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A new leafhopper (Hemiptera: Cicadellidae) from late Eocene Rovno amber described based on an adult and associated last-instar nymph from Perebrody (Ukraine)

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Abstract

Rovnoxestus rasnitsyni **gen. et sp. nov.** is described from Eocene Rovno amber based on an adult female and fifth-instar nymph collected at a recently discovered locality at Perebrody, Rovno Province, Ukraine. The new fossil taxon is tentatively placed in Aphrodinae and resembles *Xestocephalites* Dietrich & Gonçalves from Eocene Baltic amber but has the hind femur macrosetal formula 2+2+1 and hind tarsomere I in both nymph and adult with an elongated inner preapical seta. This is the first species of Eocene leafhopper for which both the adult and nymph are described in detail.

Keywords: Homoptera, Auchenorrhyncha, morphology, taxonomy, fossil

Introduction

Leafhoppers (Cicadellidae) are the largest family of Hemiptera, with >2600 extant genera and >23,000 species (Dmitriev, 2003). Although they are presently among the most abundant herbivores in habitats ranging from tropical rainforest to temperate and alpine grassland, their fossil record remains very sparse, with fewer than 100 fossil taxa described (Dietrich & Perkovsky, 2019). The oldest undoubted Cicadellidae are known from Lower Cretaceous compression fossils (Hamilton, 1990, 1992). A few species have also been described from mid-Cretaceous Kachin amber (Poinar & Brown, 2020; Wang *et al*., 2018; Chen *et al*., 2019, 2021). Recent molecular divergence time analyses (Dietrich *et al*., 2017) place the origins of most major cicadellid lineages (*i.e*., subfamilies) during the lower to mid-Cretaceous. Species belonging to modern leafhopper genera have been described from Miocene-age Dominican amber (Dietrich & Vega, 1995) but fossils from the older Eocene and Cretaceous ambers, so far, appear to represent extinct lineages and are often difficult to associate with modern tribes. Eocene ambers, in particular, have so far yielded several leafhopper fossils that have combinations of morphological characters unknown in modern forms (*e.g*., Szwedo & Gębicki, 1998, 2002). Thus, these early Cenozoic amber fossils document an important stage in the evolution of Cicadellidae.

Most known genera and species of Eocene-age Cicadellidae have been described from the well-known Baltic amber from northern Europe (reviewed by Szwedo, 2002; Dietrich & Gonçalves, 2014) but, so far, only one cicadellid has been described from Rovno amber, which is similar in age (35–37 Ma) but distributed farther south, mostly in Ukraine (Dietrich & Perkovsky, 2020). Based on FTIR spectroscopy and stable isotope analysis, Mänd *et al*. (2018) reported that Rovno amber is of the same age as Baltic amber and derived from related plant species but has a more southern and, therefore, different geographical origin. The new locality (Perebrody) is situated on the Lva River. The Lva originates on the border of Zhitomir province, so this source of amber may represent the easternmost in Rovno province with possible similarity to the Olevsk amber forest in Zhitomir province. To date, only two new genera and four new species of gall midges (Cecidomyiidae), a new anthribid beetle, one species of mite, two caddisfly species (Trichoptera) including a new *Electrotrichia* (Melnitsky *et al*., 2021), and two ant species including a new *Formica*, have been reported from amber originating in Zhitomir province (Olevsk and nearby Gulyanka localities) (Fedotova & Perkovsky, 2015, 2017;

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Perkovsky, 2017; Legalov *et al*., 2021; Radchenko *et al*., 2021).

The new fossil taxon from Eocene Rovno amber described herein is important because it is only the second leafhopper species reported from this fauna (Dietrich & Perkovsky, 2020), exhibits traits not previously reported in Eocene leafhoppers, and is distinct from known leafhoppers described from the better-studied and geographically proximate Baltic amber of the same age.

