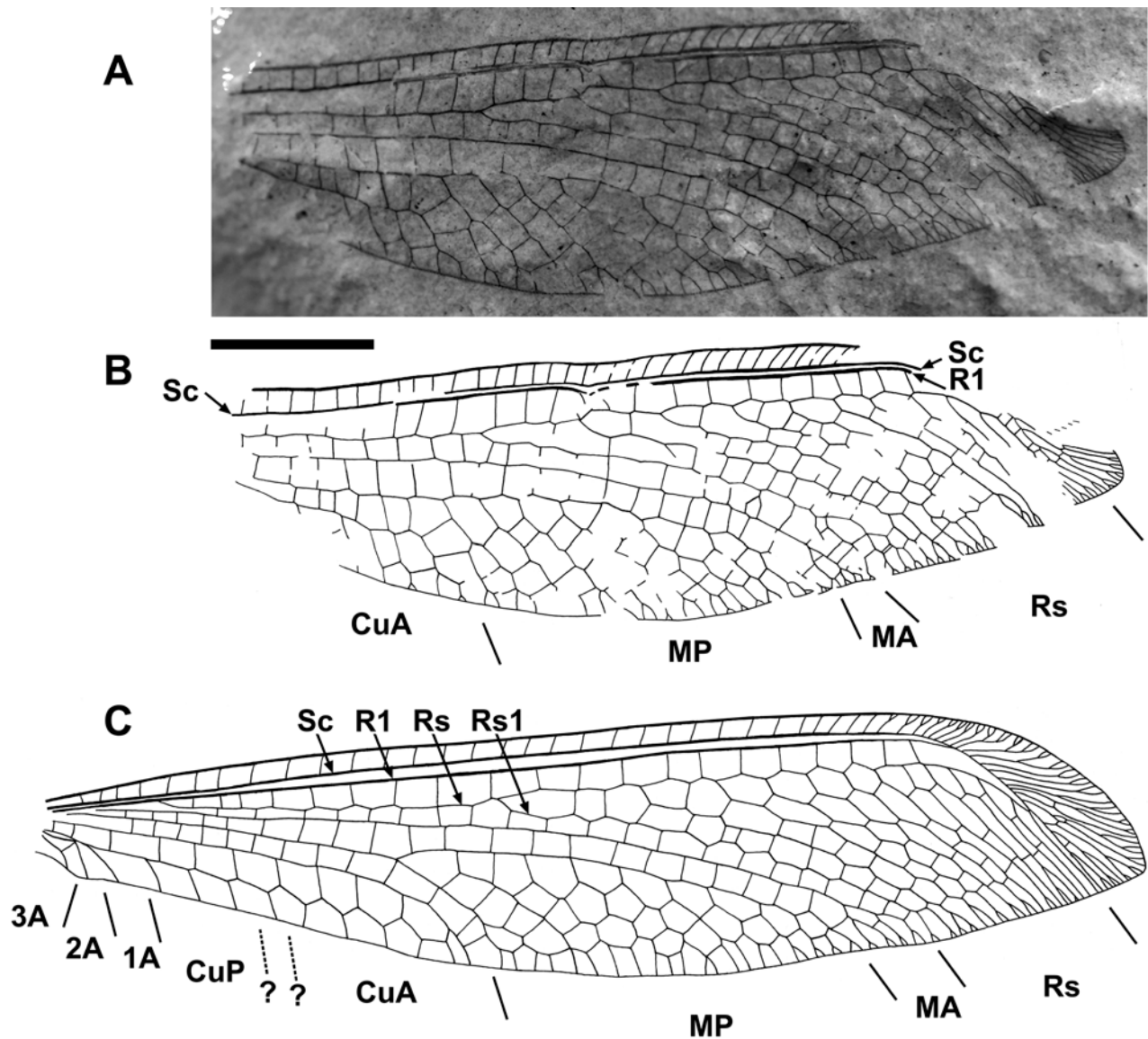


FIGURE 1. Hind wings of *Nymphes georgei* sp. nov. and *N. aperta*. **A**, photograph of holotype specimen SR09-07-08. **B**, *N. georgei* sp. nov., holotype specimen SR09-07-08. **C**, *N. aperta* (re-drawn from New, 1982: Fig. 42; vein labelling is ours). Scale bar = 5 mm (for A–B; C, scale not provided by New, 1982).

