Zootaxa 5706 (2): 175–188
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5706.2.2
http://zoobank.org/urn:lsid:zoobank.org:pub:9F2CA2DA-4B2D-4187-AB12-898047C7FDFD

Aetheapnomyia Harbach & Greenwalt (Diptera: Culicidae: Culicinae: Aedini) revisited based on a new record from Rovno amber

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Abstract

The extinct genus *Aetheapnomyia* Harbach & Greenwalt, 2012 (Diptera: Culicidae) and its type species, *At. hoffeinsorum* (Szadziewski, 1998), originally described from Baltic amber, are more fully described based on a specimen of the type species recently found in Rovno amber. Dipteran inclusions in Baltic and Rovno ambers are reviewed and the possible affinities of *Aetheapnomyia* with extant aedine mosquitoes are explored.

Key words: flies, fossil, mosquito, palaeontology, taxonomy

Introduction

The flies (Diptera) of Rovno amber are still far from being known satisfactorily and, as in the case of other ambers, knowledge of individual taxa is uneven. Out of the 14–16 currently recognised infraorders (depending on the taxonomic concept applied), seven are represented in Rovno amber. Those infraorders/superfamilies and the number of genera and species of each are summarised in Table 1. In total, 161 species of Diptera are known from Rovno amber. It is worth noting that some species found in Rovno amber and listed in Table 1 were originally reported as coming from Baltic amber, due to an outdated concept of treating both ambers as one.

In contrast to the rich fauna of extant Culicidae, represented by 3,727 currently recognised species (Harbach 2024), only 28 species of fossil mosquitoes have been described to date, including two from Rovno amber: *Culiseta gedanica* Szadziewski & Giłka, 2011 and *Culex ekaterinae* Giłka, Harbach & Perkovsky, 2021 (Giłka *et al*. 2021). Below, we provide the description of another fossil species embedded in Rovno amber, found in a mine in the Zarechnoye District. The species is placed in the genus *Aetheapnomyia* Harbach & Greenwalt, 2012, which was established for a fossil mosquito originally placed in the subgenus *Finlaya* Theobald, 1903 of *Aedes* Meigen, 1818. A more detailed description of the species, *Aetheapnomyia hoffeinsorum* (Szadziewski, 1998), is presented here based on a specimen recently found in Rovno amber, along with a refined generic diagnosis and information supporting the concept of *Aetheapnomyia* and its recognition as a distinct genus of Aedini.

Accepted by B. Sinclair: 3 Sept. 2025; published: 10 Oct. 2025

TABLE 1. Tabulation of fossil Diptera recorded in Rovno amber prior to the present paper.

Infraorder/ superfamily	**Family**	**Number of genera and species**	**References**
Asilomorpha	Mythicomyiidae	4 genera and 4 species (1 genus and all species unknown from Baltic amber)	Evenhuis 2013; Perkovsky *et al*. 2025
Bibionomorpha	Anisopodidae	1 genus and 1 species (species unknown from Baltic amber)	Wojtoń *et al*. 2019
	Bibionidae	1 genus and 1 species	Skartveit 2021
	Cecidomyiidae	52 genera and 92 species (21 genera and all species unknown from Baltic amber)	Fedotova & Perkovsky 2004, 2005, 2008, 2009, 2012a, 2012b, 2012c, 2014, 2015, 2017; Fedotova *et al*. 2024; Perkovsky & Fedotova 2004, 2008a, 2008b, 2016
Culicomorpha	Ceratopogonidae	18 genera and 29 species (1 genus and 1 species unknown from Baltic amber)	Sontag & Szadziewski 2011; Perkovsky 2013, 2017
	Chironomidae	6 genera and 9 species (1 genus and 4 species unknown from Baltic amber)	Zelentsov *et al*. 2012; Giłka *et al*. 2013; Baranov & Perkovsky 2014; Baranov *et al*. 2014; Zakrzewska & Giłka 2014; Andersen *et al*. 2015; Zakrzewska *et al*. 2016; Dietrich & Perkovsky 2020; Melnitsky *et al*. 2025b
	Corethrellidae	1 genus and 2 species (both species unknown from Baltic amber)	Baranov *et al*. 2016
	Culicidae	2 genera and 2 species (1 species unknown from Baltic amber)	Giłka *et al*. 2021
	Dixidae	1 genus and 1 species	Dubovka, SIZK DU-146, det. E. Perkovsky
	Simuliidae	2 genera and 3 species (all species unknown from Baltic amber)	Perkovsky & Sukhomlin 2015, 2016
Empidoidea	Dolichopodidae	3 genera and 4 species	Shamshev & Perkovsky 2022; Grichanov 2023
	Empididae	1 genus and 1 species (both unknown from Baltic amber)	Plant *et al*. 2011
	Hybotidae	1 genus and 1 species (both unknown from Baltic amber)	Shamshev *et al.* 2025
Muscomorpha	Campichoetidae	1 genus and 1 species	Perkovsky 2011
	Diopsidae	1 genus and 1 species	Perkovsky *et al*. 2015
	Phoridae	1 genus and 1 species	Perkovsky *et al*. 2015
Psychodomorpha	Psychodidae	2 genera and 3 species (1 genus and 2 species unknown from Baltic amber)	Azar *et al*. 2013; Wagner 2021
Tipulomorpha	Limoniidae	2 genera and 5 species	Manukyan 2018 Kopeć *et al.* 2019

