



This work is licensed under a Creative Commons Attribution 3.0 License.

Research article

urn:lsid:zoobank.org:pub:EF7DE41B-DDA5-48B8-8135-AB012C9C512A

New Baltic amber leafhoppers representing the oldest Aphrodinae and Megophthalminae (Hemiptera, Cicadellidae)

Christopher H. DIETRICH¹ & Ana Clara GONÇALVES²

^{1,2}Illinois Natural History Survey, Prairie Research Institute, University of Illinois,
1816 S. Oak St., Champaign, IL 61820

¹Email: chdietri@illinois.edu (corresponding author)

²agalliinae@yahoo.com.br

¹urn:lsid:zoobank.org:author:82FCB86C-54B4-456A-AE5E-D7847D271CB9

²urn:lsid:zoobank.org:author:A69C5C0D-76BC-420B-8FC8-E651DAC3D85F

Abstract. Three fossil leafhopper inclusions from Eocene Baltic amber, representing three new extinct genera and species, are described and illustrated. *Eomegophthalmus lithuaniensis* gen. et sp. nov. is tentatively placed in Megophthalminae, although it may represent the stem group from which Megophthalminae, Ulopinae, and Membracidae arose. *Xestocephalites balticus* gen. et sp. nov. and *Brevaphrodella nigra* gen. et sp. nov. are placed in Aphrodinae: Xestocephalini based on the structure of the head, leg chaetotaxy, and male genital capsule. These new genera and species represent the oldest known representatives of their respective subfamilies and the latter is the oldest known brachypterous adult leafhopper.

Keywords. Morphology, fossil, evolution, phylogeny, Paleogene.

Dietrich C.H. & Gonçalves A.C. 2014. New Baltic amber leafhoppers representing the oldest Aphrodinae and Megophthalminae (Hemiptera, Cicadellidae). *European Journal of Taxonomy* 74: 1-13. <http://dx.doi.org/10.5852/ejt.2014.74>

Introduction

The fossil record of leafhoppers (Cicadellidae), as reported in the literature, is very sparse, consisting of a few reports of rock fossils from the lower Cretaceous of Brazil, Eurasia and Australia (Shcherbakov 1986; Hamilton 1990, 1992), a single wing impression from the upper Cretaceous of western North America (Oman 1937), several genera and species from Eocene Baltic amber (Keilbach 1982; Spahr 1988, Szwedo 2002) and several genera and species from Oligo-Miocene Dominican amber (Dietrich & Vega 1995). Several fossil leafhoppers from Miocene deposits in Europe and North America have also been described (Metcalf & Wade 1966). Known Cretaceous leafhopper fossils are mostly either too poorly preserved to facilitate placing them to subfamily or, with the exception of two Brazilian fossils placed in Ledrinae (Shcherbakov 1992), have generalized morphology without distinctive features that would allow them to be placed with certainty in modern subfamilies. In contrast, representatives of several extant subfamilies have been reported from Baltic and Dominican amber. The cicadellid subfamilies (*sensu* Dietrich 2005) reported thus far from Baltic amber (reviewed by Szwedo 2002)

are Bathysmatophorinae, Macropsinae, Mileewinae, Ledrinae, and Typhlocybinae (*sensu* Dietrich 2005, 2011; Wei *et al.* 2010). An extinct subfamily, Nastlopiinae, description based on a first instar nymph (Szwedo & Gebicki 2002), needs more study to determine its status and relationship to other groups. Oligo-Miocene Dominican amber has yielded representatives of Aphrodinae (Xestocephalini), Cicadellinae (Cicadellini), Deltocephalinae (Athysanini), Evacanthinae (Nirvanini), Iassininae (Krisnini), Megophthalminae (Agalliini), Neocoelidiinae (Krocodonini) and Typhlocybinae (Dikraneurini; Dietrich & Vega 1995 and unpublished observations). While Dominican amber fossils are mostly referable to modern genera, most of the fossil leafhoppers present in the older (Eocene) Baltic amber appear to belong to extinct genera and, in some cases, cannot be assigned with confidence to modern tribes. This suggests that much tribe- and genus-level diversification in leafhoppers occurred during the Paleogene. Thus, Eocene Baltic amber documents an important stage in the evolution of the major lineages of Cicadellidae.

Germar & Berendt (1856) were the first authors to report on Cicadellidae from Baltic amber, describing seven species and placing two of these in *Typhlocyba* Germar, 1833, two in *Jassus* Fabricius, 1803, two in *Tettigonia* Fabricius, 1775, and one in *Bythoscopus* Germar, 1833. Unfortunately, the type material for these species was apparently destroyed during World War II and the original descriptions and illustrations are not sufficiently detailed to allow for their proper placement although, as noted by Szwedo (2002), the two species of *Typhlocyba* are probably correctly placed in subfamily Typhlocybinae, and *Bythoscopus* may be placed with reasonable confidence in Macropsini, but they cannot be placed to genus based on the information available at present. The original illustrations of *Tettigonia proavia* Germar-Berendt, 1856 and *T. terebrans* Germar-Berendt, 1856 (Germar & Berendt 1856) indicate that they belong to Bathysmatophorinae. *Tettigonia terebrans* appears to be similar to *Ambercarda skalskii* Szwedo & Gebicki, 1998, so far the only other bathysmatophorine formally described from Baltic amber. Germar & Berendt mentioned that their two “*Jassus*” species were somewhat similar to modern European species of Deltocephalinae (*Speudotettix* Ribaut, 1942 and *Thamnotettix* Zetterstedt, 1840), but they did not mention or illustrate characters that would unequivocally place these species in that subfamily. Their drawings and descriptions of these two taxa are consistent with Deltocephalinae, but they could also apply to other subfamilies; thus these two “*Jassus*” species should be treated as *species incertae sedis*.