Material and methods

The studied leafhopper specimens were mined at Perebrody (Lva River valley), in the north of Rovno province, Ukraine, near the border with Belarus; they are the first reported insects from this locality. The holotype adult was found in a partially clear, partially blackened by plant debris piece with weight 7.4 g and size 35×25×12 mm after primary treatment. The paratype nymph is in a clear piece with weight 8.7 g and size 65×31×16 mm after primary treatment; syninclusions were cut and housed with separate inventory numbers. Morphological terminology follows Dietrich (2005) for adult characters and Dmitriev (2002) for nymphs. Photographs were taken using a Leica Z16 APO microscope equipped with a Leica DFC 450 camera and processed by LAS Core software.

The holotype adult female and paratype nymph are housed in the Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine (SIZK).

Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Auchenorrhyncha Duméril, 1805
Infraorder Cicadomorpha Evans, 1946
Superfamily Membracoidea Rafinesque, 1815
Family Cicadellidae Latreille, 1825
Subfamily Aphrodinae Haupt, 1927

Rovnoxestus gen. nov.

(Figs 1–4)

Type species. *Rovnoxestus rasnitsyni* **sp. nov.** here designated.

Etymology. The genus name, a masculine noun, was formed by combining the name of the fossil amber, Rovno, with an abbreviation of the name of a possibly related modern genus, *Xestocephalus*; from Greek: ξεστός, smooth, polished.

Diagnosis. The new genus differs from other fossil and modern cicadellid genera in having the following combination of traits: head slightly broader than pronotum with anterior margin slightly produced and rounded to face, ocelli on anterior margin well separated from eyes, lateral frontal sutures extended to ocelli; forewing fully developed, venation somewhat elevated and complete, appendix very narrow; hind wing well developed with submarginal vein narrowly separated from apical margin; front tibia with stout anteroventral seta near midlength; hind femur macrosetal formula 2+2+1, tarsomere I with elongate ventromesal seta at apex.

Rovnoxestus resembles *Xestocephalites* Dietrich & Gonçalves, 2014 from Eocene Baltic amber in overall habitus and in having a stout anteroventral seta near the midlength of the front femur, but differs in having the head wider than the pronotum, the pronotum relatively long, the hind femur macrosetal formula 2+2+1, and hind tarsomere I with an elongate ventroapical seta.

Rovnoxestus rasnitsyni sp. nov.

Material. Holotype (male): SIZK Pe-27, late Eocene Rovno amber. Ukraine: Rovno prov.: Perebrody. Syninclusions: male Sciaridae, two unidentified Nematocera, one Scelionidae, stellate hairs. Paratype: fifth instar nymph SIZK Pe-118, late Eocene Rovno amber. Ukraine: Rovno prov.: Perebrody. Syninclusions: two Psychodidae, female of Chironomidae, Collembola: Entomobryomorpha, two Empididae, stellate hairs.

The holotype specimen is a complete, intact, adult female embedded in a piece of pale greenish yellow amber with extensive milky veil and plant/soil debris obscuring many morphological details of the specimen, particularly the face and ventral part of the thorax. The paratype is a complete, intact, fifth-instar nymph with the entire dorsum completely visible but with most of the venter concealed by a milky veil that obscures several details of the facial structure and leg chaetotaxy.

Etymology. The species name is a Latin noun in the genitive case honoring Prof A.P. Rasnitsyn in recognition of his many important contributions to knowledge of the fossil record of insects.

Description. Measurements (mm).

Adult: Body length 6.1; head width (dorsal aspect) 1.4, head length (medial) 0.4, pronotum maximum width 1.4, pronotum length (medial) 0.9; front femur length 0.95, tibia length 1.0; middle femur length 0.9; tibia length 1.3; hind femur length 1.6, tibia length 2.9; forewing length 4.7. Overall coloration uniformly black.