Material and methods

The specimen dealt with here is an inclusion in a large piece of dark tea-coloured amber. The adult male is well preserved but lies just above an internal crack that prevents isolation of the specimen into a smaller piece of amber and hinders observation from different aspects. The piece of amber was ground and polished manually, so that the inclusion and its diagnostic structures could be examined and documented at high magnification. Photographs were taken using a PZO Biolar SK14 microscope with a Sony NEX-3N digital camera, and a Leica M205A stereomicroscope with a DCF 495 camera. The images were compiled using LAS Montage multifocus and Helicon Focus ver. 8.2.0 image stacking software.

Except for the maxillary palpomeres, segments of the legs, ungues and genitalia, for which lengths are given in micrometres (µm), measurements of the specimen are given in millimetres (mm), rounded to the first decimal place (body lengths) or to two decimal places (other measurements, including calculated ratios). Lengths of the body and wing were measured from the antennal pedicel to the apex of the genitalia and from the base and arculus of the wing to the apex of the wing, respectively. The morphological terminology and abbreviations follow Harbach & Knight (1980, 1982) and Harbach (2024), except for crossveins of the wing, which follow Belkin (1962). The specimen is the property of the I. I. Schmalhausen Institute of Zoology, National Academy of Sciences of the Ukraine, Kyiv (SIZK), where it will be deposited.

Results

Family: Culicidae Meigen, 1818

Subfamily: Culicinae Meigen, 1818

Tribe: Aedini Neveu-Lemaire, 1902

Aetheapnomyia Harbach & Greenwalt, 2012

Type species: *Aedes hoffeinsorum* Szadziewski, 1998 (by monotypy).

Diagnosis (based on Szadziewski 1998; Harbach 2024, 2025, and current observations, amended). Adult male: Antenna longer than proboscis, pedicel enlarged, terminal flagellomere with apical stylet-like or conical prolongation; maxillary palpus shorter than proboscis, comprised of 4(?) or 5 palpomeres (see species description and Discussion), terminal palpomere very short, about 0.3 length of preceding palpomere; proboscis noticeably swollen distally; paratergal, postspiracular and lower mesepimeral setae present; wing with cell R_2 much shorter than vein R_{2+3}; fore- and midungues long, unequal, simple, borne well before apex of tarsomere 5.

Notes. *Aetheapnomyia*, like most generic-level taxa of Aedini (Reinert *et al*. 2009), is mainly a polythetic taxon that is diagnosed by a unique combination of characters. At present, the only possible unique (wholly diagnostic) character may be the preapical attachment of the fore- and midungues. *Aetheapnomyia hoffeinsorum* was originally described as a species of *Aedes* (*Finlaya*), but, as explained by Harbach & Greenwalt (2012), the absence of spotted wings precludes it from being placed in the subgenus *Finlaya*, and the unique combination of short maxillary palpi, greatly reduced palpomere 5, proboscis swollen distally, cell R_2 of the wing much shorter than vein R_{2+3} and the preapical attachment of the fore- and midungues preclude it from being placed in the extant genus *Aedes*. Szadziewski (1998) described the antenna as shorter than the proboscis, which is inconsistent with detailed measurements in his paper. The genitalia bear some resemblance to certain extant species of the *Ochlerotatus* Group of subgenera of the genus *Aedes* (see the Discussion).

Aetheapnomyia hoffeinsorum (Szadziewski, 1998)

(Figs 1–4)

Aedes (*Finlaya*) *hoffeinsorum* Szadziewski, 1998: 235 (♂, ♀; Baltic amber).

Aetheapnomyia hoffeinsorum of Harbach & Greenwalt, 2012: 33 (comb. nov., gen. nov.); Giłka *et al.* 2021: 259 (checklist of fossil mosquitoes); Harbach 2024, 2025 (taxonomy).

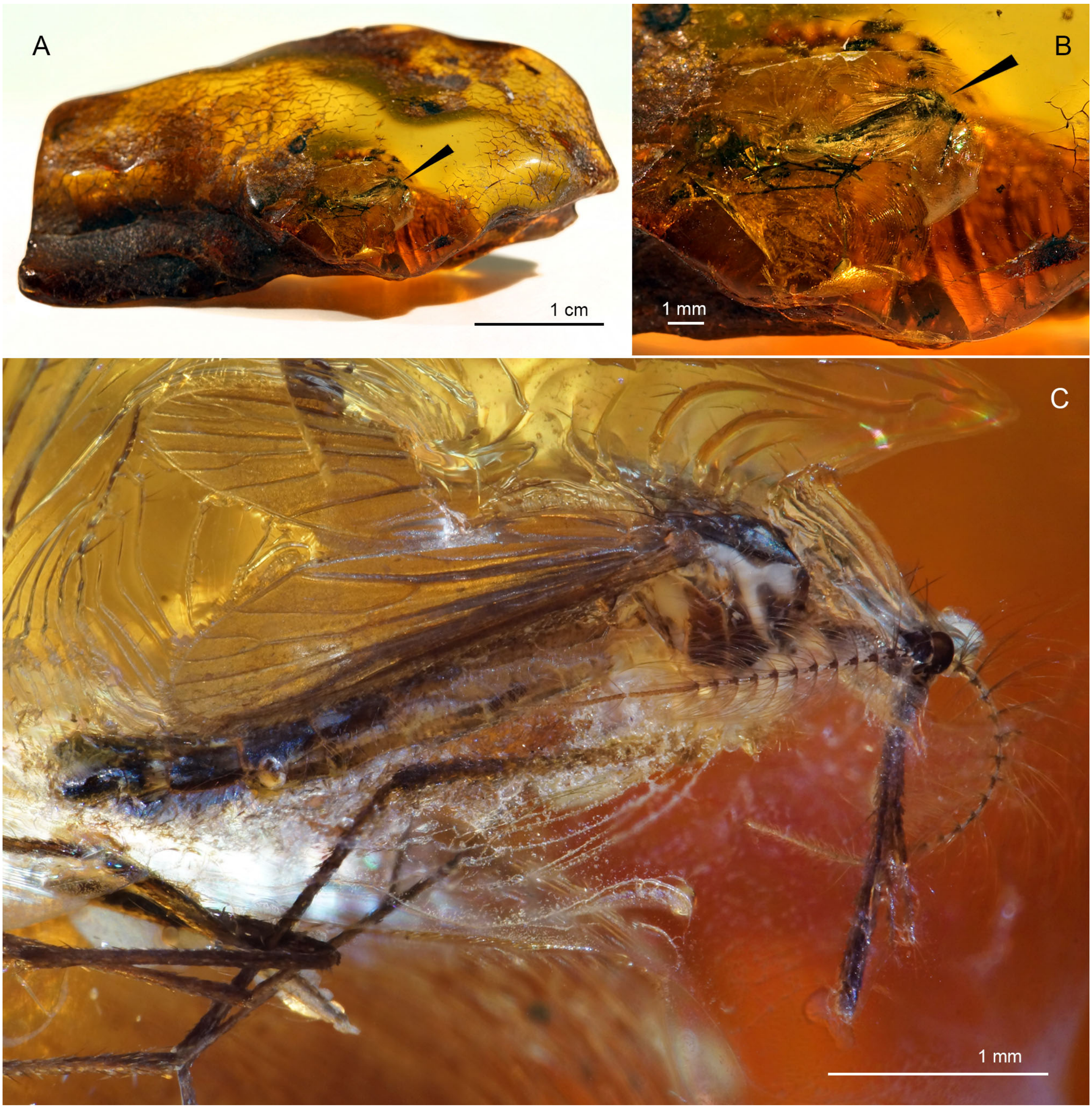

FIGURE 1. Male of *Aetheapnomyia hoffeinsorum*: **A, B,** inclusion in amber (indicated with arrowheads); **C,** habitus.