Type locality and horizon. Tom Thumb Tuff Member of the Klondike Mountain Formation, exposure A0307, Republic, Washington, U.S.A.; Ypresian.

Diagnosis. Hind wing separable from those of *N. myrmeleonoides*, *N. modesta*, *N. paramyrmeleonides* by absence of tornus, subcostal crossveins; from those of *N. aperta* by branches of MP originated at more obtuse angle, area between distal portion of CuA, MP, then MP1 broader; from those of *N. nigrescens* by distal origin of Rs1, slightly distal to termination of CuA [Rs1 originated much proximal to termination of CuA in *N. nigrescens*].

Description. Hind wing elongate, without tornus, with apex shifted posteriad; preserved portion 27 mm long (estimated complete length about 34–35 mm), 8.2 mm wide. Trichosors prominent along entire preserved margin: one between each vein tip apically along posterior margin, many (up to about five) between veinlet tips along anterior margin, posterior margin in mid- and basal wing. Each vein/veinlet tip thickened like trichosors. Macrotrichia along veins rather short. Costal space narrow. Subcostal veinlets simple, perpendicular to Sc basally, bent apically. Sc+R1 entering margin far beyond apex; veinlets of Sc+R1 deeply

forked, each branch with shallow marginal fork; two crossveins preserved between veinlets of Sc+R1. Subcostal space narrow, without crossveins. R1 space broad, with numerous crossveins arranged rather regularly. Rs probably originated near wing base, with 10 branches dichotomously branched distally. Rs1 originated far distant from wing base, rather profusely branched distally. MA slightly concave, somewhat arced, only few branched distally. MP slightly convex, markedly arced distal to its proximal branch, with seven branches, partly dichotomously branched. MP space triangular, enclosed by distal portion of MP, basalmost branch of MP. Radial, medial crossveins numerous, arranged irregularly. MP, CuA approach to each other toward wing base; several crossveins between them. CuA probably slightly concave (poorly preserved), pectinately branched (two branches preserved); each branch connecting by crossvein to other (three crossveins preserved). CuP, anal veins not preserved. Membrane hyaline.

Comments. The extant genera of Nymphidae are divided into the morphologically distinct *Nymphes*-group (*Nymphes*, *Nesydrion* Gerstaecker, 1885a, *Austronymphes*) and *Myiodactylus*-group (*Myiodactylus* Brauer, 1866, *Osmyllops* Banks, 1913, *Nymphydron* Banks, 1913, *Norfolius* Navás, 1922) (New 1984). Formerly, the *Myiodactylus*-group was considered to constitute a separate family, the Myiodactylidae (Handlirsch 1906–1908; Withycombe 1925; Tillyard 1926), and has subsequently been treated as a subfamily of Nymphidae (Henry 1982; Makarkin 1990).

Nymphes georgei belongs confidently to the *Nymphes*-group by the following hind wing features: the MP space has a characteristic triangular area enclosed by the distal portion of MP and the basal-most branch of MP [absent in *Myiodactylus*-group]; Rs1 is originated distant from wing base [relatively close to wing base, much proximal to termination of CuA in *Myiodactylus*-group]; costal space is narrow [broad in *Myiodactylus*-group]. Fortunately, the venation of hind wings of all species of Nymphidae (both fossil and extant, except the Early Cretaceous *Olindanymphes makarkini* Martins-Neto, 2005) is well known, allowing some confidence in its generic affinity.

All preserved character states indicate that the hind wing venation of this species is indistinguishable from that of *Nymphes* species. Indeed, the hind wing venation of *Nymphes* possesses a distinctive combination of the long stem of Rs (*i.e.*, Rs1 is originated distally) and the presence of crossveins between branches of CuA. The venation of *N. nigrescens* differs greatly from that of other species of the genus. For example, Rs originates much more distally in its hind wing, costal crossveins are present in the apical portions of both wings, and there are no crossveins connecting branches of CuP in the forewing. New (1982) mentioned that this species “may eventually be separated into a new genus” (p. 718). The genus *Nymphes* is also heterogeneous for the presence/absence of subcostal crossveins in both wings and M is either deeply forked or simple in the forewing. While understanding that further examination might then indicate that *Nymphes* should be broken into smaller genera, this is outside of the scope of this study, and here, we assign *N. georgei* to this genus as currently defined. However, the *Nymphes* affinity of this new species should be considered *formally* tentative, as the specimen is represented by only an incomplete hind wing; we should not exclude a venational convergence between this fossil species and species of *Nymphes*.

