

<https://doi.org/10.11646/palaeoentomology.3.2.7>

<http://zoobank.org/urn:lsid:zoobank.org:pub:1AB433B7-1FE2-46DC-9870-CACF1499B76F>

A new genus and species representing the first leafhopper (Hemiptera: Cicadellidae) from Eocene Rovno amber

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Abstract

Rovnotettix brachypterus gen. et sp. nov. is described and illustrated from Eocene Rovno (Ukraine) amber and tentatively placed in subfamily Bathysmatophorinae, tribe Malmaemichungiini. The new fossil is the first cicadellid described from Rovno amber from the Volyn region and the second brachypterus leafhopper adult described from the fossil record. It does not appear to be closely related to *Brevaphrodella* Dietrich & Gonçalves from Eocene Baltic amber, indicating that multiple flightless cicadellid lineages, now mostly associated with dry habitats with patchy vegetation, had evolved in Europe by the Eocene.

Keywords: Homoptera, Auchenorrhyncha, morphology, taxonomy, flightless

Introduction

Although leafhoppers (Cicadellidae) are currently among the most diverse and abundant families of herbivorous insects, their fossil record remains poorly studied with major gaps. Improved knowledge of leafhopper fossils is needed not only to elucidate morphological character evolution through time but also to improve calibrations for ongoing molecular divergence time analyses of this group (Dietrich *et al.*, 2017, Skinner *et al.*, 2019). The oldest true leafhoppers are recorded from the Lower Cretaceous of Brazil and Australia (Hamilton, 1990, 1992) and the first leafhoppers from Cretaceous amber have only recently been described (Poinar & Brown, 2017; Wang *et al.*, 2018; Chen *et al.*, 2019). In contrast, many species and genera of Cicadellidae have been described from late Eocene Baltic amber (reviewed by Szwedo, 2002; Dietrich & Gonçalves, 2014; Dietrich & Thomas, 2018). The first genus and species of Cicadellidae from Eocene

Sakhalinian amber was also described recently (Dietrich & Perkovsky, 2019). Unlike the more recent (Miocene) Dominican amber, in which most of the leafhoppers can be accommodated in modern genera (Dietrich & Vega, 1995), Eocene-age amber has yielded genera that mostly represent extinct lineages with combinations of morphological characters not found in the modern fauna. Thus, these faunas document an important transitional stage in the evolution of leafhoppers.

Rovno amber, dated at 35–37 Ma, is a southern analogue of the better known and more intensively studied Baltic amber (Perkovsky *et al.*, 2007; Nadein *et al.*, 2016). Over the past 20 years, 292 new species have been described from Rovno amber (Perkovsky & Rasnitsyn, 2013; Jałoszyński & Perkovsky, 2016; Perkovsky, 2015, 2018; Lyubarsky & Perkovsky, 2020, in press; Colombo *et al.*, 2020, in press). Nearly all Rovno amber inclusions studied so far have originated from Klesov and the Horyn River basin (Perkovsky *et al.*, 2010; Perkovsky, 2017), but new collections have recently been made from the more western basins of the Styr and Stokhod rivers and especially the Veselukha river floodplain in between. These new collections (mostly from Voronki and Velyki Telkovichyi) have yielded a number of new species of beetles, neuropterans and snakeflies (Jałoszyński & Perkovsky, 2019; Legalov *et al.*, 2019; Makarkin & Perkovsky, 2020; Perkovsky & Makarkin, 2019, 2020), as well as some species previously recorded from Baltic amber (Perkovsky & Olmi, 2018; Martynova *et al.*, 2019) or from Baltic and Bitterfeld amber (Radchenko & Perkovsky, 2018, 2020, in press). Inclusions from the Volyn region were not previously reported, although the first lacertid from Rovno amber (deposited in a private collection) was found at an even more western locality.

Some new taxa have also been described from nearby

Belarus (Perkovsky, 2017 and references therein) and the Zhitomir region (Fedotova & Perkovsky, 2015, 2017). The new genus and species of leafhopper described below was collected in the river basin next to the Stokhod large river basin from a site 1.5 km west of Kovel situated on the river Turia (Volyn region). Some other inclusions known from the same recently-discovered locality include numerous Phoridae, including *Aenigmatias* Meinert, 1890, the first Rovno amber dragonfly (Vasilenko, pers. com.), and a non-biting midge belonging to a boreal genus, *Apsectrotanypus* cf. *pecularis* (V. Baranov, pers. com.).

Hemipterans (except *Germaraphis* aphids: Perkovsky & Wegierek, 2018 and references therein) from Rovno amber remain understudied in comparison with hymenopterans. Only two heteropteran species (Putschkov & Popov, 2003; Herczek *et al.*, 2013), one aleyrodid genus and species (Drohojowska *et al.*, 2015), and one dictyopharid species also recorded from Baltic amber (Emeljanov & Shcherbakov, 2011) have been described so far, compared to 54 named hymenopteran species (nearly half of the known Rovno fauna). Seventy-four hymenopteran genera are recorded. One tribe and one subfamily of Hymenoptera are recorded in the Eocene only from Rovno amber and 21 of the 74 hymenopteran genera recorded from Rovno amber are the only known Eocene representatives of these genera (Perkovsky, 2018; Radchenko & Dlussky, 2019; Colombo *et al.*, 2020 in press; Radchenko & Perkovsky, 2020, in press). If the tentative placement of the new cicadellid described below in Malmaemichungiini can be verified, it would represent the third tribe of insects recorded in the fossil state known only from Rovno amber (Legalov *et al.*, 2018).