Material examined. Adult male, complete specimen (visible only from lateral side, visibility of head and genitalia limited by resin layers between which the specimen is located; right midleg attached, remaining legs present but detached, lying next to specimen), preserved in a piece of amber 46 × 20 × 17 mm (Eocene, Priabonian, 33.9–37.8 Mya), Zarechnoye District, Rovno Region, Ukraine (SIZK Z-9; Fig. 1A–C). Syninclusions: Coleoptera *incertae sedis*, 1 specimen; Hymenoptera *incertae sedis*, 1 specimen.

Description. Adult male. *Colour*: Body, mouthparts and legs brown to dark brown or black; wing membrane uniformly coloured, without spots; scales of thorax and wing pale, scales darker on mouthparts, legs and abdomen.

Size: Body length, excluding proboscis, 4.4 mm, body + proboscis 5.9 mm, thorax + abdomen 3.9 mm.

Antenna (Figs 1C, 2A–C): Length including pedicel 2.14 mm; flagellum 1.99 mm, comprised of 13 flagellomeres, flagellomeres 12 and 13 longest (0.39 and 0.58 mm, respectively), their combined length slightly less than total length of preceding flagellomeres (ratio 0.95); flagellar whorls well-developed, flagellomeres 1–12 each with whorl of many long setae, flagellomere 13 with whorl of several shorter setae and conical apical prolongation; antenna about 1.43 × length of proboscis.

FIGURE 2. Male of *Aetheapnomyia hoffeinsorum*: **A,** head; **B,** antenna; **C,** flagellomeres 12 and 13; **D,** labella of proboscis; **E,** palpomeres 4 and 5.

Proboscis (Figs 1C, 2A, D): Length 1.50 mm, longer than maxillary palpus (ratio 1.30), flattened dorsoventrally and gradually broadened toward apex; labella of typical aedine form, with well-defined proximal and distal sclerites, proximal sclerite crescentic in lateral view, dorsal sclerite slightly longer than proximal sclerite, shaped like convex surface of bowl of a spoon, both sclerites largely covered with setae.

FIGURE 3. Male of *Aetheapnomyia hoffeinsorum*: **A,** wings; **B,** venation of distal half of wing.

Maxillary palpus (Fig. 2A, E): Length 1.15 mm, shorter than proboscis (ratio 0.77), with 5(?) palpomeres (possibly only 4, see Discussion) combined length of palpomeres 1–3 882 μm, about 0.59 length of proboscis; palpomere 4 (209 μm) more than 3 times longer than palpomere 5 (67 μm), ratio 3.12; palpomere 1 (= palpifer ?, see Discussion) short, somewhat bulbous; palpomeres 2–4 slender, each gently broadening toward apex; palpomere 5 greatly reduced, ovoid with rounded apex, bearing up to 5 long setae distally.

Thorax (Figs 1C, 2A): Integument dark brown (some areas obscured by milky amber); paratergite with pale scales; postspiracular, prealar, upper and lower mesokatepisternal and upper and lower mesepimeral setae present; some pale scales on upper mesokatepisternal, lower mesokatepisternal, and upper and lower mesepimeral areas.

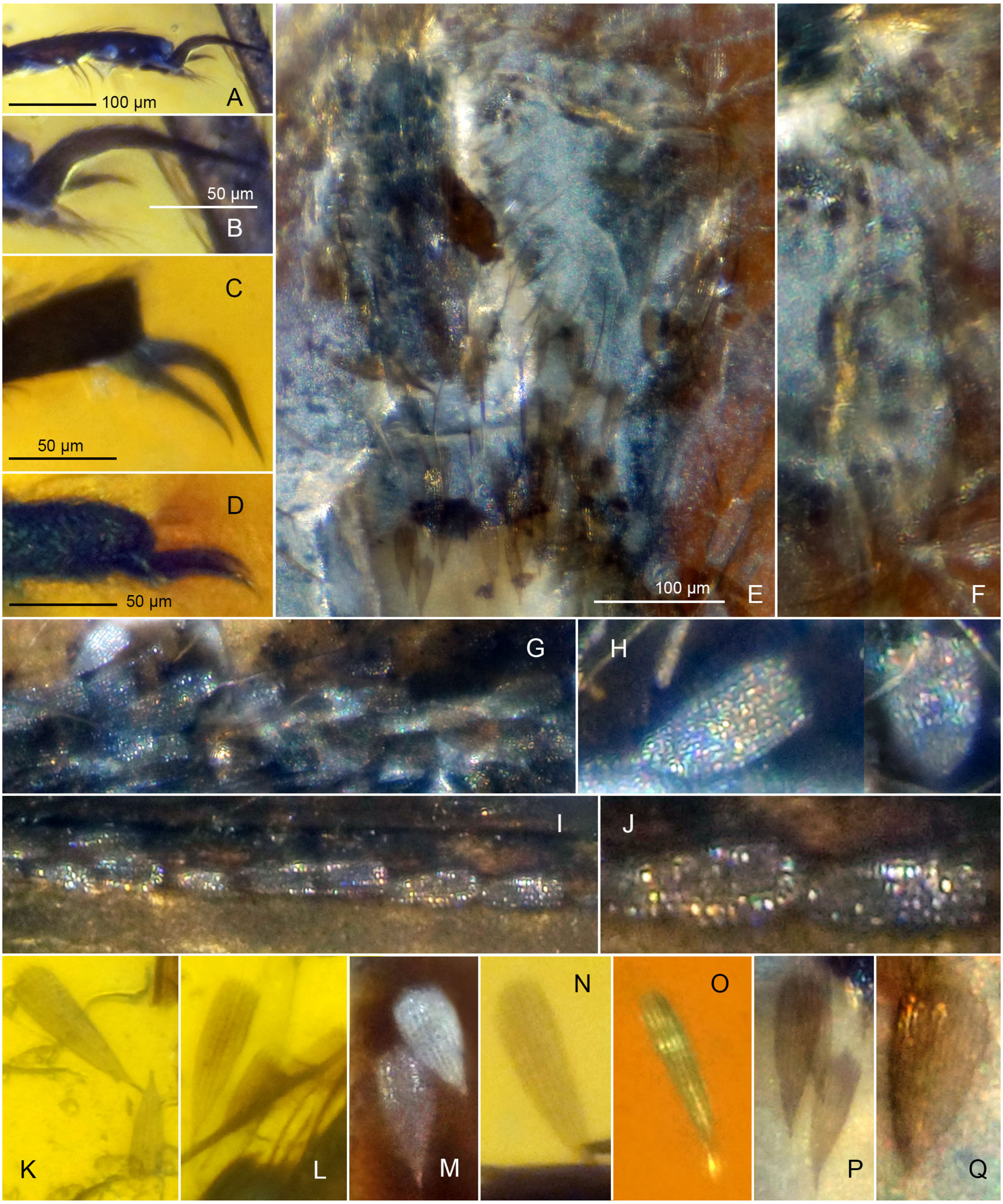

FIGURE 4. Male of *Aetheapnomyia hoffeinsorum*. **A–D,** ungues of foreleg (A–C) and hindleg (D), and ungues magnified (B–D); **E,** genitalia in dorsolateral view (largely obscured by milky amber); **F**, gonostylus magnified ×2; **G–Q,** scales on costa (G, magnified ×3 in H), radius (I, magnified ×3 in J), proboscis (K), maxillary palpus (L), thorax (M), legs (N, O) and abdomen (P, Q).

Wing (Fig. 3A, B): Length 2.60 mm (base to tip), 2.29 mm (arculus to tip), maximum width 0.63 mm; scales spatulate, slender, apically rounded or slightly apically triangulate, apices minutely pectinate; cells R_2 and R_3

distinctly shorter than vein R_{2+3} ($R_2/R_{2+3} = 0.80$, $R_3/R_{2+3} = 0.90$); arrangement of veins in area of radiomedial and mediocubital crossveins as shown in Fig. 3; mediocubital crossvein [base of M_{3+4} of Harbach & Knight 1980] unusually short; cubitus posterior (plical vein of Belkin 1962) developed as strongly as cubitus anterior, with scales at least on proximal part; anal vein (1A) ending 1/3 (0.35) of distance between intersection of mediocubital crossvein and cubitus and base of M_{3+4} toward apex of wing.

Legs (Figs 1C, 4A–D): Entirely dark-scaled; fore- and midungues borne well before apex of tarsomere 5, long, curved, unequal on foreleg (lengths 90 µm and 120 µm) and midleg (longer unguis 110 µm, shorter unguis unmeasurable), short and equal on hindleg (~60 µm); all ungues simple, without teeth. Lengths of segments of legs in Table 2.

TABLE 2. Lengths (µm) of segments of the legs of the male of *Aetheapnomyia hoffeinsorum*. Ta = tarsomere.

	Femur	Tibia	Ta1	Ta2	Ta3	Ta4	Ta5
Foreleg	-	1495	900	320	215	150	195
Midleg	~1500	1670	1195	520	320	150	185
Hindleg	1400	1730	1310	620	425	245	220

Abdomen (Fig. 1C): Laterotergite of segment I apparently without scales, with setae only; tergum II with a few basolateral pale scales; terga III–VIII apparently without pale bands, entirely dark-scaled; scaling of sterna uncertain, but some dark scales evident on lateral areas of sterna III–VI.

Genitalia (Fig. 4E, F): Observable in dorsolateral view (in part obscured by layer of milky amber); gonocoxite elongate, length ~300 µm; gonostylus slender, slightly arched, about half length of gonocoxite, with long, slender terminal gonostylar claw; claspette moderately long with narrow columnar stem and terminal flattened filament (see Szadziewski 1998: fig. 3).

Scales (Fig. 4G–Q): Variable in shape, depending on location on wing veins (Fig. 4G–J), proboscis (Fig. 4K), maxillary palpus (Fig. 4L), thorax (Fig. 4M), legs (Fig. 4N, O) or abdomen (Fig. 4P, Q); ranging from broadly spatulate (twice as long as wide at most) with apex slightly triangulate or rounded, to slender (several times as long as wide) with apex more or less convex; apices pectinate.

Discussion

Taxonomy

The genus *Aetheapnomyia* was established by Harbach & Greenwalt (2012), based on a combination of unusual characters exhibited by the type species, especially the unique attachment of the fore- and midungues well before the apex of the fifth tarsomere. *Aetheapnomyia* is undoubtedly correctly classified as a genus of the tribe Aedini, subfamily Culicinae, based on the presence of postspiracular setae and scales on the paratergite.

Phylogenetic analyses of morphological and molecular data indicate that Aedini is a monophyletic group (see Harbach 2024: 42 for references). The tribe is divided into two genus groups, the *Aedes* and *Ochlerotatus* Groups, based on morphological features of the adults and larvae. The division of the tribe into the two groups is supported by the molecular phylogenetic study of Soghigian *et al.* (2017), Clades A and B, respectively.

The segmentation of the maxillary palpus of extant mosquitoes was elucidated by Harbach & Kitching (1998). Five palpomeres is the maximum number present in both males and females – the loss or reduction of distal palpomeres has given rise to maxillary palpi with fewer palpomeres. The palpus is five-segmented in most Aedini; however, in most extant *Aedes* it has either four or five palpomeres, but in certain subgenera the males may have only three palpomeres, three with a vestigial fourth palpomere or four with a vestigial fifth palpomere. Furthermore, in males with five-segmented palpi, there is clear evidence of ankylosis between the second and third palpomeres. These observations are important here because it is uncertain whether the maxillary palpus of *At. hoffeinsorum* consists of four or five palpomeres. The small bulbous proximal "segment" may be the palpifer. This possibility is supported by the equally long following two segments that are clearly not ankylosed. A few pale scales are associated with the proximal segment, but it is not clear whether they are attached or have come from another area of the specimen. Whether four- or five-segmented, the maxillary palpus of *At. hoffeinsorum* is unusual among Aedini: if the basal bulbous lobe is the palpifer, it is exceptionally large compared to the structure in extant species; if the following two segments are palpomeres 2 and 3, the absence of ankylosis may be a unique feature of *Aetheapnomyia*.

With a degree of uncertainty, the characteristics of the male genitalia of *At. hoffeinsorum*, especially the long gonostylar claw and the development of the claspette noted above, suggest that *Aetheapnomyia* belongs to the *Ochlerotatus* Group (as characterised by Reinert 2000, as the genus *Ochlerotatus* Lynch Arribálzaga, 1891), which does not include the genus *Aedes* in which *At. hoffeinsorum* was originally placed. However, the affinities of *Aetheapnomyia* with other genera and species of the *Ochlerotatus* Group are indeterminate, and it must be borne in mind that some aedine species, as noted by Belkin (1962), show affinities with other tribes of Culicinae.

Palaeontological context

Rovno amber originated on the Volhynian Upland (Chemyreva *et al*. 2024) and has been dated to the Priabonian Age (33.9–37.8 Mya) (Perkovsky *et al*. 2024a). Most Rovno amber containing Diptera, as well as most other inclusions studied thus far, have been mined in Klesov (Sarny District, Rovno Region) (Perkovsky *et al*. 2010; Mitov *et al*. 2021). The new findings, including mosquitoes, come from the Varash District (former Zarechnoye and Vladimirets districts) located in the northwestern part of the Rovno Region (Lyubarsky & Perkovsky 2020; Olmi *et al*. 2022; Fedotova *et al*. 2024 and references therein). The new mosquito specimen described above was found in the former Zarechnoye District. Extensive amber mining in the district during the past 11 years has resulted in many interesting findings, especially from Kukhotskaja Volia. Unfortunately, much of this amber have been mixed with material from the Vladimirets District or even from outside the Varash District. To date, only two liverwort plant species (one of which is new) have been definitively associated with this deposit (Mamontov *et al*. 2020).

Numerous endemic species and genera (*e.g.* Melnitsky *et al*. 2024a, 2024c, 2024d, 2025a; Vilhelmsen *et al.* 2024; Legalov *et al.* 2025; Shavrin *et al.* 2025; Zaitsev *et al.* 2025), as well as new Eocene species common to Rovno and Baltic ambers (Telnov *et al.* 2023; Alekseev *et al.* 2025; Melnitsky *et al*. 2024a), are added to the fossil fauna in Rovno amber every year. It is well understandable, given that Rovno and Baltic ambers are of the same age, but the Volhynian Upland was separated from Russo-Scandia by Subparathethys (Simutnik *et al.* 2025 and references therein). Moreover, the climate of the Rovno amber forest was warmer (see below). Like most dipterans, mosquitoes are good fliers with the ability to disperse and a significant tolerance to changeable temperatures. The climate of the Baltic amber forest appears to have been warm enough for two of the three Rovno culicid species, so these mosquitoes are represented in both of the faunas compared here.

At the time of this writing, 162 species representing 101 genera of the seven superfamilies/infraorders mentioned in the Introduction and summarised in Table 1 (now with the inclusion of the genus and species described in the present paper) are known from Rovno amber; of these, 27 genera (27%) and 112 species (69%) have not been recorded from Baltic amber.

Especially interesting is the discovery of the moth fly *Neoarisemus groehni* Wagner, 2021 (Psychodidae, Psychodinae) in Rovno amber. It is the only known extinct species of *Neoarisemus* Botoşaneanu & Vaillant, 1970. Twenty of the 27 currently known extant species of *Neoarisemus* occur in the mountains of central, eastern and southern Africa, and Madagascar. The distributions of the other seven species are patchy. One is known from the Neotropical Region (Mexico, Nicaragua), one from the Nearctic Region (Canada, USA), one from the Oriental Region (mainland Southeast Asia) and four from warm-temperate and subtropical areas of the Palearctic Region (Mediterranean Basin, central Asia and Ryukyu Islands). The geological and geographical distribution of the genus strongly indicates a southward migration to Africa during the Miocene (as for many other taxa, see, e.g. Lyubarsky *et al*. 2024a, 2024b; Perkovsky *et al*. 2024b; Telnov & Perkovsky 2025) following the establishment of a stable land connection between Africa and Asia. The absence of *Neoarisemus* and many other cryophobic taxa from Baltic amber, which are present in Rovno amber (*e.g.* Matalin *et al*. 2021; Lyubarsky *et al*. 2023; Jenkins Shaw *et al*. 2024), can likely be explained by a warmer climate of the Rovno amber forest (Mänd *et al*. 2018; Sokoloff *et al*. 2018). Interestingly, the hybotid dance fly genus *Eodromyia* Myskowiak, Garrouste & Nel, 2018 (Hybotidae, Tachydromiinae), present in Rovno amber, was earlier known only from the Eocene Oise amber forest with a paratropical climate (Shamshev *et al*. 2025).

Acknowledgements

We thank Alex Kondratyuk (Berezne, Ukraine) for help with obtaining the mosquito fossil and Dr Emilia Sułek (Warsaw, Poland) for taking care of the amber specimen during the trip from Kyiv to Gdańsk. The comments and suggestions by two anonymous reviewers and the editor are greatly appreciated.

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