Based on the original descriptions and illustrations, additional cicadellid species described from Baltic amber by Bervoets (1910) may be tentatively placed as follows: *Bythoscopus punctatus* Bervoets, 1910 and *Pediopsis minuta* Bervoets, 1910 belong in tribe Macropsini; *Eupteryx minuta* Bervoets, 1910 belongs in subfamily Typhlocybinae (tribal placement uncertain); *Acocephalus resinusus* Bervoets, 1910 may belong in Bathysmatophorini, but the original description and illustration are not sufficient to confirm this placement.

More recently described cicadellids from Baltic amber (Szwedo & Gebicki 1999; Gebicki & Szwedo 2001) were placed in Ledrinae and Mileewinae, respectively. Although the subfamily placements of these fossils appear to be correct, the placement of the two ledrine nymphs in the modern genus *Camptelasmus* Spinola, 1850 is questionable, given that the type material of the type species of this genus is lost, and nymphs of modern representatives have not been previously described (Jones & Deitz 2009). Jones & Deitz (2009) excluded *Camptelasmus* from Ledrinae and considered the genus to be of uncertain position within Cicadellidae. The nymphs described and illustrated by Szwedo and Gebicki (1999) do not resemble those of other known members of Ledrini (*sensu* Jones & Deitz 2009, = Petalocephalini), which are much more strongly flattened with lamelliform extensions of the tergites but, nevertheless, are consistent with Ledrinae in having the frontoclypeus narrower than the distance between the frontoclypeus and the eye, and in having setal row AD of the hind tibia with enlarged, spiniform bases. These fossils should be considered unplaced within Ledrinae until the nymphs of modern ledrines are better known.

The fossil taxa from Eocene Baltic amber described herein are remarkable in that they represent the oldest known representatives of Aphrodinae and Megophthalminae and exhibit morphological character combinations not found in modern representatives of their respective groups. The geologic age of Baltic amber is generally considered to be Late Eocene (37.7±3 Ma; Perkovsky *et al.* 2007) although some evidence suggests that a Middle Eocene (44.1±1 Ma) or even older origin is possible (reviewed by Szwedo & Sontag 2009; Weitschat & Wichard 2010).

Material and Methods

All specimens studied were obtained by the first author from amber dealers in Palanga, Lithuania, where the material was originally collected. The specimens are deposited in the Insect Collection of the Illinois Natural History Survey (INHS). Digital photographs were taken using a Q-Imaging digital camera attached to an Olympus SZX-12 stereomicroscope.

Abbreviations

AD	=	anterodorsal
AM1	=	apical anteromedial
AV	=	anteroventral
CuA	=	anterior Cubitus
M	=	Media
PD	=	posterodorsal
PV	=	posteroventral
R	=	Radius

Results

Order Hemiptera Linnaeus, 1758
Suborder Auchenorrhyncha Dumeril, 1806
Infraorder Cicadomorpha Evans, 1946
Superfamily Membracoidea Rafinesque, 1815
Family Cicadellidae Latreille, 1825
Subfamily Megophthalminae Kirkaldy, 1906

Eomegophthalmus gen. nov.

urn:lsid:zoobank.org:act:8F89B113-8148-4FA5-9B5F-275F46E02416

Type-species

Eomegophthalmus lithuaniensis sp. nov.

Diagnosis

Same as for *Eomegophthalmus lithuaniensis* sp. nov., due to monotypy of this genus.

Etymology

The genus name, a feminine Latinized Greek noun, combines *eos* (“dawn”) with *Megophthalmus*, the name of a related modern genus, and refers to the apparent position of the genus as the earliest known representative of its lineage.

Eomegophthalmus lithuaniensis sp. nov.

urn:lsid:zoobank.org:act:2A1548C9-BC26-4F05-BB99-E0EE5FB55AB9

Figs 1A-B, 2A-F

Diagnosis

This species resembles extant members of the tribe Megophthalmini in having the crown of the head short and broad, the eyes relatively large and extended well laterad of the pronotum, the ocelli on the face distant from the eyes, and lateral frontal sutures of the head distinctly carinate. It is however easily distinguished by its relatively large and more dorsally placed ocelli, elongate wings, and short, broad second valvulae.

Etymology

The species name refers to the country in which the holotype was collected.

Material examined

Holotype female, Eocene Baltic amber, Palanga, Lithuania (INHS).

Description

MEASUREMENTS. (in mm). Body length including forewings at rest 9.0; head width 2.9; pronotum width 2.5; front femur length 1.1, tibia 1.4; middle femur length 1.4, tibia 2.0; hind femur length 2.0, tibia 3.5, tarsus 1.1; forewing length 7.1; ovipositor length 2.0.