Head in dorsal view (Figs 1C, 3A) broader than pronotum, anterior margin parabolically rounded, crown moderately convex, slightly longer in middle than next to eyes, width between eyes approximately twice median length, eye width slightly less than crown width between eyes. Ocelli large, on anterior margin of head, separated from eyes by two ocellar diameters. Face slightly convex,

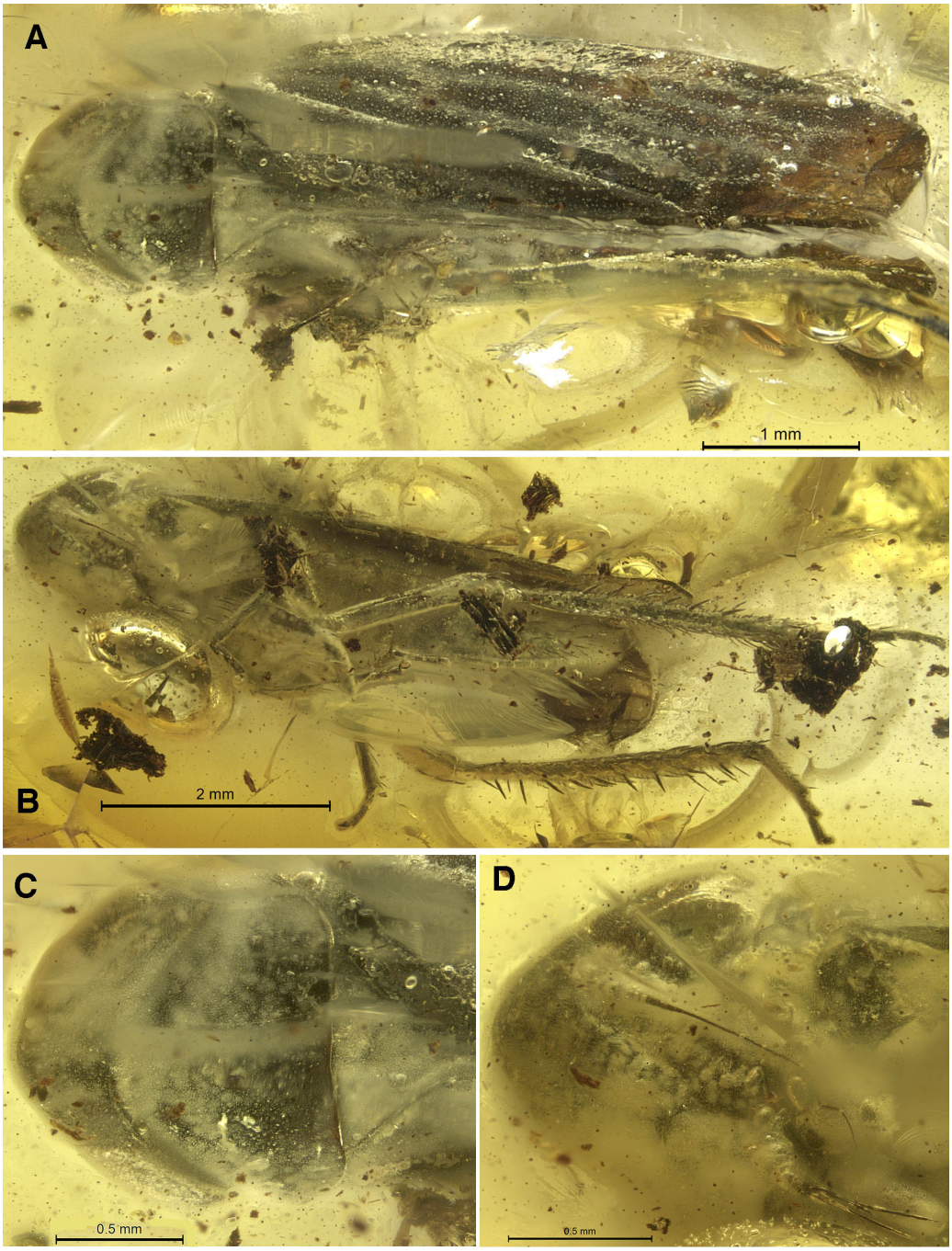

FIGURE 1. *Rovnoxestus rasnitsyni* **sp. nov. A**, Dorsal habitus. **B**, Ventrolateral habitus. **C**, Details of head and thorax, dorsal view. **D**, Face, ventrolateral view.

frontoclypeus (Figs 1D, 3C) slightly longer than width between antennal bases, shagreen with some indistinct transverse rugae; lateral frontal sutures extended to ocelli. Antennae shorter than head width, arising from shallow pits closer to anterodorsal than to ventral corners of eyes. Rostrum slightly tapered, extended to middle trochanters.