The new genus and species described below is only the second hemipteran genus and the first leafhopper known only from Rovno amber. The fossil is also important because it is only the second brachypterous adult leafhopper described from the fossil record and is quite different from the previously described one, *Brevaphrodella nigra* Dietrich & Gonçalves, 2014 from Baltic amber, in several respects.

Material and methods

Morphological terminology follows Dietrich (2005). Photographs were taken using a Leica Z16 APO microscope equipped with a Leica DFC 450 camera and processed by LAS Core software.

The holotype is 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 Bathysmatophorinae Anufriev, 1978

Tribe Malmaemichungiini Kwon, 1983

Rovnotettix gen. nov.

(Figs 1, 2)

Type species. *Rovnotettix brachypterus* sp. nov., by monotypy.

Etymology. The genus name, a masculine noun, was formed by combining the name of the fossil amber, Rovno, with *-tettix*, Greek for “cicada”; a common suffix used for cicadellid genus names.

Diagnosis. The new genus differs from other fossil and extant Cicadellidae in having the following combination of traits: head wider than pronotum with anterior margin angulate in dorsal and lateral views, vertex extended behind compound eye; ocelli absent; lorum large, flat and extended to lateral margin of face; gena emarginate below eye exposing proepisternum; rostrum extended past middle coxae; forewing short, heavily sclerotized and elytralike with venation not delimited, apex obliquely truncate; hind femur with apical and preapical pair of macrosetae, tibia with alternating short and long setae in row PV; male subgenital plates separate from each other and articulated to valve, tapered in ventral view, compressed and curved dorsad distally, with scattered macrosetae.

Rovnotettix differs from *Brevaphrodella* in its more elongate, less depressed overall body form and narrow gena, which does not conceal the proepisternum and somewhat longer forewings (extended to sternite VI rather than V). The specimen photographed by Szwedo (2002) appears to be more similar to *Rovnotettix* in overall body form but its wings are also shorter, exposing abdominal segment III and the (male?) genital capsule is much more elongated.

Rovnotettix brachypterus sp. nov.

Material. Holotype male SIZK Kov-1. Eocene Rovno amber. Ukraine: Volyn Region, 1.5 km west of Kovel.

The holotype inclusion is very well preserved with little apparent distortion and most parts of the exoskeleton clearly visible. The anterior view of the head and front legs and the lateral and dorsal views of the abdominal terminalia are obscured by fractures.