STRUCTURE. Body elongate, somewhat depressed, uniformly dark brown. Head broad and short, much wider than pronotum; eyes bulbous; crown very short and poorly developed, coronal suture not visible, posterodorsal margin of head elevated and forming vertical rim above pronotum; ocelli large, slightly closer to midline than to eyes, in depressions near dorsal margin of face; antennal ledges oblique, flattened, slightly extended over antennal pits; antenna nearly as long as width of head; frontoclypeus narrow, rugulose, elevated and shelflike ventrolaterally in relation to gena, concave dorsomedially, extended to dorsal margin of face in anteroventral view, evenly tapered from antennal pit to anteclypeus; lateral frontal sutures complete, weakly carinate, extended from antennal pit to midline; ocellocular area broad; clypeal suture complete; anteclypeus tapered, slightly convex, apex rounded, extended slightly beyond lower margin of gena; lorum flat, well separated from genal margin, ventral 2/3 bordering anteclypeus; gena very narrow; maxillary cleft absent. Proepisternum small, flat, largely exposed. Pronotum depressed, transversely rugulose, anterior margin roundly produced but not extended anterad of eyes, lateral margin short, carinate. Exposed part of mesonotum and scutellum depressed, scutellum acuminate. Episternum divided by suture into anepisternum and katepisternum, without processes. Front femur with numerous scattered, poorly undifferentiated setae on dorsal and anterior surface, ventral rows poorly differentiated, AM1 slightly enlarged; tibia slender, dorsal surface flat, longitudinal rows present but poorly differentiated and surfaces of tibia between rows with numerous scattered fine setae, ventral setae scattered and short. Middle leg similar to front leg in shape and chaetotaxy. Hind femur apical macrosetae 2+0; hind tibia compressed, with setal rows PD, AD, AV and PV with 15, 10, 11, and ~53 setae, respectively; with PD and AD closer to each other than distance from AD to AV; PD setae slightly smaller than those of AD; AD macrosetae with bases enlarged but not spinelike, intercalary setae absent; AV extended from basal third to apex; PV setae fine and subequal in length with macrosetae of similar lengths; pecten with single row of macrosetae with spinelike bases, 2 lateral setae longer than 4 medial setae; tarsus ca. 1/3 length of tibia; tarsomere I without dorsoapical pair of setae, ventral setae scattered, pecten with 3 platellae. Forewings elongate, macropterous, with venation poorly delimited, texture glabrous except rugulose near base of clavus; vein R branched in basal 1/3, with 6 branches, 4 extended to costal margin with basal branch arising near midlength, crossvein s present; M with 2 branches; only distal r-m crossvein visible; inner apical cell long, tapered in distal 3/4, not extended to

wing apex; CuA connected to submarginal vein slightly distad of apex of clavus; clavus occupying ~3/4 total wing length; appendix absent. Hind wing macropterous but not well preserved in holotype.

FEMALE GENITALIA. Ovipositor with first valvulae sculpturing imbricate; second valvulae abruptly broadened near base and tapered distally, with 2 large teeth near base and several smaller serrations more distad.

MALE. Unknown.

Age and occurrence

Baltic region. Baltic amber, Middle Eocene, ca. 44 Ma.

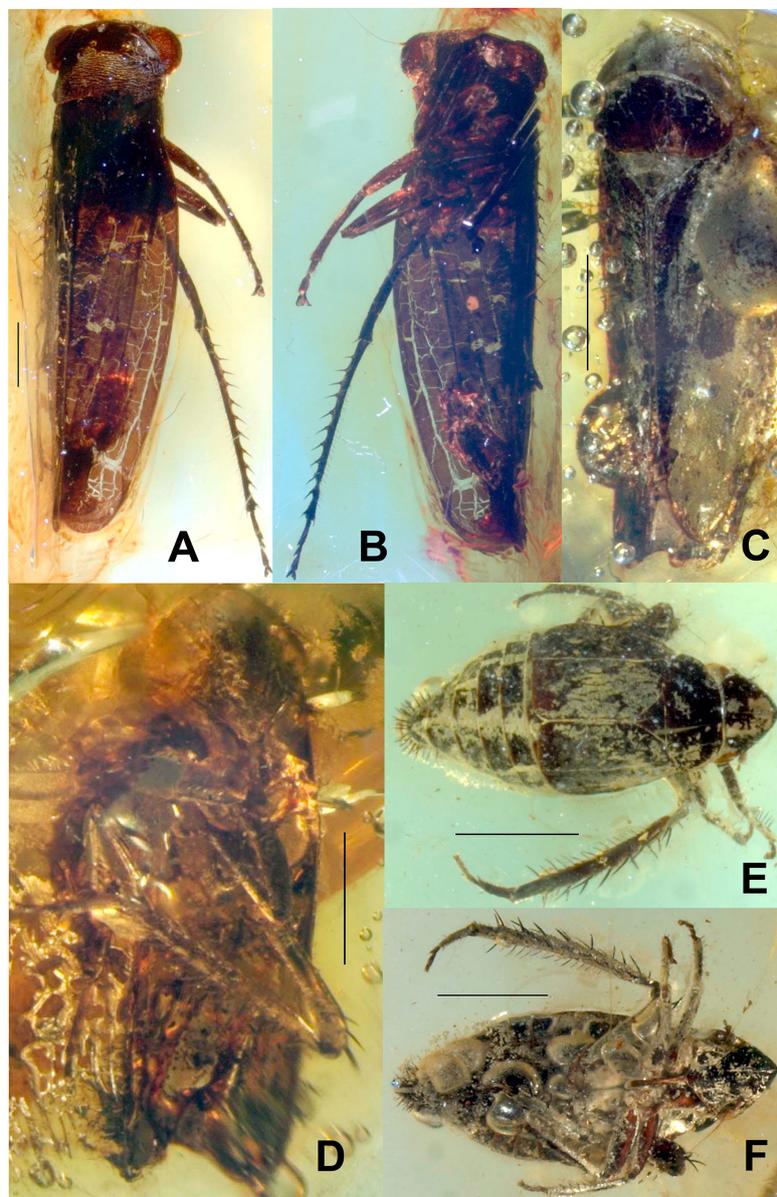


Fig. 1. Habitus in dorsal and ventral view. A-B. *Eomegophthalmus lithuaniensis* sp. nov. ♀. C-D. *Xestocephalites balticus* sp. nov. ♂. E-F. *Brevaphrodella nigra* sp. nov. ♂. Scale bars = 1 mm.