Pronotum slightly more than twice as long as crown, lateral margin moderately long, divergent posterad (Figs 1C, 3A). Exposed part of mesonotum shorter than scutellum, scutellar sulcus arcuate (Fig. 3A).

Forewing macropterous, texture granulose, mostly opaque except near apex; clavus approximately two thirds total length; venation somewhat elevated and moderately well delimited, three anteapical cells present, appendix very narrow, wing apices not overlapping at rest, inner apical cell extended to apical margin (Fig. 3F). Hind wing membrane with reticulate pattern, submarginal vein narrowly separated from margin, complete distally.

Front femur with anteroventral macroseta near midlength and some additional ventral setae more distad; tibia row PD with three widely spaced macrosetae in

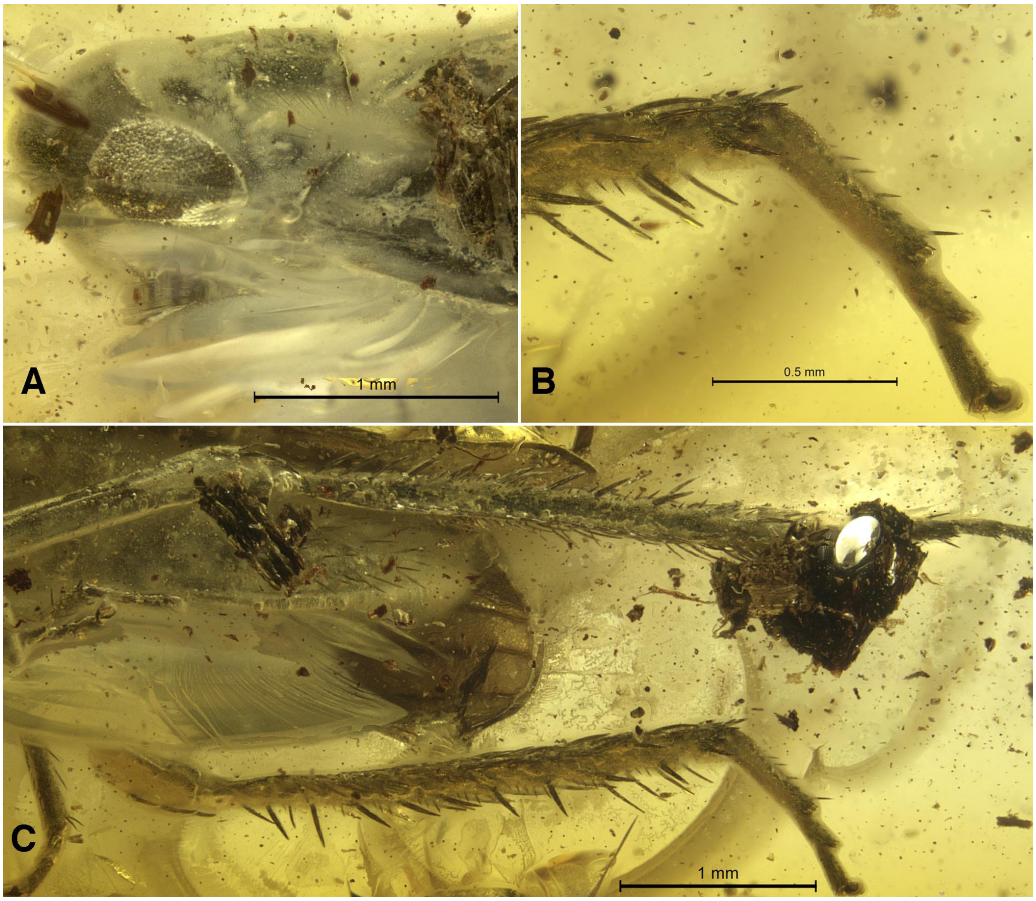

FIGURE 2. *Rovnoxestus rasnitsyni* **sp. nov. A**, Head and thorax, lateral view. **B**, Hind tarsus and apex of tibia, ventrolateral view. **C**, Posterior part of body showing legs, hind wing apex, and pygofer.