The venation of *N. georgei* is most similar to that of *N. aperta* in wing shape, size and many venational details, including the absence of the subcostal crossveins (cf. Figs. 1B and 1C).

Other extant genera have somewhat different venation. For example, all species of *Nesydrion* have numerous subcostal crossveins and do not possess any crossveins between the branches of CuA [contrary in *N. georgei*]; the single species of *Austronymphes* has these crossveins, but the stem of Rs is short. Also, the hind wings of these two genera are broader than that of *N. georgei* in association with the rather distinct tornus in most species. The venation of all known fossil genera is considerably different from that of *N. georgei*.

Nymphes georgei is significant in that it shows that this genus (or one very close), currently found only in Australia (continental and Tasmania), was present in the Eocene of North America. This is an emergent pattern among some insects known from Eocene Republic and other Okanagan Highlands fossil localities, *e.g.*, bulldog ants (Hymenoptera: Formicidae: Myrmeciinae; Archibald *et al.* 2006), and mastotermitid termites (Isoptera: Mastotermitidae; Wilson 1977). This is in accord with a broader pattern of a number of insects that had a Northern Hemisphere distribution in the Mesozoic and/or Eocene, and are today restricted to

the Australian region, *e.g.*, Tettigarctidae (Hemiptera) (Menon 2005); Plectrotarsidae (Trichoptera) (Sukacheva & Jarzembowski 2001); the genus *Peradenia* Naumann et Masner, 1985 and its family Peradeniidae (Hymenoptera) (Johnson *et al.* 2001); and, indeed, other biota, *e.g.*, the family and genus level similarities between the Lutetian flora of Messel, Germany, and that of the modern Australian region (Burrows 1998). This is the first fossil record of *Nymphes*, and so details of its change in distribution through the Cenozoic remain obscure (*Nymphidae* is also now established in North America for the first time; the biogeographic history of the family will be examined in a future work).

Genus *Pronymphes* Krüger, 1923

Type species. *Nymphes mengeanus* Hagen in Pictet-Baraban & Hagen, 1856, by original designation.

Diagnosis. Separated from other nymphid genera by the following combination of character states of its wing venation: subcostal crossveins absent, except one basal [numerous crossveins present in *Nesydrion*]; only one crossvein between each branch of CuA in forewing, MP in hind wing [more than one in all extant genera; absent in *Liminymphe* Ren & Engel, 2007]; CuP in forewing long, pectinate [short, with only one to two branches in *Mesonymphes* Carpenter, 1929, *Olindanymphe* Martins-Neto, 2005]; CuP short, with only terminal fork in hind wing [very long, pectinate in *Cretonymphes* Ponomarenko, 1992, *Santananymphe* Martins-Neto, 2005]; R1 space moderately broad [very narrow in *Elenchonymphes* Engel & Grimaldi, 2008].

Included species. Two species, *Pronymphes mengeana*, and *P. hoffeinsorum* **sp. nov.** from Priabonian Baltic amber.

Comments. A diagnosis has not been previously provided for this genus. The gender of *Pronymphes* is feminine, as is the Latin noun *nymphes* from which it is derived, meaning brides, young women (ICZN 1999: Article 31.1.1), see also Oswald (2007).

Pronymphes hoffeinsorum **sp. nov.**

Figs. 2–4

Etymology. The specific epithet is formed from the surname of Christel and Hans-Werner Hoffeins, in recognition of their contributions to amber research.

Holotype. Specimen BaB 1544-2, collected by Christel and Hans-Werner Hoffeins, deposited in SDEI. An incomplete, crumpled insect in a yellow, translucent piece of amber: distal portion of abdomen; distal two third of left forewing, covered by a partial left hind wing; fragmentary right fore- and hind wings overlapping. Syninclusions include stellate hairs and nemathelminthes.

Type locality and horizon. Baltic amber (Yantarny [=Palmnicken], Kaliningradskaya Oblast', Russia); Priabonian.

Diagnosis. Forewing separable from that of *P. mengeana* by fork of M located much distally, only slightly proximal to origin of Rs1 [far proximal to origin of Rs1 in *P. mengeana*].

Description. Distal portion of abdomen (preserved portion 4 mm long); terminal, genitalic segments obscured, probably female judging from prolonged laterally 8th tergite (Fig. 4).

Forewing. Maximal preserved length of left forewing 12.1 mm (estimated length about 19 mm), 5.5 mm wide. Wing margin with distinct trichosors: one between tips of each two veins along apical margin; three to four between tips of veinlets/veins (one between branches of shallow marginal forks) along costal, hind margin. Each vein/veinlet tip thickened like trichosors. Macrotrichia along veins rather long. Costal space relatively narrow, dilated towards base. Subcostal veinlets bent, simple medially, shallowly forked distally. Sc+R1 entering margin nearly at apex; proximal four veinlets of Sc+R1 shallowly forked, next three veinlets deeply dichotomously branched; no crossveins preserved between veinlets of Sc+R1. Subcostal space rather broad, no crossveins. R1 space broaden towards base, with eight crossveins arranged rather regularly between

origin of Rs1, fusion of Sc; R1, long hypostigmal cell, three crossveins distal to it. Rs with eight branches, not or few branched distally. Rs1 origin far distant from wing base, with only very shallow marginal fork. M forked slightly proximal to origin of Rs1. MA with two distal branches, shallowly forked. MP with three branches: proximal-most deeply forked, two next shallowly branched; between these branches one crossvein. MP space small, triangular, enclosed by distal portion of MP, basal-most branch of MP. Radial, medial crossveins numerous; crossveins in distal portion of radial space forming outer gradate series. Between MP, CuA several crossveins. CuA occupying relatively small space, with five irregular branches, shallowly to deeply branched; each branch connecting by crossvein to other (four crossveins in total, one in left forewing anomalously incomplete). CuP pectinately branched, with simple branches, not connecting by crossveins. Membrane hyaline, without pattern.

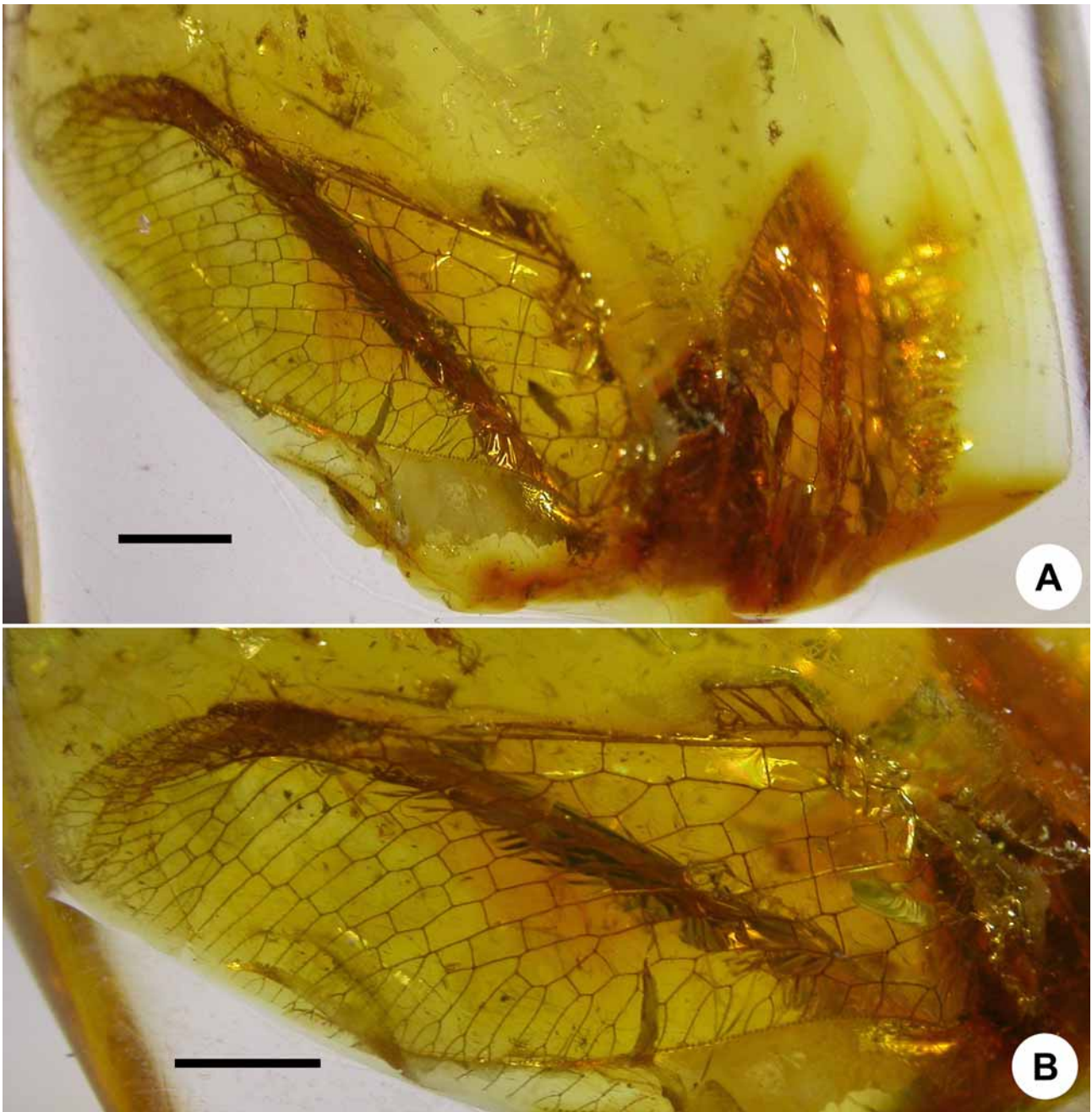


FIGURE 2. *Pronymphes hoffeinsorum* sp. nov., photographs of holotype specimen BaB 1544-2. **A**, specimen as preserved. **B**, left wings (mainly the forewing visible). Scale bar = 2 mm.

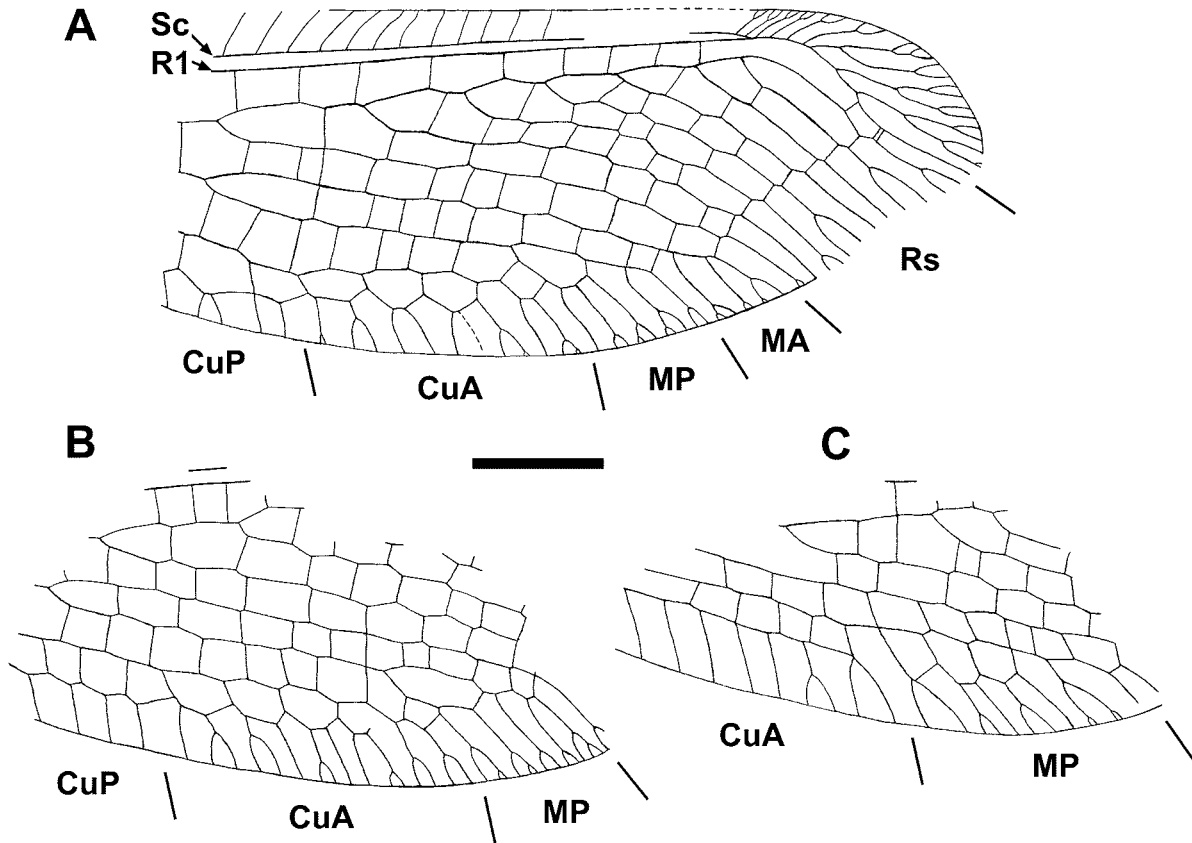


FIGURE 3. Drawings of wings of *Pronymphes hoffeinsorum* sp. nov., holotype specimen BaB 1544-2. **A**, left forewing. **B**, right forewing. **C**, right hind wing. Trichosors and hairs omitted. Scale bar = 2 mm.

Hind wing without distinct tornus; 8.1 mm long as preserved (estimated length about 18 mm), 4 mm wide as preserved (estimated length about 4.5 mm). One to four distinct trichosors between each two veins along preserved apical, hind margins. Venation of apical-most portion of hind wing similar to that of forewing. R1 space rather broad in middle portion, with crossveins arranged rather regularly. Rs with three preserved branches. Rs1 origin far distant from wing base, slightly proximal to end of CuA. Preserved MA straight, with one or two branches distally. MP with five branches, one simple, other forked; between some branches one crossvein (three crossveins preserved totally). MP space triangular, small, enclosed by distal portion of MP, basalmost branch of MP. Radial, medial crossveins numerous. Between MP, CuA several crossveins. CuA pectinately branched (seven branches preserved), not connected by crossveins. CuP, anal veins not preserved. Membrane hyaline, without pattern.

Comments. Judging from Pictet-Baraban and Hagen's original description and figure (1856: Pl. 8, Fig. 15) and the redescription of Krüger (1923), *Pronymphes mengeana* is represented by a possibly incomplete body and the basal half of both right wings. Its type seems to be lost. Unfortunately, mainly the proximal parts of the wings of *P. mengeana* and the distal parts of *P. hoffeinsorum* are preserved. In spite of this, there is enough available comparative venation to strongly associate these as congeners and to confidently distinguish them as separate species. Given the incomplete nature of these specimens, placement of the new species in *Pronymphes* remains tentative.

The forewing of *P. mengeana* was estimated by Krüger (1923) as 27 mm long under the assumption that the 9 mm of preserved portion was a third of its complete length. However, comparing this with wings of modern species we find it more reasonable to assume that the preserved portion actually represents about half its complete length, in which case the wing would have not exceeded 20 mm long.

We conclude from analysis of *P. hoffeinsorum* and published figures of *P. mengeana* that the genus is

valid, and that *Pronymphes* belongs to *Nymphes*-group (see above). MacLeod (1971) argued in favor of a close affinity between *Pronymphes* and *Nesydrion*. The venation of these genera is indeed similar, but not identical (see diagnosis of the genus *Pronymphes*, note comparisons of crossveins in the subcostal space and between branches of CuA in the forewing and branches of MP in the hind wing). Moreover, *Pronymphes* is smaller than any species of *Nesydrion*: the minimal forewing length in *Nesydrion* (i.e., *N. diaphanus* Gerstaecker, 1885) is 23 mm (New 1982).