Remarks

The structure of the head (crown absent, ocelli on face distant from eyes) places this leafhopper within the lineage comprising Eurymelinae, Megophthalminae, Ulopinae, and treehoppers. The carinate facial sutures extended ventrad of the ocelli suggest that it is closest to Megophthalmini but, unlike *Eomegophthalmus* gen. nov., modern members of that tribe have the gena expanded and concealing the proepisternum and the wings reduced in size. The presence of macropterous forewings with supernumerary crossveins suggests a relationship to Adelungiini, but modern members of the latter tribe have the head smoothly rounded and shagreen in texture (except in *Adelungia* Melichar, 1902, which has a compressed, bladelike median dorsal process), and lack conspicuous transverse rugae on the pronotum. The broad second valvulae are more membracid-like than those of modern Megophthaminae, which have the second valvulae relatively narrow with serrations restricted to the distal half. The relatively dorsal position of the ocelli also suggests a relationship with Ulopinae and Membracidae. Thus, the subfamily placement must be considered tentative until the relationship of *Eomegophthalmus* gen. nov. to other leafhoppers can be elucidated by phylogenetic analysis.

Specimen notes

The type specimen, embedded in a clear piece of orange-yellow polished amber with most aspects of the body visible, apparently underwent considerable decay prior to fossilization. The abdomen is missing except for most of the first and second valvulae of the ovipositor, which are exposed and situated in their original resting position near the apex, beneath the wings. The rest of the exoskeleton is remarkably well preserved, although there is some distortion of the head and thorax due to compression, and the forewing integument has numerous small fractures that appear as white areas and give the specimen the appearance of having reticulate forewing venation. Close examination suggests that only a few of these fractures correspond to veins.

Subfamily Aphrodinae Haupt, 1927 (=Acocephalinae Dohrn, 1859)

Tribe Xestocephalini Baker, 1915

Xestocephalites gen. nov.

urn:lsid:zoobank.org:act:3D2E3FA1-905A-4892-AF4F-DCD7CFC9F04F

Type-species

Xestocephalites balticus sp. nov.

Diagnosis

Same as for *Xestocephalites balticus* sp. nov., due to monotypy of this genus.

Etymology

The genus name, a masculine Latin noun, was formed by replacing the suffix of *Xestocephalus*, a related modern genus, with *-ites* (“stone”), a common suffix used to designate fossil taxa.

Xestocephalites balticus sp. nov.

urn:lsid:zoobank.org:act:FC8D9A1F-FF96-4DD0-8A1D-5C587489CC76

Figs 1C-D, 2G-I

Diagnosis

This species resembles the modern genus *Xestocephalus* Van Duzee, 1892 in the structure of the head and in the leg chaetotaxy but differs in having the head wider than the pronotum, the crown more

strongly depressed, the forewing elongate, and the front femur lacking an enlarged ventral seta near the midlength.

Etymology

The species name refers to the Baltic region, where the holotype originated.

Material examined

Holotype male, Eocene Baltic amber, Palanga, Lithuania (INHS).

Description

MEASUREMENTS. (in mm). Body length including forewing at rest 5.3; head width 1.5; pronotum width 1.4; front femur length 0.8, tibia 0.9; middle femur length 0.8, tibia 1.1; hind femur length 1.5, tibia 2.1, tarsus 0.7; forewing length 4.2.

STRUCTURE. Body elongate, weakly depressed, dark brown colored, without conspicuous pattern. Head slightly wider than pronotum; crown well developed, roundly produced, longer medially than next to eye, uniformly shagreen; ocelli well developed but small, on crown just posterad of anterior margin, slightly closer to midline than to eye; transition from crown to face rounded; antennal ledges oblique, weakly developed; antennal pits deep; antenna shorter than half width of head; frontoclypeus weakly convex; lateral margins evenly tapered ventrad from antennal pits to just dorsad of clypeal suture, thence abruptly narrowed; clypeal suture weakly delimited; lateral frontal sutures extended dorsomesad from antennal pits to near dorsal margin of face; anteclypeus parallel-sided, weakly convex, apex rounded, extended slightly beyond genal margin; lorum flat, narrowly separated from genal margin ventrally, bordering anteclypeus for half length; gena broadly rounded; rostrum extended to just beyond base of hind legs. Pronotum depressed smooth, with sparse fine punctures and very inconspicuous transverse striations lateral margin less than half-length of eye, carinate. Exposed part of mesonotum and scutellum together slightly shorter than broad. Front femur chaetotaxy poorly visible in holotype, without conspicuous large ventral setae, tibia without conspicuous dorsal preapical macrosetae, ventral rows with several conspicuous macrosetae. Hind femur macrosetae 2+1+1; hind tibia flattened and bowed, with setal rows PD, AD, AV with 12, 11, and 17 setae, respectively (PV not visible on specimen); with macrosetae of dorsal rows approximately equal in length, AD and PD with approximately equal numbers of macrosetae extended from near base to apex, without short intercalary setae between successive large macrosetae, AV with 3 stout preapical macrosetae in addition to numerous close set, slender setae of approximately equal length; tarsomere I elongate, with conspicuous dorsoapical pair of macrosetae and well differentiated ventral longitudinal row of short, stout setae. Forewings macropterous, venation not visible in holotype; clavus occupying $\frac{3}{4}$ length of wing, appendix absent. Male subgenital plates short and broad, somewhat compressed, fused along midline, with numerous conspicuous long, fine setae along dorsal and apical margins and few stout setae ventromedially, apices obliquely truncate.

FEMALE. Unknown.

Age and occurrence

Baltic region. Baltic amber, Middle Eocene, ca. 44 Ma.