distal half (possibly more basally), AD with single distal macroseta, AV with at least 12 long setae, PV with a few shorter, more widely spaced setae. Middle tibia row PD with several macrosetae, AD with only distal macroseta present. Hind femur macrosetal formula 2+2+1 with penultimate pair close-set (Fig. 3E). Tibial row AD with 11 macrosetae and 3–5 small setae between successive macrosetae, distal setae in each intercalary series progressively larger; row PD with 20 setae approximately uniform in length, slightly longer and thinner than AD macrosetae; AV with ~19 close-set setae; PV with ~29 setae (Figs 2C, 3E); tarsus *ca*. half length of tibia, tarsomere I as long as II and III combined, with dorsoapical pair of macrosetae, two ventral longitudinal rows of stout setae and pecten with 3 platellae, inner preapical ventral seta elongate (Figs 2B, 3D).

Female pygofer elongate with numerous scattered macrosetae, ovipositor approximately half total length of abdomen, extended slightly beyond pygofer (Fig. 2C).

5th instar nymph: Body. Length 5.6 mm. Body slender, not flattened, without flattened setae, with only macrosetae organized into longitudinal rows (Fig. 4A, B).

Head. Without macrosetae. Crown (Fig. 4A) more than 1.5× wider than long, angulately rounded. Crown lateral margin carinately elevated above eye level. Lateral edges long, parallel to each other, only slightly shorter than middle line of head. Ecdysial line on dorsal surface of head. Angle formed by ecdysial line almost 180 degrees. Acrometope present, about 1/3 of the crown length. Median longitudinal carina on crown absent. Ocelli at fore margin of head, close to eyes. Crown-face transition narrowly rounded. Face (Fig. 4C) longer than wide, without longitudinal carina. Postclypeus longer than wide. Antennae attached near upper margins of eyes, first antennal segment visible from above, antennae short, not or just reaching apex of anteclypeus. Antennal flagellum not segmented.

Thorax. Thorax (Fig. 4A) without macrosetae on dorsum. Pronotum lateral margin shorter than pronotum medially.

Wings. Forewing pad moderately long, 1.6× as long as pterothorax (Fig. 4A).

Legs. Fore tibia rounded dorsally. Hind femur setal formula 2+2+1, setae of penultimate pair set close to each other. Cross section of hind tibia narrowly rectangular (distance AD-AV much greater than AD-PD). Hind tibia AD row with 9–11 macrochaetae. PD row of hind tibia with intercalary setae shorter than macrosetae (Fig. 4E).

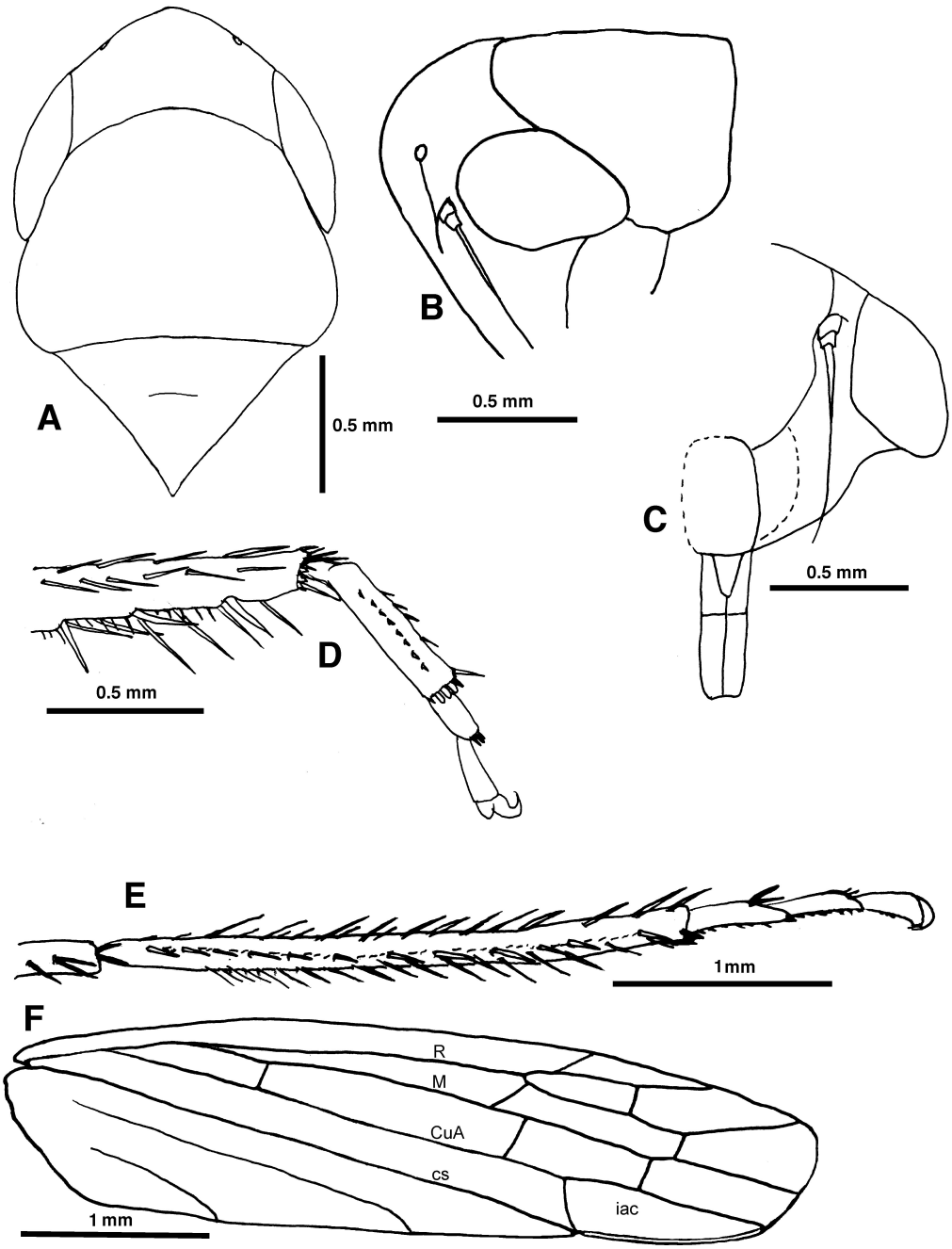

FIGURE 3. *Rovnoxestus rasnitsyni* **sp. nov. A**, Head, pronotum, mesonotum and scutellum, dorsal view. **B**, Head and pronotum (in part), dorsolateral view. **C**, Face, anteroventral view (partially reconstructed. **D**, Hind tarsus and apex of tibia, ventrolateral view. **E**, Hind femur, tibia and tarsus, dorsolateral view. **F**, Forewing. Abbreviations: cs, claval sulcus; iac, inner apical cell.

AD row of hind tibia with 1–3 setae between each pair of macrosetae. PV row of hind tibia with setae increasing in size towards apex of tibia. Pecten of hind tibia with platellae. Ventral surface of hind tarsomere I with two well developed longitudinal rows of setae, without platellae, last seta of PV row significantly enlarged. Apex of hind tarsomere I not pointed; pecten consists of several platellae (Fig. 4D).

Abdomen. Lateral margins of abdominal tergites not flattened. Abdomen without dorsomedial carina, without setal tubercles, with macrosetae of moderate size, about 1/3 of tergite length. Abdomen with eight longitudinal rows of macrosetae situated at hind margin and hind corners of each tergite (Fig. 4B). Fore and lateral margins of abdominal tergites without macrosetae.

Nymph terminalia. Pygofer dorsally more than 2× as long as tergite VIII, incised along the midline, with 2 groups of numerous macrosetae. Pygofer appendages set close to each other. Gonapophyses I shorter than pygofer length.

Coloration. Main coloration brownish. Red pigment absent. Without distinct color pattern; entire body,

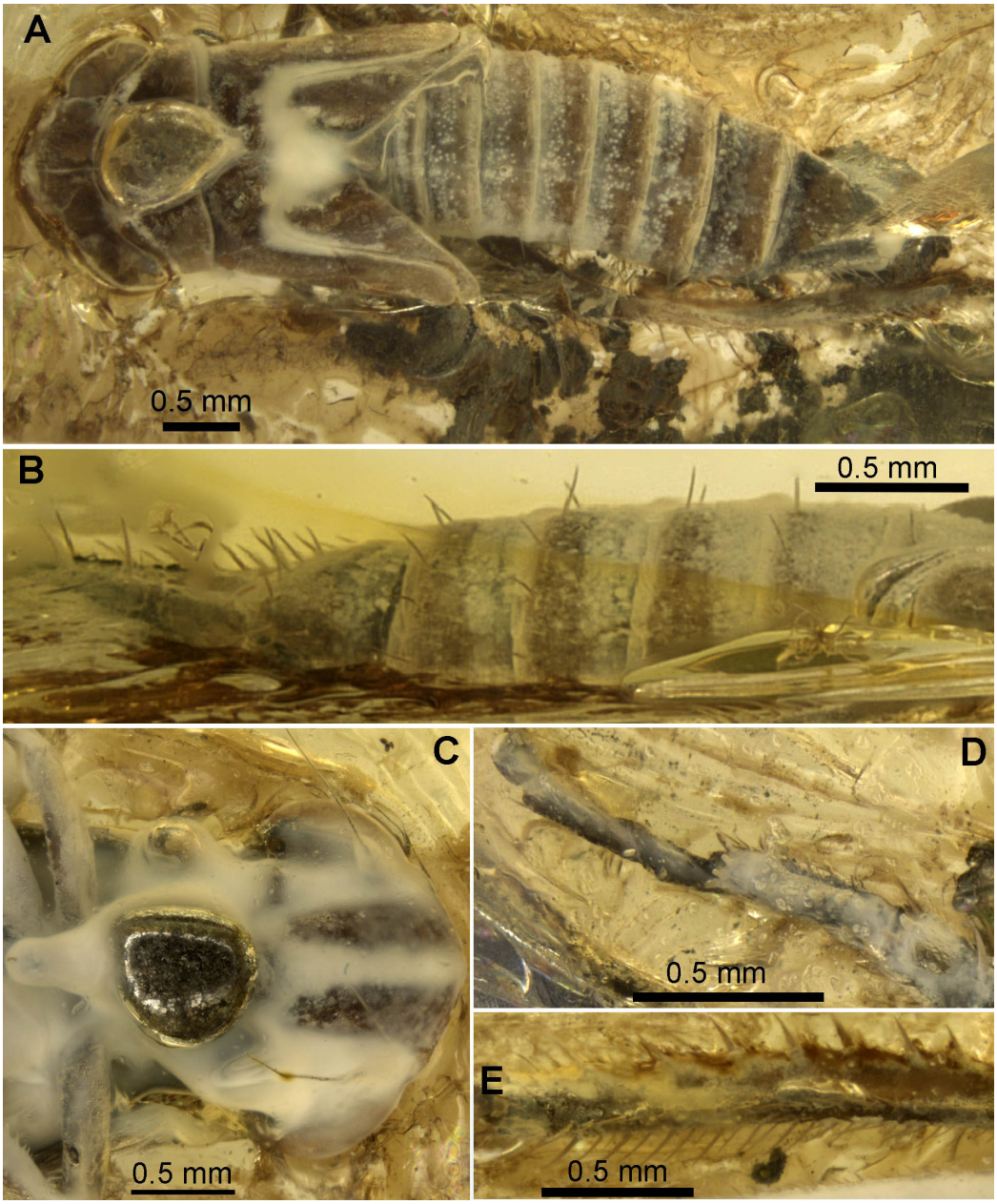

FIGURE 4. *Rovnoxestus rasnitsyni*, fifth instar nymph. **A**, Dorsal habitus. **B**, Dorsal part of abdomen, lateral view. **C**, Head and anterior part of thorax, ventral view. **D**, Left hind tarsomere, ventral view. **E**, Right hind tibia, ventrolateral view.

especially abdominal tergites covered with small pale dots. Setal areolae on abdomen not developed. Hind margin of metanotum without dark spots. Posterior half of each abdominal tergites slightly darker than anterior half, which has more pale dots. Legs without dark setal areolae.

Discussion

Placement of *Rovnoxestus* to subfamily is tentative. Based on the adult morphological characters visible in the holotype, it could belong either to Aphrodinae or Deltocephalinae Dallas, 1870. The former subfamily is doubtfully monophyletic and defined mainly based on a combination of plesiomorphic and apomorphic traits, including presence of ocelli on the anterior margin of the crown well separated from the eyes, hind femoral macrosetae with a 2+2+1 arrangement, complete forewing venation and ligulate male subgenital plates, but has not been recovered as monophyletic in recent phylogenetic analyses of Cicadellidae. The latter subfamily is a well-supported monophyletic group defined by several morphological synapomorphies but most of these are in the male terminalia (triangular male subgenital plates, styles broadly bilobed basally) and females cannot be

placed with certainty without details of the forewing venation (presence of a crossvein connecting vein Pcu to CuP. Unfortunately, these details are not clearly visible on the fossil. In overall habitus, the new genus resembles *Xestocephalites* Dietrich & Gonçalves, 2014 (tentatively included in Aphrodinae: Xestocephalini), described from Eocene Baltic amber but differs in having the crown more obviously produced, the pronotum relatively long, the hind femoral macrosetae 2+2+1 and hind tarsomere I with an elongate inner ventroapical seta. The latter feature appears to be unique among known Eocene leafhopper fossils. Some undescribed cicadellids from mid-Cretaceous Kachin amber have a pair of elongate setae in the same position (unpublished observations).

The fifth-instar nymph from the type locality is similar to the adult holotype in overall size and body structure, including leg chaetotaxy, so it seems likely that the two specimens are conspecific. The nymph does not closely resemble any modern cicadellid for which nymphs have been studied previously, but it shares some traits with the modern aphrodine tribe Portanini, all extant species of which are restricted to the Neotropical region. These traits include lack of macrochaetae on the head and thorax, and placement of the antennae relatively high on face, so that antennal bases are visible in a dorsal view of the head. Nevertheless, nymphs of modern Portanini have the antennae much longer than those of the fossil, a trait also shared with Neocoelidiinae, another group presently endemic to the New World. The abdomen of the fossil nymph has the macrochaetae organized into 8 longitudinal rows (only 2 rows are present in modern nymphs of Portanini), the pecten of the hind tibia of the fossil nymph has platellae (regular macrochaetae are present in modern nymphs of Portanini). As in the adult, the pecten of hind tarsomere I in the nymph has platellae and one large inner regular seta. Most modern leafhoppers have a similar arrangement of setae on the pecten of the first hind tarsomere but the adult and nymph of *Rovnoxestus* are unique in having the inner seta of the pecten relatively long. Although, as described above, several traits visible in the adult holotype are consistent with Deltocephalinae, no characters of the adult or nymph definitely support placement in this subfamily. Therefore, *Rovnoxestus* is tentatively included in Aphrodinae based its overall similarity to *Xestocephalites* and the abovementioned head characters consistent with Portanini present in the nymph.

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