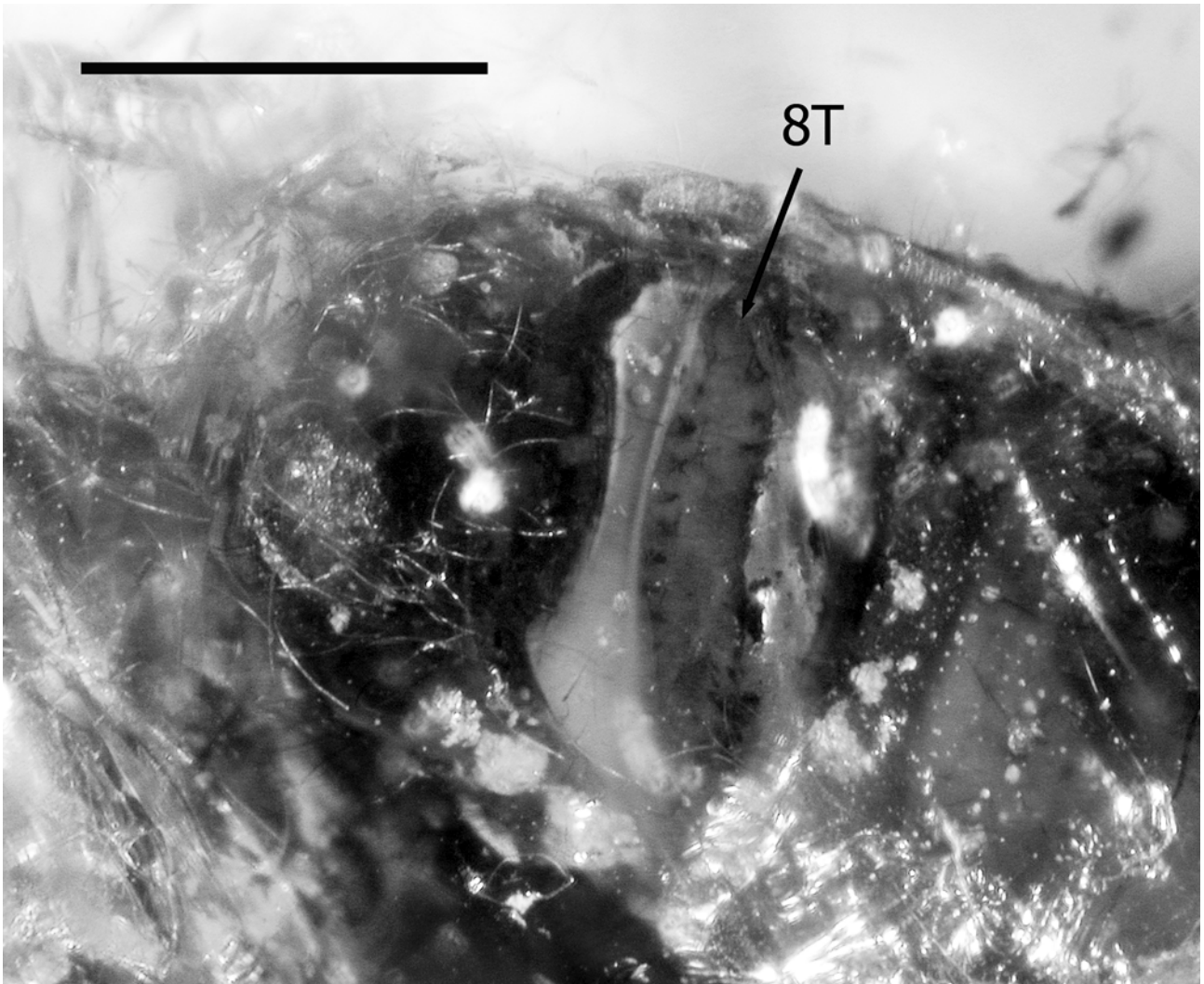


FIGURE 4. Apex of abdomen of *Pronymphes hoffeinsorum* sp. nov., holotype specimen BaB 1544-2. 8T, 8th tergite. Scale bar = 1 mm.

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