Remarks

This genus is referable to Aphrodinae based on the position of the ocelli on the crown slightly posterad of the anterior margin and distant from the eye. Among modern aphrodines, it most closely resembles *Xestocephalus* (*Xestocephalini*) in the structure of the head. *Xestocephalus* differs in having the head less strongly depressed and narrower than the pronotum with the gena broader and the anteclypeus

strongly flattened. *Xestocephalites* gen. nov. also differs from most modern aphrodines in having the wings fully macropterous. Species of the related tribe Portanini also have fully developed wings, but differ in having the head narrower, the ocelli on the margin of the crown, and the lorum greatly enlarged.

Specimen notes

The type specimen is embedded in a clear orange-yellow piece of amber but it is partly degraded with the left front leg (femur and segments distad) detached, and parts of the dorsum, including the forewings, largely concealed by air bubbles such that the wing venation is not visible. The anterior margin of the head is obscured by a horizontal fracture plane.

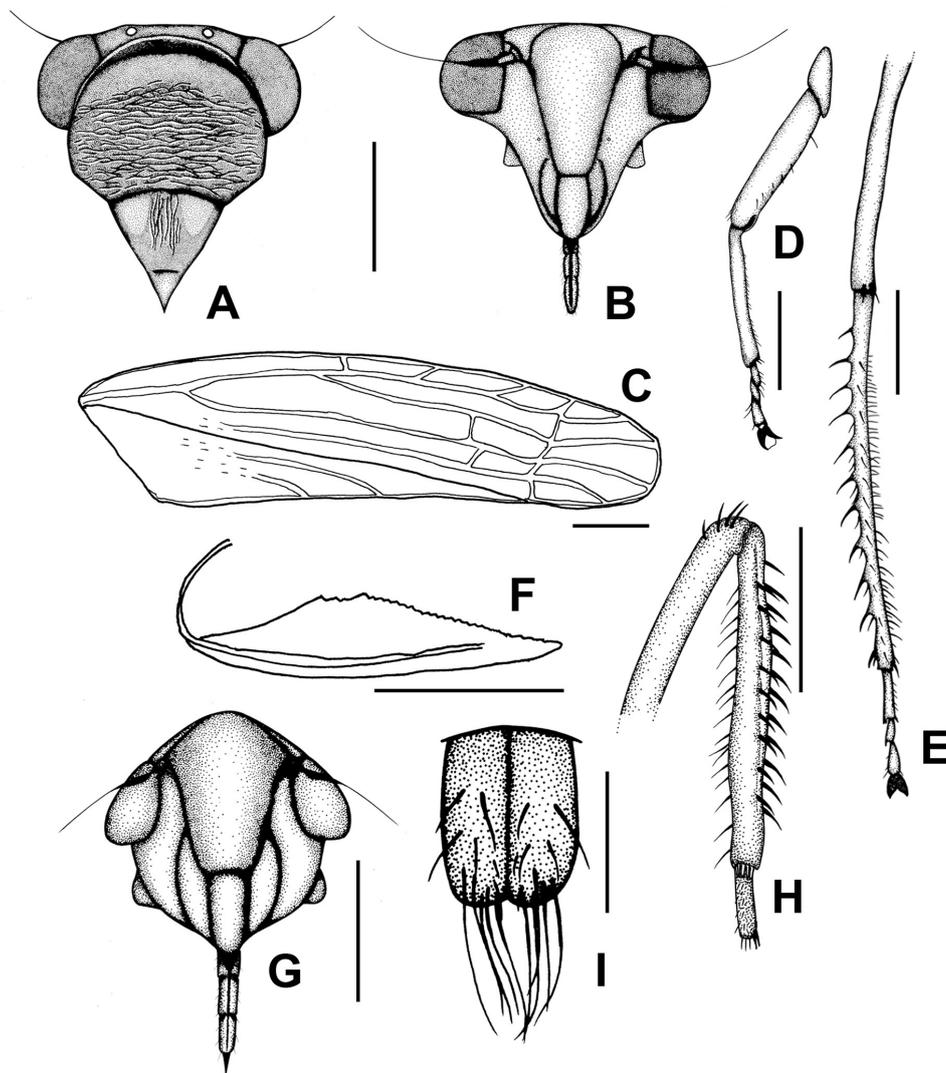


Fig. 2. A-F. *Eomegopthalmus lithuaniensis* sp. nov. ♀. A. Crown, pronotum, and mesonotum, dorsal view. B. Face, anteroventral view. C. Right forewing, lateral view. D. Prothoracic leg, lateral view. E. Metathoracic leg, dorsal view. F. Second valvulae of ovipositor, general lateral view. G-I. *Xestocephalites balticus* sp. nov. ♂. G. Face. H. Apical portion of femur, tibia, and first tarsomere of metathoracic leg, lateral view. I. Subgenital plates, ventral view. Scale bars: A-H = 1 mm; I = 0.5 mm.

Brevaphrodella gen. nov.

[urn:lsid:zoobank.org:act:898D14D3-6580-4EE5-8C6D-D9FBDE5EB92E](https://doi.org/10.3896/abris.2019.14D3-6580-4EE5-8C6D-D9FBDE5EB92E)

Type-species

Brevaphrodella nigra sp. nov.

Diagnosis

Same as for *Brevaphrodella nigra* sp. nov., due to monotypy of this genus.

Etymology

The genus name, a feminine Latin noun, combines *brevis* (“short”), *Aphrodes* (the name of a related extant leafhopper genus), and *-ella* (a diminutive suffix), referring to the small size and short forewings of the genus.

Brevaphrodella nigra sp. nov.