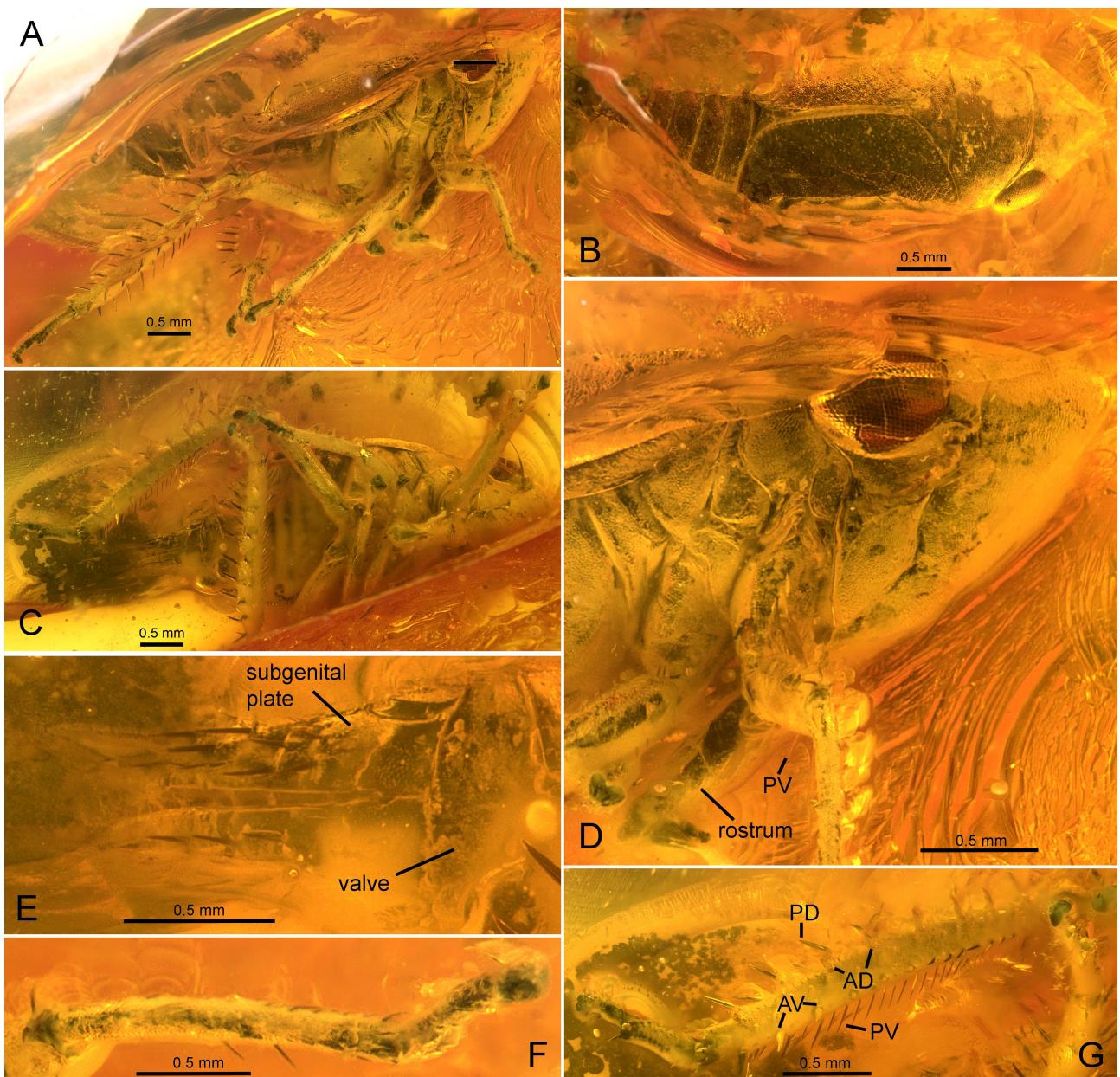


FIGURE 1. *Rovnotettix brachypterus* gen. et sp. nov., male holotype. **A**, Lateral habitus. **B**, Dorsal habitus. **C**, Ventral habitus. **D**, Enlarged lateral view of head and thorax. **E**, Male terminalia, ventral view. **F**, Right front tibia and tarsus, posterolateral view. **G**, Right hind leg, ventral view with rows of tibial macrosetae labeled. AD, anterodorsal row; AV, anteroventral row; PD, posterodorsal row; PV, posteroventral row.

Etymology. The species name, an adjective, is a latinization of the Greek compound word meaning “short-winged.”

Description. Measurements (mm). Body length 4.5; head width (dorsal aspect) 1.7, head length (medial) 0.7; pronotum maximum width 1.6, pronotum length (medial) 0.8; front femur length 1.15, tibia length 1.4; middle femur length 0.95; tibia length 1.2; hind femur length 1.7, tibia length 2.5; forewing length 2.05.

Head in dorsal view (Figs 1B, 2B) wider than pronotum, crown produced and angulate in dorsal view, longer medially than next to eye, somewhat depressed, texture finely granulose throughout, vertex with narrow

extension behind compound eye, distance between compound eyes more than twice eye width, coronal suture weakly delimited, transition from crown to face rounded; ocelli not visible; frontoclypeus (Figs 1A, D, 2A) weakly convex, distinctly taller than maximum width, only narrowly separated from eyes, texture finely granulose without obvious muscle impressions; lateral frontal sutures, distinct, extended dorsad from antennal ledges and extended posteromesad slightly onto crown; antennal base near mid-height of eye; antenna slightly shorter than head width; antennal ledge poorly developed, narrow and slightly oblique; gena narrow and obtusely emarginate below eye, exposing small, ovoid proepisternum; lorum

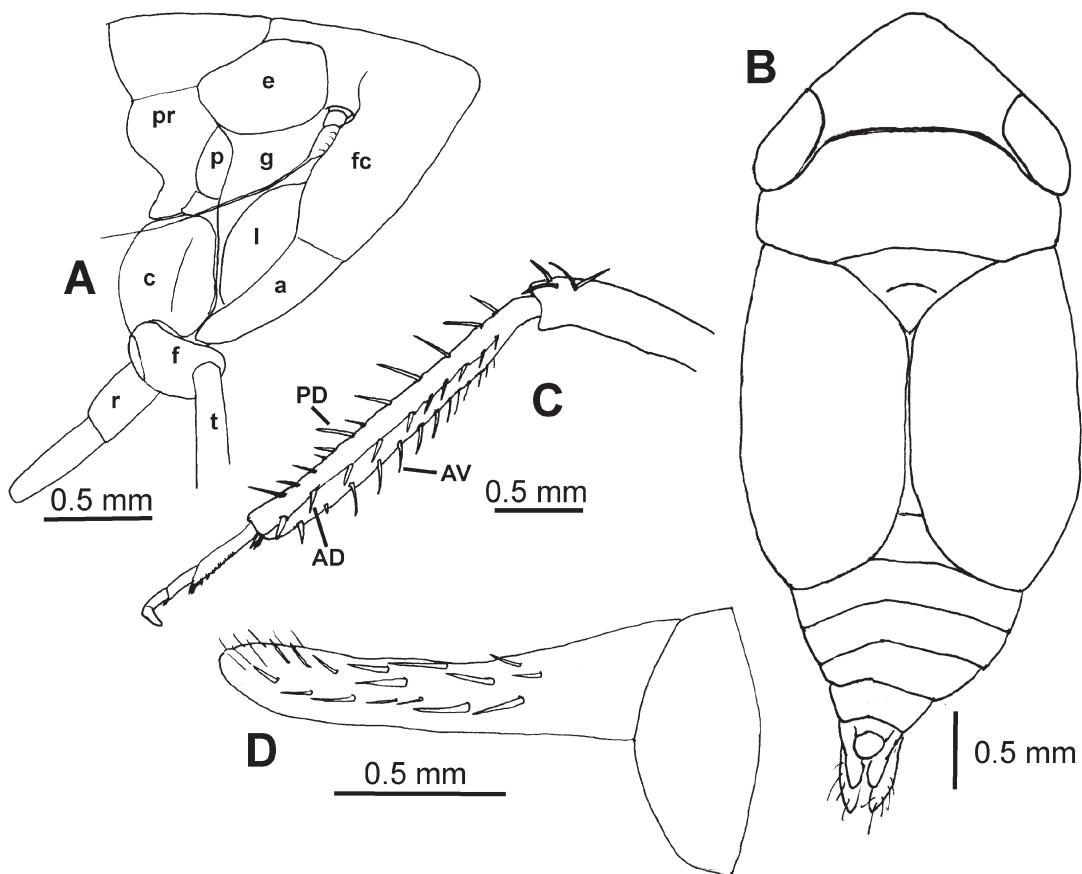


FIGURE 2. *Rovnotettix brachypterus* gen. et sp. nov. **A**, Head and prothorax, lateral view. **B**, Dorsal habitus (partially reconstructed). **C**, Femur (part), tibia and tarsus of right hind leg, lateral view. **D**, Valve and right subgenital plate, ventral view. AV, anteroventral row; AD, anterodorsal row; PD, posterodorsal row; a, anteclypeus; c, coxa; e, eye; f, femur; fc, frontoclypeus; g, gena; p, proepisternum; pr, pronotum; r, rostrum; t, tibia.

(Figs 1D, 2A) large, extended to lateral margin of face, portions of inner margin bordering anteclypeus and postclypeus approximately equal; clypeal suture well delimited, slightly arcuate; anteclypeus weakly convex, parallel-sided, apex convex and extended beyond lower margin of maxillary plate, apex truncate; rostrum (Figs 1A, D, 2A) long, stout, tapered, extended well past middle coxae.

Pronotum (Figs 1B, D, 2A, B) weakly convex, anterior margin in dorsal view somewhat trapezoidal, texture finely granulose with some indistinct, irregular transverse striations; lateral margins slightly divergent, weakly carinate behind eyes, more than half as long as eyes; posterior margin slightly concave. Mesonotum and scutellum (Figs 1B, 2B) finely granulose, scutellar suture distinct and slightly arcuate. Forewing (Figs 1B, 2B) short, elytralike, venation not visible, texture uniformly granulose with scattered punctations each associated with a short seta, extended to base of abdominal tergite VI, apex obliquely truncate.

Legs with chaetotaxy of femora and tibiae well differentiated. Front femur (Fig. 1D) with dorsoapical

pair of macrosetae and dorsal preapical row of evenly spaced setae extended over most of length, ventral surface with two prominent PV setae widely spaced near midlength (anterior surface not visible in fossil). Front and middle tibia (Fig. 1A, C, F) with dorsal and ventral rows of several evenly spaced macrosetae (femoral setae not visible in specimen). Hind femur (Figs 1G, 2C) with close-set apical and anteapical pairs of distal macrosetae; tibial rows PD, AD, AV and PV with approximately 13, 10 and 13 and 24 macrosetae, respectively; AD with 4–5 short setae between successive macrosetae in distal half; PD row setae alternating short and long in distal half, all longer than AD setae; AV with six distal setae distinctly stouter and more widely spaced than setae in basal half and with 1–2 short setae between successive stout setae; apical pecten with setae even; tarsomere I longer than II and III combined, with AV row of short plantar setae and PV irregular band of setae, posteroapical ventral angle with single enlarged seta.

Male genital capsule (Fig. 1E) with scattered stout setae; valve short and broad in ventral view, posterior

margin broadly convex; subgenital plates articulated to valve, in ventral view much longer than pygofer, with numerous scattered stout setae, compressed and upturned apically with rounded apices.

Color: overall color uniform, no spots or other patterns evident. Crown anterior margin forming right angle in dorsal view.

Discussion

Rovnotettix gen. nov. is the first cicadellid described from Rovno amber. It is the third brachypterous adult leafhopper known from the fossil record. The other two, one illustrated by Szwedo (2002) but not formally described, and *Brevaphrodella nigra* Dietrich & Gonçalves (2014), are from Baltic amber and differ as indicated in the above diagnosis.

The new genus is tentatively included in the modern cicadellid subfamily Bathysmatophorinae, tribe Malmaemichungiini, based on the narrow gena, lack of ocelli, exposed proepisternum, short, elytra-like forewing, elongate first hind tarsomere with numerous short plantar setae in one row and one band and triangular subgenital plate with scattered stout setae (Wei *et al.*, 2010). The lack of ocelli and elytra-like forewings are possible synapomorphies shared with *Malmaemichungia* Kwon, 1983 and other extant genera of the tribe. *Rovnotettix* differs from modern members of Malmaemichungiini in its much smaller body size, less strongly depressed crown and longer forewing. Extant Malmaemichungiini also have the ovipositor extended well beyond the posterior margin of the pygofer, a probable synapomorphy shared with the nominotypical tribe of Bathysmatophorinae (Wei *et al.*, 2010). Unfortunately, the state of this character in *Rovnotettix* is unknown and the placement of the genus in Bathysmatophorinae will remain tentative until a female is discovered. Most of the other morphological characters visible in the fossil (e.g., tapered anteclypeus extended ventrad of face margin, exposed proepisternum, subgenital plates with depressed base and compressed apex) are consistent with placement in Bathysmatophorinae but are plesiomorphies shared with several other cicadellid subfamilies.

Previous studies of Eocene Baltic amber (Szwedo, 2002, 2005; Szwedo & Gębicki, 1998) suggest that Bathysmatophorinae were more morphologically diverse and abundant during the Eocene than they are in the modern fauna. Modern Bathysmatophorinae are mostly restricted to the eastern Palearctic and western Nearctic regions with only one species (*Bathysmatophorus reuteri* Sahlberg, 1871) having a more widespread distribution including western Europe. Malmaemichungiini presently

appear to be restricted to Korea and central China (Wei *et al.*, 2010).

Overall, *Rovnotettix* is superficially similar to many extant brachypterous grass-specialist Deltcephalinae (e.g., *Athysanella* Baker, 1898) but is easily distinguished by the structure of the head, which lacks ocelli and has the anteclypeus extended well beyond the normal curve of the maxillary plates and the rostrum elongate.

In the Recent fauna, brachyptery in leafhoppers is usually associated with dry habitats, particularly grasslands and deserts (Oman, 1987 and CHD pers. obs.). Insect genera in which most modern species are associated with dry areas are known from Baltic amber, e.g., the bethylid genus *Glenosema* Kieffer, 1905 (Azevedo & Noort, 2019; Colombo & Azevedo, 2019) but in Rovno amber such elements are much more common (Perkovsky *et al.*, 2010 and references therein; Lyubarsky & Perkovsky, 2012; Perkovsky, 2013; Lyubarsky & Perkovsky, 2019 and references therein) and include five families or subfamilies of xerophilic Heteroptera (Herczek *et al.*, 2013) etc. Presence of brachypterous leafhoppers during the Eocene may reflect a transition from closed forests to more open habitats in temperate and subtropical latitudes during this epoch.

Acknowledgments

We thank Ekaterina V. Martynova (SIZK) for providing the photos of the holotype. The senior author acknowledges support from US National Science Foundation Grant DEB-1639601.

References

Anufriev, G.A. (1978) Les cicadellides de la Territoire Maritime. *Horae Societatis Entomologicae Unionis Soveticae*, 60, 1–215.

Azevedo, C.O. & Noort, S. van (2019) Review of Afrotropical *Glenosema* Kieffer (Hymenoptera, Bethylidae) with description of 13 new species. *Zootaxa*, 4585 (3), 401–437. <https://doi.org/10.11646/zootaxa.4585.3.1>

Chen, J., Wang, B., Jones, J.R., Zheng, Y., Jiang, H., Jiang, T., Zhang, J. & Zhang, H.C. (2019) A representative of the modern leafhopper subfamily Ledrinae in mid-Cretaceous Burmese amber (Hemiptera, Cicadellidae). *Cretaceous Research*, 95, 252–259. <https://doi.org/10.1016/j.cretres.2018.11.022>

Colombo, W.D. & Azevedo, C.O. (2019) Synopsis of the fossil Scleroderminae (Hymenoptera, Bethylidae) with description of a new genus and four new species from Baltic amber. *Historical Biology*, 31, 1–10. <https://doi.org/10.1080/08912963.2019.1650275>

Colombo, W.D., Gobbi, F.T., Perkovsky, E.E. & Azevedo, C.O. (2020) Synopsis of the fossil Pristocerinae (Hymenoptera, Bethylidae), with description of two new genera and six species from Burmese, Taimyr, Baltic and Rovno ambers. *Historical Biology*, in press.
<https://doi.org/10.1080/08912963.2019.1650275>

Dietrich, C.H. (2005) Keys to the families of Cicadomorpha and subfamilies and tribes of Cicadellidae (Hemiptera: Auchenorrhyncha). *Florida Entomologist*, 88, 502–517.
[https://doi.org/10.1653/0015-4040\(2005\)88\[502:KTTFOC\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2)

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.
<https://doi.org/10.5852/ejt.2014.74>

Dietrich, C.H. & Perkovsky, E.E. (2019) First record of Cicadellidae (Insecta: Hemiptera: Auchenorrhyncha) from Eocene Sakhalinian amber. *ZooKeys*, 886, 127–134.
<https://doi.org/10.3897/zookeys.886.38828>

Dietrich, C.H. & Thomas, M.J. (2018) New eurymeline leafhoppers (Hemiptera, Cicadellidae, Eurymelinae) from Eocene Baltic amber with notes on other fossil Cicadellidae. *ZooKeys*, 726, 131–143.
<https://doi.org/10.3897/zookeys.726.21976>

Dietrich, C.H. & Vega, F.E. (1995) Leafhoppers (Homoptera: Cicadellidae) from Dominican amber. *Annals of the Entomological Society of America*, 88, 263–270.
<https://doi.org/10.1093/aesa/88.3.263>

Dietrich, C.H., Allen, J.M., Lemmon, A.R., Moriarty Lemmon, E., Takiya, D.M., Evangelista, O., Walden, K.K.O., Grady, P.G.S. & Johnson, K.P. (2017) Anchored hybrid enrichment-based phylogenomics of leafhoppers and treehoppers (Hemiptera: Cicadomorpha: Membracoidea). *Insect Systematics and Diversity*, 1, 57–72.
<https://doi.org/10.1093/isd/ixx003>

Drohojowska, J., Perkovsky, E.E. & Szwedo, J. (2015) New genus and species of Aleyrodidae from the Eocene Baltic amber (Hemiptera: Sternorrhyncha: Aleyrodomorpha). *Polish Journal of Entomology*, 84 (4), 259–269.
<https://doi.org/10.1515/pjen-2015-0022>

Duméril, A.M.C. (1805) *Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques. "1806".* Allais, Paris, i–xxxii, 1–344.
<https://doi.org/10.5962/bhl.title.44835>

Emeljanov, A.F. & Shcherbakov, D.E. (2011) A new genus and species of Dictyopharidae (Homoptera) from Rovno and Baltic amber based on nymphs. *ZooKeys*, 130, 175–184.
<https://doi.org/10.3897/zookeys.130.1775>

Evans, J.W. (1946) A natural classification of leafhoppers (Jassoidea, Homoptera). Part I. External morphology and systematic position. *Transactions of the Entomological Society of London*, 96, 47–60.
<https://doi.org/10.1111/j.1365-2311.1946.tb00442.x>

Fedotova, Z.A. & Perkovsky, E.E. (2015) New gall midges (Diptera, Cecidomyiidae, Stomatosematidi, Brachineuridi) from the Late Eocene amber of Gulyanka (Zhitomir Region, Ukraine). *Paleontological Journal*, 49 (3), 270–278.
<https://doi.org/10.1134/S0031030115030041>

Fedotova, Z.A. & Perkovsky, E.E. (2017) New genus and species of gall midges (Diptera, Cecidomyiidae, Porricondylinae, Holoneurini) from the Late Eocene amber of Olevsk (Zhitomir Region, Ukraine). *Vestnik Zoologii*, 51 (1), 23–30.
<https://doi.org/10.1515/vzoo-2017-0004>

Hamilton, K.G.A. (1990) Homoptera. In: Grimaldi, D.A. (Ed.), Insects from the Santana Formation. Lower Cretaceous of Brazil. *Bulletin of the American Museum of Natural History*, 195, 82–122.

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, 423–430.
<https://doi.org/10.1093/aesa/85.4.423>

Herczek, A., Popov, Y.A. & Perkovsky, E.E. (2013) Another new representative of the isometopine genus *Archemeyiomma* (Hemiptera: Heteroptera: Miridae) from Late Eocene Rovno (Ukraine) amber. In: Azar, D., Engel, M.S., Jarzemowski, E., Krogmann, L., Nel, A. & Santiago-Blay, J. (Eds), *Insect evolution in an amberiferous and stone alphabet*. Proceedings of the 6th International Congress on Fossil Insects, Arthropods and Amber. Brill, Leiden & Boston, pp. 47–54.
https://doi.org/10.1163/9789004210714_005

Johnson, K.P., Dietrich, C.H., Friedrich, F., Beutel, R., Wipfler, B., Peters, R.S., Allen, J., Petersen, M., Donath, A., Walden, K.K.O., Kozlov, A., Podsiadlowski, L., Mayer, C., Meusemann, K., Vasilikopoulos, A., Waterhouse, R.M., Cameron, S., Weirauch, C., Swanson, D.R., Percy, D., Hardy, N., Terry, I., Liu, S., Zhou, L.X., Misof, B., Robertson, H.M. & Yoshizawa, K. (2018) Phylogenomics and evolution of hemipteroid insects. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 12775–12780.
<https://doi.org/10.1073/pnas.1815820115>

Ignatov, M.S., Lamkowski, P., Ignatova, E.A. & Perkovsky, E.E. (2019) Mosses from Rovno amber (Ukraine), 4, *Sphagnum heinrichsii* sp. nov. *Arctoa*, 28, 1–11.
<https://doi.org/10.15298/arctoa.28.01>

Jałoszyński, P. & Perkovsky, E.E. (2016) Diversity of Scydmaeninae (Coleoptera: Staphylinidae) in Upper Eocene Rovno amber. *Zootaxa*, 4157 (1), 1–85.
<https://doi.org/10.11646/zootaxa.4157.1.1>

Jałoszyński, P. & Perkovsky, E.E. (2019) The Mastigitae genus *Baltostigus* in Upper Eocene Rovno amber (Coleoptera: Staphylinidae: Scydmaeninae). *Zootaxa*, 4661 (3), 594–600.
<https://doi.org/10.11646/zootaxa.4661.3.12>

Kwon, Y.J. (1983) Classification of leafhoppers of the subfamily Cicadellinae from Korea (Homoptera: Auchenorrhyncha). *Korean Journal of Entomology*, 13 (1), 15–25.

Latreille, P.A. (1825) *Familles naturelles du règne animal, exposées succinctement et dans un ordre analytique, avec l'indication de*

leurs genres. J.B. Baillière & Baudouin Frères, Paris, 570 pp.
<https://doi.org/10.5962/bhl.title.16094>

Legalov, A.A., Nazarenko, V.Y. & Perkovsky, E.E. (2018) A new genus of fungus weevils (Coleoptera: Anthribidae) in Rovno amber. *Fossil Record*, 21, 207–212.
<https://doi.org/10.5194/fr-21-207-2018>

Legalov, A.A., Nazarenko, V.Y. & Perkovsky, E.E. (2019) New weevils (Coleoptera: Curculionidae) from Rovno Amber. *Paleontological Journal*, 53 (10), 1045–1059.
<https://link.springer.com/article/10.1134/S0031030119100101>

Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum caracteribus, differentiis, synonymis, locis*, Tomus I. Editio decima, reformata. L. Salvii, Holmiae [= Stockholm], 824 pp.
<https://doi.org/10.5962/bhl.title.542>

Lyubarsky, G.Y. & Perkovsky, E.E. (2012) The first Eocene species of the genus *Cryptophagus* (Coleoptera, Clavicornia, Cryptophagidae). *Vestnik Zoologii*, 46 (1), 83–87.
<https://doi.org/10.2478/v10058-012-0007-z>

Lyubarsky, G.Y. & Perkovsky, E.E. (2019) *Spaniophagus*, first new Eocene genus of silken fungus beetle from Baltic amber (Coleoptera: Clavicornia: Cryptophagidae). *Russian Entomological Journal*, 28 (3), 263–268.
<https://doi.org/10.15298/rusentj.28.3.05>

Lyubarsky, G.Y. & Perkovsky, E.E. (2020) First Rovno amber species of the genus *Telmatophilus* (Coleoptera: Clavicornia: Cryptophagidae) from Veselukha floodplain. *Invertebrate Zoology*, in press.

Makarkin, V.N. & Perkovsky E.E. (2020) A new species of *Proneuronema* (Neuroptera: Hemerobiidae) from late Eocene Rovno amber. *Zootaxa*, 4718 (2), 292–300.
<https://doi.org/10.11646/zootaxa.4718.2.11>

Martynova, K.V., Perkovsky, E.E., Olmi, M. & Vasilenko, D.V. (2019) New records of Upper Eocene Chrysidoidea Wasps (Hymenoptera: Chrysidoidea) from basins of Styr and Stokhod Rivers (Rovno Amber). *Paleontological Journal*, 53 (10), 998–1023.
<https://doi.org/10.1134/S0031030119100125>

Nadein, K.S., Perkovsky, E.E. & Moseyko, A.G. (2016) New Late Eocene Chrysomelidae (Insecta: Coleoptera) from Baltic, Rovno and Danish ambers. *Papers in Palaeontology*, 2, 117–137.
<https://doi.org/10.1002/spp2.1034>

Oman, P. (1987) Alary polymorphism in the Cicadellidae and its ecological implications. In: Wilson, M.R. & Nault, L.R. (Eds), *Proceedings of the 2nd International Workshop on Leafhoppers and Planthoppers of Economic Importance, Provo, Utah, USA, 28 July–1 August 1986*. Commonwealth Institute of Entomology, London, pp. 55–63.

Perkovsky, E.E. (2015) Toponyms and ethnonyms in the names of Rovno amber animals and plants. *Vestnik Zoologii*, 49 (5), 407–412.
<https://doi.org/10.1515/vzoo-2015-0046>

Perkovsky, E.E. (2017) Rovno amber caddisflies (Insecta, Trichoptera) from different localities, with information about three new sites. *Vestnik Zoologii*, 51, 15–22.
<https://doi.org/10.1515/vzoo-2017-0003>

Perkovsky, E.E. (2018) Only a half of species of Hymenoptera in Rovno amber is common with Baltic amber. *Vestnik Zoologii*, 52, 353–360.
<https://doi.org/10.2478/vzoo-2018-0037>

Perkovsky, E.E. & Makarkin, V.N. (2019) A new species of *Succinoraphidia* Aspöck & Aspöck, 2004 (Raphidioptera: Raphidiidae) from the late Eocene Rovno amber, with venation characteristics of the genus. *Zootaxa*, 4576 (3), 70–580.
<https://doi.org/10.11646/zootaxa.4576.3.9>

Perkovsky, E.E. & Makarkin, V.N. (2020) A new species of *Sympherobius* Banks (Neuroptera: Hemerobiidae) from the late Eocene Rovno amber. *Palaeoentomology*, 3 (2), in press.

Perkovsky, E.E. & Olmi, M. (2018) Discovery of the first pincer wasp (Hymenoptera, Dryinidae) from Rovno amber. *Zootaxa*, 4457 (2), 296–304.
<https://doi.org/10.11646/zootaxa.4457.2.5>

Perkovsky, E.E. & Rasnitsyn, A.P. (2013) First records of Scolebythidae and Chrysidae (Hymenoptera, Chrysidoidea) in Rovno amber. *Vestnik Zoologii*, 47, 113–118.
<https://doi.org/10.2478/vzoo-2013-0010>

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.

Perkovsky, E.E. & Wegierek, P. (2018) Aphid-Buchnera-ant symbiosis, or why are aphids rare in the tropics and very rare further south? *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 107, 297–310.
<https://doi.org/10.1017/S1755691017000147>

Poinar, G. Jr. & Brown, A. (2017) A new genus of leafhoppers (Hemiptera: Cicadellidae) in mid-Cretaceous Myanmar amber. *Historical Biology*, 2017, 1–4.
<https://doi.org/10.1080/08912963.2017.1384472>

Putschkov, P.V. & Popov, Y.A. (2003) The first find Microphysidae from Ukrainian (Rovno) amber (Heteroptera, Cimicomorpha). *Annals of the Upper Silesian Museum, Bytom, Entomology*, 12, 81–85.

Radchenko, A.G. & Dlussky, G.M. (2019) First record of the ant genus *Crematogaster* (Hymenoptera: Formicidae) from the Late Eocene European ambers. *Annales Zoologici*, 69 (2), 417–421.
<https://doi.org/10.3161/00034541ANZ2019.69.2.0008>

Radchenko, A.G. & Perkovsky, E.E. (2018) First record of fossil ant species *Eocenomyrma rugosostriata* (Mayr) (Hymenoptera: Formicidae) from the Rovno amber. *Russian Entomological Journal*, 27, 285–288.
<https://doi.org/10.15298/rusentj.27.3.08>

Radchenko, A.G. & Perkovsky, E.E. (2020) New records of the fossil ant genus *Prionomyrmex* Mayr (Hymenoptera, Formicidae, Myrmeciinae) from Late Eocene European ambers. *Paleontological Journal*, 54, in press.

Rafinesque, C.S. (1815) *Analyse de la nature ou tableau de l'univers et des corps organisés*. [Privately published by the author], Palermo, 224 pp.
<https://doi.org/10.5962/bhl.title.106607>

Rasnitsyn, A.P. & Quicke, D.L.J. (Eds) (2002) *History of insects*. Kluwer Academic Publishers, Dordrecht, 517 pp.
<https://doi.org/10.1007/0-306-47577-4>

Skinner, R.K., Dietrich, C.H., Walden, K.K.O., Gordon, E., Sweet, A.D., Podsiadlowski, L., Petersen, M., Simon, C., Takiya, D.M. & Johnson, K.P. (2019) Phylogenomics of Auchenorrhyncha (Insecta: Hemiptera) using transcriptomes: examining controversial relationships via degeneracy coding and interrogation of gene conflict. *Systematic Entomology*, 45, 85–113.
<https://doi.org/10.1111/syen.12381>

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). *Denisia*, 4, 37–56.

Szwedo, J. (2005) *Jantarivacanthus kotejai* gen. et sp. n. from Eocene Baltic amber, with notes on the Bathysmatophorini and related taxa (Hemiptera: Cicadomorpha: Cicadellidae). *Polskie Pismo Entomologiczne*, 74, 251–276.

Szwedo, J. & Gębicki, C. (1998) *Ambericarda skalskii* gen. et sp. n. from Baltic amber Homoptera: Cicadellidae). *Polskie Pismo Entomologiczne*, 67, 179–184.

Wang, X., Dietrich, C.H. & Zhang, Y. (2019) The first fossil Coelidiinae: a new genus and species from mid-Cretaceous Myanmar amber (Hemiptera, Cicadellidae). *Cretaceous Research*, 95, 146–150.
<https://doi.org/10.1016/j.cretres.2018.11.005>

Wei, C., Zhang, Y. & Dietrich, C.H. (2010) A new brachypterous leafhopper of the tribe Malmaemichungiini (Hemiptera: Cicadellidae: Bathysmatophorinae), representing the first record of the tribe from China. *Zootaxa*, 2689, 48–56.
<https://www.mapress.com/j/zt/article/view/10219>