[urn:lsid:zoobank.org:act:0E415A40-3645-4C63-9B59-6F15E2512BB2](https://doi.org/10.3896/abris.2019.0E415A40-3645-4C63-9B59-6F15E2512BB2)

Figs 1E-F, 3

Diagnosis

Although the placement in Aphrodinae is somewhat tentative because the ocelli are not visible on the specimen, the overall structure of the head (flattened, produced crown; broad, flattened face with wide, angulate gena); leg chaetotaxy (2+2+1 hind femoral macrosetal formula); and male genital capsule (with numerous, scattered macrosetae and ligulate subgenital plates) are consistent with Aphrodinae. The presence of a single enlarged ventral seta near the midlength of the front femur suggests that the new genus is related to *Xestocephalus* and supports its placement in tribe Xestocephalini.

Etymology

The species name refers to the black overall coloration of the holotype.

Material examined

Holotype male, Eocene Baltic amber, Palanga, Lithuania (INHS).

Description

MEASUREMENTS. (in mm). Body length including forewings at rest 3.7; head width 0.9; pronotum width 1.0; front femur length 0.7, tibia 0.7; middle femur length 0.7, tibia 0.8; hind femur length 1.1, tibia 1.9, tarsus 0.7; forewing length 1.2.

STRUCTURE. Body small, depressed, ovoid, entirely black. Head triangularly produced; crown weakly convex, shagreen; coronal suture not visible; eyes small, anterior margin slightly emarginate adjacent to antennal base; ocelli not visible. Antennal pits deep, pedicel enlarged, base of flagellum divided into 5 subsegments. Lorum large, flat, narrowly separated from gena ventrally; gena angulate below eye, concealing proepisternum. Anteclypeus flat, tapered distally, apex rounded, extended slightly beyond gena. Rostrum long, extended to base of hind coxae. Pronotum with lateral margins divergent posteriorly, long, carinate. Mesonotum reduced, almost completely concealed by pronotum, scutellum small. Forewing short, coriaceous, elytral-like, apex truncate, extended nearly to posterior margin of abdominal tergite IV, venation not delimited. Front femur with AM1 small, near midheight of femur, intercalary row well differentiated with 5-6 setae; AV with single long stout seta near midlength; hind tibia with setal rows PD, AD, AV and PV with 15, 10, 11, and ~53 setae, respectively; with dorsal preapical macrosetae 1+2, row AV with 13 setae becoming longer from base to apex, basal 5 abruptly

shorter than others. Middle trochanter with stout ventroapical seta; femur with 4 AV and 1 PV setae, tibia with pair of dorsal setae near base and another near apex, AV with several setae. Hind femur macrosetae 2+2+1, penultimate pair close-set with posterior seta much smaller than anterior; tibia rows AD and PD with approximately equal numbers of macrosetae; AD macrosetae each with one intercalary seta, AD1 slightly offset toward middle of dorsal surface and distad of PD1, pecten with two pairs of shorter setae between two longer lateral and on long medial seta; tarsomere I with dorsoapical pair of macrosetae and two well differentiated rows of short, stout ventral setae; pecten with 5 tapered setae, medial seta longest. Male pygofer with numerous large macrosetae scattered over distal half. Valve concealed by sternite VIII. Subgenital plates ligulate, boatlike, with numerous large macrosetae scattered over most of length, mesal margins straight and closely appressed, apex evenly tapered.

FEMALE. Unknown.

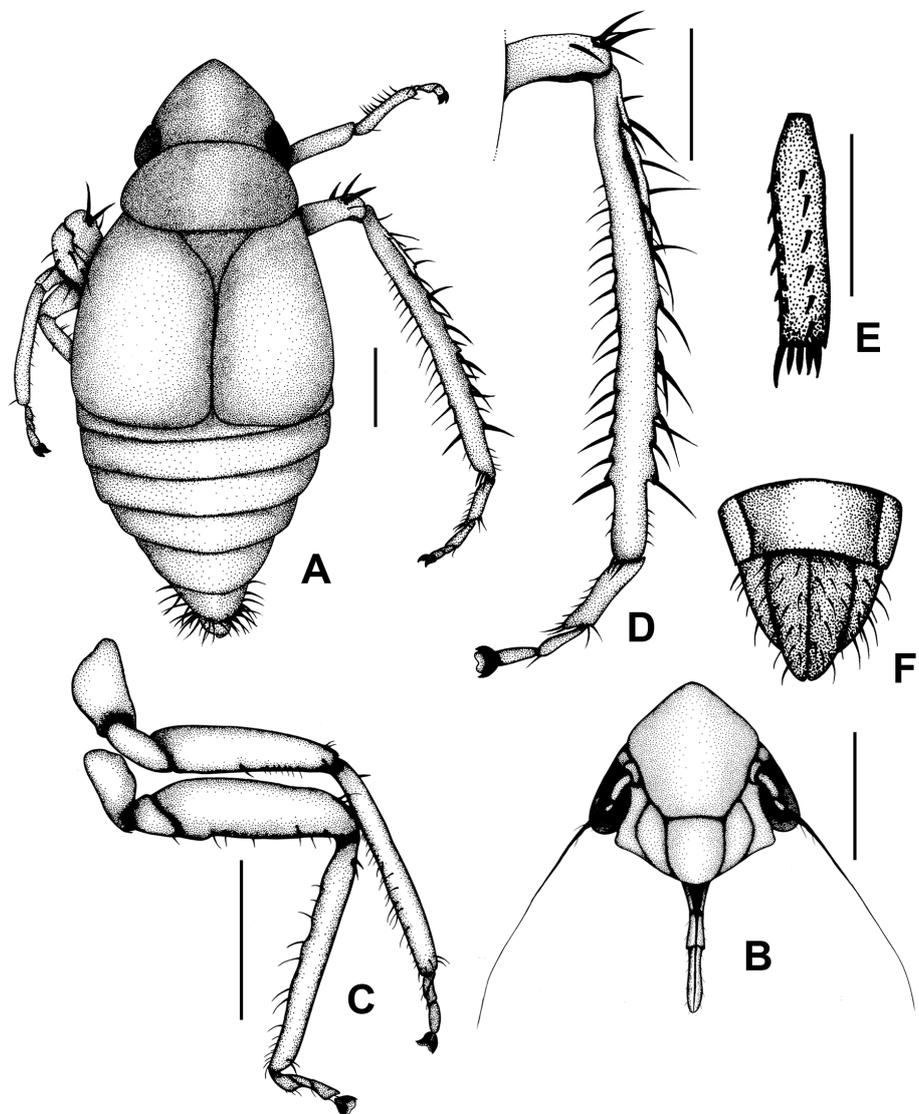


Fig. 3. *Brevaphrodella nigra* sp. nov. ♂. **A.** Body in dorsal view. **B.** Face. **C.** Pro- and mesothoracic legs in ventral view. **D-E.** Metathoracic leg. **D.** Apical portion of femur, tibia, and tarsomeres, dorsolateral view. **E.** First tarsomere, ventral view. **F.** Subgenital plates, and valve, ventral view. Scale bars: A-D, F = 0.5 mm; E = 0.25 mm.

Age and occurrence

Baltic region. Baltic amber, Middle Eocene, ca. 44 Ma.

Remarks

Placement of *Brevaphrodella* gen. nov. in Aphrodinae is somewhat tentative because the ocelli are not visible on the specimen. Either they are absent or greatly reduced (as in some modern brachypterous leafhoppers), or they are on the anterior margin of the head and not visible due to the presence of a fracture plane concealing this part of the head in the only available specimen. Nevertheless, the overall structure of the head (flattened, produced crown; broad, flattened face with wide, angulate gena); leg chaetotaxy (2+2+1 hind femoral macrosetal formula); and male genital capsule (with numerous, scattered macrosetae and ligulate subgenital plates) are consistent with Aphrodinae. The presence of a single enlarged ventral seta near the midlength of the front femur suggests that the new genus is related to *Xestocephalus* and supports its placement in tribe Xestocephalini. This appears to be the oldest known example of a brachypterous adult leafhopper, along with the specimen of an undescribed species and genus from Baltic amber illustrated by Szwedo (2002: fig. 24).

Specimen notes

The holotype is a specimen in excellent condition with apparently very little decomposition or loss of original color, embedded in a clear, light yellow piece of amber with dorsum and venter clearly visible but with numerous air bubbles concealing parts of the venter and a fracture plane obscuring the view of the anterodorsal margin of the head. The abdomen appears to have longitudinal pale stripes but these are asymmetrical and appear to be caused by pockets of air between the integument and the matrix.

Discussion

Although, to date, very few fossil Cicadellidae from Eocene Baltic amber have been described and illustrated adequately, leafhoppers are quite common in the Baltic amber fauna and the fossil taxa described so far from this source appear to be of great importance to the study of leafhopper phylogeny. The species represented by these fossils lived during a time when modern subfamilies and tribes were first beginning to appear; thus the fossils document evolutionary changes in morphology that were associated with the transition from the more morphologically generalized leafhoppers recorded from the Cretaceous period (Hamilton 1990, 1992) and the thoroughly modern leafhoppers recorded from the more recent Dominican amber (Dietrich & Vega 1995). Because the preservation of Baltic amber fossils is often very good, detailed study of their morphology is beginning to yield insights into the evolution of characters important for inferring the ecology and behavior of leafhoppers as well as for diagnosing higher taxa.

Eomegophthalmus gen. nov. exhibits a unique combination of features shared with some modern leafhopper subfamilies, as well as the treehopper families Aetalionidae, Melizoderidae and Membracidae. This provides further support for phylogenetic results suggesting that treehoppers arose from within a lineage comprising Megophthalminae and Ulopinae (Dietrich *et al.* 2001).

Xestocephalites gen. nov. and *Brevaphrodella* gen. nov. reveal that diversification of the lineage, that eventually gave rise to the large modern leafhopper subfamily Deltocephalinae, involved parallel acquisition of characters such as brachyptery and specialized leg chaetotaxy that now occur in several independent lineages of leafhoppers.

These recent discoveries, in addition to those recently published by Szwedo and colleagues, suggest that Baltic amber may soon yield representatives of other modern leafhopper subfamilies and tribes, most of which remain undocumented in the fossil record.

Acknowledgements

Fellowships from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) to A. C. G. through Ciência sem Fronteiras (CsF) program, process 237427/2012-5, and from Lemann Foundation, are acknowledged. S.W. Heads and J. Thomas provided helpful advice on photographing specimens. We also thank the anonymous reviewers for constructive comments that greatly improved the manuscript.

References

- Bervoets R. 1910. Diagnoses de quelques nouvelles espèces de cicadines de l'ambre de la Baltique. *Annales Historico-Naturales Musei Hungarici* 8: 125-128.
- Dietrich C.H. 2005. Keys to the families of Cicadomorpha and subfamilies and tribes of Cicadellidae (Hemiptera: Auchenorrhyncha). *Florida Entomologist* 88 (4): 502-517. [http://dx.doi.org/10.1653/0015-4040\(2005\)88\[502:KTTFOC\]2.0.CO;2](http://dx.doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2)
- Dietrich C.H. 2011. Tungurahualini, a new tribe of Neotropical leafhoppers, with notes on the subfamily Mileewinae (Hemiptera: Cicadellidae). *ZooKeys* 124: 19-39. <http://dx.doi.org/10.3897/zookeys.124.1561>
- Dietrich C.H., Rakitov R.A., Holmes J.L. & Black W.C. IV. 2001. Phylogeny of the major lineages of Membracoidea (Insecta: Hemiptera: Cicadomorpha) based on 28S rDNA sequences. *Molecular Phylogenetics and Evolution* 18 (2): 293-305. <http://dx.doi.org/10.1006/mpev.2000.0873>
- Dietrich C.H. & Vega F.E. 1995. Leafhoppers (Homoptera: Cicadellidae) from Dominican amber. *Annals of the Entomological Society of America* 88 (3): 236-270.
- Gebicki C. & Szewo J. 2001. The first record of fossil Mileewinae from Eocene Baltic amber (Hemiptera: Membracoidea: Cicadellidae). *Annales Zoologici* 51 (4): 417-422.
- Germar E.F. & Berendt G.C. 1856. Die im Bernstein befindlichen Hemipteren und Orthopteren der Vorwelt. In: Berendt G.C. (ed.) *Die im Bernstein befindlichen organischen Reste der Vorwelt gesammelt in Verbindung mit Mehreren, bearbeitet und herausgeben von G. C. Berendt* 2 (1): 1-40. Nicolaische Buchhandlung, Berlin.
- Hamilton K.G.A. 1990. Homoptera. In: Grimaldi D.A. (ed.). *Insects from the Santana Formation. Lower Cretaceous of Brazil*: 82-122. Bulletin of the American Museum of Natural History 195, American Museum of Natural History, New York.
- Hamilton K.G.A. 1992. Lower Cretaceous Homoptera from the Koonwarra Fossil Bed in Australia, with a New Superfamily and Synopsis of Mesozoic Homoptera. *Annals of the Entomological Society of America* 85 (4): 423-430.
- Jones J.R. & Deitz L.L. 2009. Phylogeny and systematics of the leafhopper subfamily Ledrinae (Hemiptera: Cicadellidae). *Zootaxa* 2186: 1-120.
- Keilbach R. 1982. Bibliographie und Liste der Arten tierischer Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsorte. *Deutsche Entomologische Zeitschrift, Neue Folge* 29 (1-3): 129-286. <http://dx.doi.org/10.1002/mmnd.19820290121>
- Metcalf Z.P. & Wade V. 1966. *A Catalogue of the Fossil Homoptera (Homoptera: Auchenorrhyncha)*. General Catalogue of the Homoptera: a supplement to Fascicle I, North Carolina State University, Raleigh.
- Oman P.W. 1937. Fossil Hemiptera from the Fox Hills sandstone (Cretaceous) of Colorado. *Journal of Paleontology* 11 (1): 38.
- Perkovsky E.E., Rasnitsyn A.P., Vlaskin A.P. & Taraschuk M.V. 2007. A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. *African Invertebrates* 48 (1): 229-245.

- Shcherbakov D.E. 1986. Cicadina (= Auchenorrhyncha). In: Rasnitsyn A.P. (ed.) *Insects in the Early Cretaceous ecosystems of West Mongolia*: 47-50. Transactions of the Joint Soviet-Mongolian Palaeontological Expedition 28, Nauka Moscow (in Russian).
- Shcherbakov D.E. 1992. The earliest leafhoppers (Hemiptera: Karajassidae n. fam.) from the Jurassic of Karatau. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1: 39-51.
- Spahr U. 1988. Ergänzungen und Berichtigungen zu R. Keilbachs Bibliographie und Liste der Bernsteinfossilien - Überordnung Hemipteroidea. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* 144: 1-60.
- Szwedo J. 2002. Amber and amber inclusions of planthoppers, leafhoppers and their relatives (Hemiptera, Archaeorrhyncha et Clypeorrhyncha). In: Holzinger W. (ed.). *Zikaden – Leafhoppers, Planthoppers and Cicadas (Insecta: Hemiptera: Auchenorrhyncha)*: 37-56. Denisia 4, Biologiezentrum/Oberösterreichisches Landesmuseum, Linz.
- Szwedo J. & Gebicki C. 1998. *Ambercarda skalskii* gen. et sp. n. from Baltic amber (Homoptera: Cicadellidae). *Polskie Pismo Entomologiczne* 67 (3-4): 179-184.
- Szwedo J. & Gebicki C. 1999. Representatives of Petalocephalini (Homoptera, Cicadellidae: Ledrinae). *Estudios del Museo de Ciencias Naturales de Alava* 14, Numero especial 2: 201-206.
- Szwedo J. & Gebicki C. 2002. Nastlopiinae nov. subfam. to comprise *Nastlopiia nigra* gen. and sp. n. from Eocene Baltic amber (Hemiptera: Cicadomorpha: Cicadellidae). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 86: 211-220.
- Szwedo J. & Sontag E. 2009. The traps of the “amber trap”. How inclusions could trap scientists with enigmas. In: *Amber - Archive of Deep Time*: 155-169. Denisia 26, Biologiezentrum/Oberösterreichisches Landesmuseum, Linz.
- Wei C., Zhang Y. & Dietrich C H. 2010. First record of the tribe Malmaemichungiini Kwon from China with description of a new species of the genus *Malmaemichungia* Kwon (Hemiptera: Cicadellidae). *Zootaxa* 2689: 48-56.
- Weitschat W. & Wichard W. 2010. Baltic amber. In: Penney D. (ed.). *Biodiversity of fossils in amber from the major world deposits*: 80-115. Siri Scientific Press, Manchester, UK.

Manuscript received: 22 August 2013

Manuscript accepted: 6 January 2014

Published on: 14 February 2014

Topic editor: Christian de Muizon

Desk editor: Charlotte Thionois

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum National d'Histoire Naturelle, Paris, France; National Botanic Garden of Belgium, Meise, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Natural History Museum, London, United Kingdom; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark.