

Biting midges (Diptera, Ceratopogonidae) in amber forest communities based on analysis of syninclusions in Late Eocene Rovno amber

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Received on November 17, 2012. Accepted on January 23, 2013.

Final version received on April 1, 2013

Summary

Over 2,500 pieces of unselected Rovno amber (Late Eocene of Ukraine) are studied for their contents of syninclusions depending on amber piece weight class and taxonomic position of syninclusion components. Unlike previous publications (Perkovsky et al. 2010a, 2012), ceratopogonid components enter analysis separately (as genera or genus groups) rather than as entire taxon. This changes the resulting pattern drastically. Instead of two correlation pleiades, the air-plankton one (include biting midges), and the ‘*Sciara* zone’ dwellers, we have six pleiades now depending on developmental environments (terrestrial saprophs *vs.* aquatic) and adult behavior (low level fliers and tree trunk visitors *vs.* air plankton and others which show no preference to tree trunks). Causes of some differences are uncertain.

Keywords

Rovno amber; Baltic amber; Late Eocene; Ceratopogonidae; paleoecology; biocenotic structure; correlation pleiades

Introduction

The present publication continues our series on syninclusions in the Rovno amber (Perkovsky 2006, 2007a, b, 2008, 2009, 2010, 2011; Perkovsky et al., 2010a, 2012). Rovno amber from northern Ukraine and south-western Belarus is a southern coeval counterpart of the Baltic amber and other European succinites (Perkovsky et al., 2007, 2010b; Perkovsky, 2011). It was demonstrated that a statistical analysis of syninclusions made possible to identify some biotopically and, sometimes, trophically intercorrelated groups within a biota of the Late Eocene amber forest (Perkovsky et al., 2010a, 2012). Among others, a group of air-plankton insects is found embracing non-biting and

biting midges (Chironomidae and Ceratopogonidae), and two different groups of tree-trunk dwellers and/or visitors, that is, Dolichopodidae + *Germaraphis* (+ *Lasius*?), and *Sciara* zone Diptera + *Glaesacarus* (+ *Formica*?). Borkent (2000) used syninclusions to determine diversity and community structure in different amber deposits. Males and females of biting midges display strikingly different activity since eclosion. That is why only in their eclosion biotopes we expect to observe them with a comparable sex ratio (40% of males and 60% females as in the material analyzed by Borkent, 2000). The number of syninclusions of various species of Ceratopogonidae reflects the diversity of ceratopogonid species present. Here we show that some taxa are unlikely to be synincluded because of differences in habitat within the amber forest. The present paper is aimed to test and develop the above results using information about syninclusia of genera and genus groups of the biting midges.

The aspects of ecology and behavior of biting midges relevant to the present study may be briefly summarized as follows. Adult females of the subfamily Ceratopogoninae other than blood-sucking *Culicoides* Latreille, 1809 are predators and feed on other flying insects of approximately the same size as themselves. In general, a female flies into a swarm of male non-biting midges (Chironomidae), grabs a male, and settles either to the ground or surrounding vegetation to feed (Borkent and Spinelli, 2007). Swarming males of Chaoboridae and *Culicoides* form their prey as well (Downes, 1978). Male *Ceratopogon* Meigen, 1803, *Brachypogon* Kieffer, 1899, *Serromyia* Meigen, 1818, *Monohalea* Kieffer, 1917, *Stilobezzia* Kieffer, 1911 have plumose antenna and swarming unlike Heteromyiini and Palpomyiini with non-plumose antenna (Downes, 1978). Feminized antennae of extinct *Eohalea* Petrunkevitch, 1957 suggest non-swarming habits and probably substrate mating (Dinwiddie and Rachootin, 2011; Perkovsky, 2013); the same is applicable to *Gedanohalea* Szadziewski, 1988 (Perkovsky, 2013). Like other Ceratopogoninae, *Culicoides* develops in aquatic and semiaquatic habitats; adult females take blood from mammals and birds; mating typically takes place in flight (Szadziewski, 1988). *Forcipomyia* Meigen, 1818 is variable in ecology and behavior, larvae of nominotypical subgenus, which covers a vast majority of the amber species, live mainly in rotten wood and both sexes visit only flowers (Szadziewski, 1988; Hagan et al., 2000). Except for *Culicoides* and *Fossihelea* Szadziewski, 1988, characteristic of the amber (or, rather, succinite) biting midges is a prevalence of females over males (Szadziewski, 1988). However the latter genus shows female majority (73%) in the Rovno amber (Sontag and Szadziewski, 2011). Moreover, a Norwegian experiment of pine trees fogged with a synthetic pyrethroid revealed a female prevalence (55.2%) in *Culicoides* as well (Hagan et al., 2000).

Methods

Sontag and Szadziewski (2011) have revised more than 700 biting midge fossils in the Rovno amber; the only important addition to their data is identification of 26 more specimens of *Eohalea* in the same material. Particularly, besides the early mentioned specimens listed in Sontag and Szadziewski (2011) and Perkovsky (2013), a female of

E. sinuosa (Meunier, 1904) was found in a sample K-967. As a result, a total share of the genus becomes 1.6 times as many as after Sontag and Szadziewski (2011). All studied material is kept at the Schmalhausen Institute of Zoology, NASU, Kiev.

Analyzed statistically is a sample of 2,535 pieces of unselected Rovno amber obtained before the end of 2010 and with each piece weighting 1.5 g or more after primary treatment (grinding and polishing), as described by Perkovsky et al. (2012). Amber pieces less than 1.5 g are excluded because they are usually free of dipteran syninclusion (Perkovsky et al., 2010a, Table 1, 2). Occurrence of dipteran inclusion in different weight fractions of the amber is studied earlier (Perkovsky et al., 2010a); the same weight fractions for piece after primary treatment are used in this paper.

Besides the biting midges included in the present analysis are (i) Chironomidae as one of the most abundant groups in ambers, (ii) the above mentioned group of the trunk dwellers and visitors which comprises Dolichopodidae flies, long-beaked aphid *Germanaphis* Heie, 1967, ant *Lasius schiefferdeckeri* Mayr, 1868 (Perkovsky et al., 2010a, 2012), and Tachydromiinae flies (Hybotidae) which also visit and often hunt on tree trunks (Kovalev, 1966), (iii) various dipteran taxa which develop in decaying plant matter (often mycophagous) and flying low over forest floor; (iv) caddis flies (Trichoptera).

Correlation of the groups involved is assessed with the χ^2 criterion using the Statistica 6.0 (2012) software. A ratio of actual and theoretical shares of particular syninclusion with its confidence level is taken as an immediate measure of correlation (cf. Tables 2 and 3, and Fig. 1).

Results

Predatory Ceratopogonini of the widespread living genera (*Ceratopogon*, *Brachypogon*, *Serromyia*, *Monohalea*, *Stilobezzia*, further referred to as the *Ceratopogon* group), swarming males of *Culicoides* spp., and female *Forcipomyia* spp. who oviposit mainly in decaying wood, are the most abundant in the Late Eocene (Priabonian) ambers of Europe. They comprise 64 per cent of all revised biting midge after Szadziewski (1988) and 74 per cent of all revised biting midge after Szadziewski (1993).

At the same time, the largest pieces of amber provide different proportions of taxa, with the above ones accounting for only 35 per cent of biting midges identified to tribal level. Within the sample studied, big pieces yield 83 per cent of *Eohelea* and *Gedanohalea*, 71.4 of male *Forcipomyia*, 50 of Heteromyiini and Palpomyiini, and 40 of female *Culicoides*. In contrast, they account for only 30.6 per cent of male *Culicoides*, 22.4 of *Ceratopogon* group (as defined above), and 15 of female *Forcipomyia* (Table 1). As a result, the biting midges with feminized male antennae take almost half of the total ceratopogonid assemblage in big pieces (40.7% *Eohelea* and *Gedanohalea* and 3.7% Heteromyiini and Palpomyiini), and 5.6% *Fossihelea* and the living fossil genus *Meunierohalea* Szadziewski, 1988, blood-sucking female *Culicoides* take 9.3 per cent, and nectar feeding male *Forcipomyia* 4.6 per cent. Heteromyiini and Palpomyiini are less common than *Eohelea* and yet better represented in big pieces comparing the

Table 1. Inclusion of biting midges in different weight fractions in studied sample of the Rovno amber. The first figure denotes males; the second, the females.

Taxa	Weight fractions			
	≥ 6.5 g	3–6.5 g	1.5–3 g	< 1.5 g
<i>Eohelea</i> & <i>Gedanohoelea</i>	8:36	1:4	0:4	2:11
<i>Fossihelea</i> & <i>Meunierohoelea</i>	2:4	1:4	0:1	0:4
<i>Culicoides</i>	11:10	10:6	15: 9	25:6
<i>Forcipomyia</i>	5:3	1:10	1:7	7:17
<i>Ceratopogon</i> group	10:14	14:33	17:29	39:75
Heteromyini & Palpomyini	0:4	2:1	0:1	0:1
Total	108	90	83	173

medium-weighted pieces, not to mention small ones with the only specimen found. These are the largest of *Ceratopogonidae* which makes their burial less likely comparing other taxa. In contrast, the pieces of less weight reveal relatively few of *Heteromyini* and *Palpomyini*, whilst *Ceratopogon* group, male *Culicoides*, and female *Forcipomyia* take as much as 73.9 per cent in pieces weighted 3–6.5 g after a primary treatment, 82 per cent in pieces of 1.5–3 g, and 90 per cent in those under 1.5 g.

It is known that big amber pieces are formed low on the tree trunk (Perkovsky, 2010). This implies that biting midges buried mostly in big pieces dwelled on a lower level of the amber forest and often contacted with a low part of amber tree trunks. This inference is in agreement with composition of the studied syninclusion which suggest higher correlation of the above taxa with those showing similar preferences (Table 2, Fig. 1).

Figure 1 shows a number of intercorrelated groups (correlation pleiades *sensu* Berg, 1960) of various biting midges with some taxa already studied in that respect (Perkovsky et al., 2010a, 2012). A central pleiad embraces *Eohelea*, *Gedanohoelea*, *Fossihelea*, *Meunierohoelea*, *Forcipomyia*, *Mycetophilidae* and *Cecidomyiidae*. Ecology of *Eohelea*, *Gedanohoelea*, *Fossihelea* (all are extinct genera) and *Meunierohoelea* is unknown, all other are forest or otherwise non-aquatic saprotrophs, which frequent a lower level of forest and easily visit tree trunks. Male *Forcipomyia* visit flowers for nectar, and the same is known for female *Cacaohoelea* Wirth and Grogan, 1988 with a distinctive patch of microtrichia on wing similar to that characteristic of extinct *Eohelea* (Borkent and Picado, 2008). Of interest is a confident correlation between *Eohelea* and gall midges (*Cecidomyiidae*), for the latter use trunk bark crevices at night and during cold snaps (Z.A. Fedotova, person. comm., 2012), and so they could serve as a food of biting midges when they hunt there, like *Tachypeza* Meigen, 1830 flies (*Hybotidae*, *Tachydromiinae*) do at tree trunks (Kovalev, 1966). Still the stronger and equally confident correlation between *Eohelea* and gall midges is found in the Kalandyk collection of the Baltic amber (E. Sontag and R. Szadziewski, person. comm., 2011). This might additionally explain correlation revealed between the gall and biting midges.

Table 2. Correlation of studied taxa of Ceratopogonidae to other groups considered, based on their co-occurrence in syninclusion.

	Trichoptera	Chironomidae	Trunk visitors	Cecidomyiidae	Phoridae	Sciaridae	Mycetophilidae
<i>Eohelena</i> & <i>Gedanohelea</i>	(1.7):-(1.78)	1.68:2.67/1.60	2.06:1.8/2.16	4.0:-/4.19	0	1.53:(0.96)/1.6	(0.77):-/(0.81)
<i>Fossilhelea</i> & <i>Meunierohelena</i>	0	1.39:-/1.52	3.3:4.6/2.9	0	0	(0.40):-/(0.48)	5.71:(5.71)/5.1
<i>Culicoides</i>	4.39:(1.7)/7.46	1.38:1.37/1.57	0.42:0.41/0.61	1.55:0/3.52	0	0.73:0.88/0.64	0
<i>Forcipomyia</i>	0	1.36:2.39/1.1	0.96:3.25/0.22	1.89:5.0/(0.84)	2.83:-/3.76	1.2:1.38/1.21	1.90:7.29/0
<i>Ceratopogon</i> group	(0.43):-/(0.60)	1.07:1.25/1.01	<u>0.62:0.52/0.65</u>	1.2:1.51/0.84	<i>0.60</i>	<u>0.6:0.55/0.54</u>	0.58:(.47)/ 0.54
Heteromyini & Palpomyini	(4.7):-/(6.2)	1.68:(1.68)/1.68	1.14:-/1.5	-	(3.85)	-	-

Figures denote ratio of actual vs. theoretical number (A:T) of respective kind of syninclusion: the first figure in a cell concerns all syninclusion, the second and third, if at all, refer to syninclusion with male and female of biting midges, respectively. Figures in bold underlined are confident at $P < 0.005$, bold at $P < 0.01$, italics underlined at $P < 0.025$, italics at $P < 0.05$, underlined at $P < 0.1$, regular at $P > 0.1$. Figures in parentheses denote A:T of unique syninclusion of respective kind.

Table 3. Correlation between the non-ceratopogonid groups considered based on their co-occurrence in syninclusia.

	Trunk visitors	Sciaridae	Cecidomyiidae	Phoridae	Mycetophilidae	Trichoptera
Chironomidae	<u>0.55</u>	<u>0.74</u>	1.02	<u>0.31</u>	0.86	1.21
Trunk visitors		<u>0.55</u>	0.99	0.90	0.71	<u>0.47</u>
Sciaridae			1.47	<u>0.71</u>	0.87	<u>0.50</u>
Cecidomyiidae				0.92	1.76	(0.26)
Phoridae					0.72	(0.38)
Mycetophilidae						0.5

The above central pleiad is better represented in the big amber pieces. This is the least applicable for fungus gnats (Mycetophilidae) which anti-correlate with the trunk visitor group (Table 3). Fungus gnats enter the central pleiad solely due to six big and particularly inclusion-rich pieces where they are found together with a variety of other arthropods, including 2 *Fossihelea*, 2 *Meunierohelea* and 3 male *Forcipomyia* (in the one piece K-5632-7 synincluded female *Fossihelea*, male *Forcipomyia*, female *Stilobezzia* and *Germanaphis* aphid). Otherwise Mycetophilidae were hardly present in the central pleiad. Out of 98 male *Forcipomyia* revised by Szadiewski (1988, 1993) in Priabonian ambers, only one was found synincluded with Mycetophilidae. A single Heteropezini gall midge (developing under bark) found in Baltic amber with biting midges is co-buried there as well; gall midges are found also in two of three male *Forcipomyia* - Mycetophilidae syninclusia in Rovno amber.

Two more groups join the central pleiad to form a larger pleiad of a lower level, the above mentioned trunk visitor group, and a pleiad of *Culicoides* biting midges together with the caddis flies which consist mainly of Polycentropodidae (72% of all identified up to family level). Both *Culicoides* and caddis flies develop in water bodies and so less common deep in forest: this might account for their correlation. Both caddis flies synincluded with female *Culicoides* and identified up to family level belong to Polycentropodidae, and one of them to *Plectrocnemia* Stephens, 1836 whose larvae now develop in cool rivers, streams and springs, which might be the case of larvae of *Culicoides* (*Oecacta*) found in Priabonian amber as well.

Within the larger pleiad of a lower level, caddis-flies are distinctly anti-correlated with the trunk visitors. Supposing the two diverging after a gradient of humidity, and having caddis-flies and *Culicoides* connected to water bodies, it is possible to infer the trunk visitors as the least hygrophilic, and the central pleiad as intermediate.

A small and tight pleiad of scuttle flies (Phoridae) and female *Forcipomyia* is distinct of the above larger (and weaker) pleiad in spite that it embraces larval saprotroph insects similar in that respect to the majority of larger pleiad. The distinction might be due to the scuttle flies and female *Forcipomyia* are buried mainly in small pieces unlike the majority of larger pleiad (except for caddis-flies and *Culicoides*). Indeed, 67 per cent

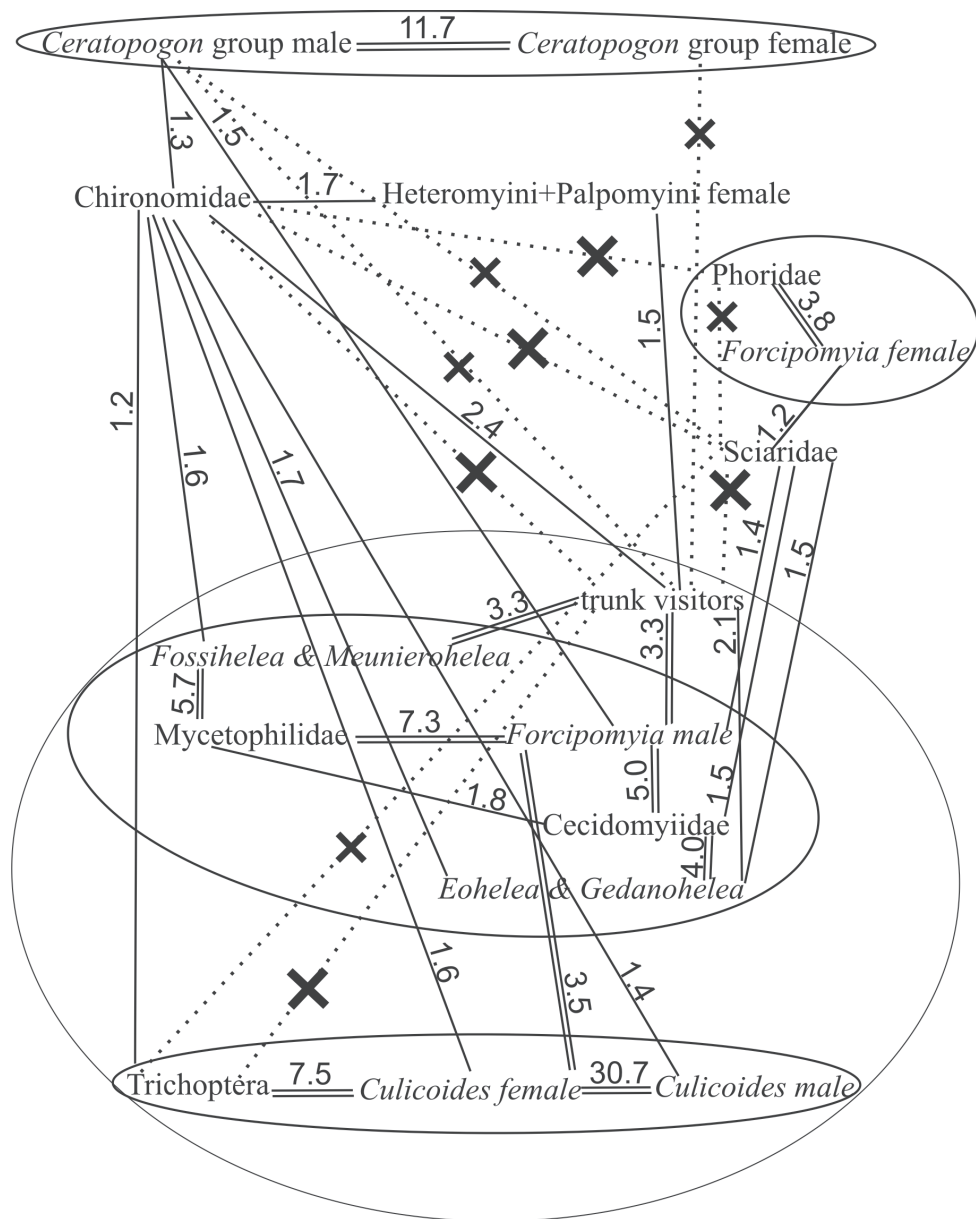


Figure 1. Correlation structure of studied fragment of the Priabonian (Late Eocene) arthropod assemblage of the Rovno amber based on composition of syninclusion. Double lines denote confident correlation ($P < 0.1$), simple line: non-confident correlation ($P > 0.1$), numbers at lines: ratio of actual and theoretical share (A:T) of syninclusion of respective groups. Dot lines denote anti-correlation (those with $A:T < 1$), those with small cross: confident ones ($P < 0.1$), with big cross: highly confident ones ($P < 0.01$). Thick ovals encircle higher correlated pleiades ($A:T > 3.7$), thin oval: less correlated one ($A:T < 3.7$). Not shown are weak correlations ($A:T < 1.2$) and anti-correlations ($A:T > 0.7$), non-confident anti-correlations ($P > 0.1$), and any of them based on unique syninclusion.

of female *Forcipomyia* are found in the pieces under 3 g, and only 8.1 in big pieces. This implies a behavioral difference between the larger pleiad which, with the above exception, intentionally visited tree trunks, and scuttle flies and female *Forcipomyia*, who only occasionally got entrapped into resin, with tree trunks not being attractive for them. In case of female *Forcipomyia*, this might be connected with their activity when seeking for oviposition sites, for three females in the Kiev collection are found buried with an egg batch nearby.

There is one more group of forest soil saprotrophs, Sciaridae, which only weakly correlates with gall midges, *Eohelea* and *Gedanohoelea*, male and female *Forcipomyia*, and strongly anti-correlates with many other groups involved. The reason for this pattern is obscure. Sciaridae are similarly abundant in both big and medium-weighted pieces of amber (Perkovsky et al., 2010a). Similar pattern is characteristic of non-biting midges (Chironomidae) which also show many weak correlative and strong anti-correlative relations. Rovno amber includes many soil-developing species of non-biting midges (40% after Zelentsov et al., 2012), in addition to more expected aquatic ones. Similarly to Phoridae, female *Forcipomyia*, *Culicoides* and caddis flies, a majority of non-biting midges are found in small and medium-weighted pieces of amber. If their relative independence of both aquatic and non-aquatic groups considered here depends on the ecologically mixed composition of the amber Chironomidae, is a subject of future research.

Isolated position of predatory midges defined above as *Ceratopogon* group is equally difficult to explain. They are hunting for small Diptera on flight, and judging from their prevalence in small amber pieces (Table 1), they used tree crowns for day rest.

Insufficient material prevents analyzing connections of Heteromyiini and Palpomyiini in the amber forest biota. It is known that they “may be found in larger water bodies (ponds and springs and larger lotic and lentic habitats such as rivers and lakes) comparing *Ceratopogonini*” (Borkent and Spinelli, 2007, p. 17). One of two specimens of *Physohelea obtusa* (Meunier, 1904) (single female) found in Rovno amber, and the only one buried in a piece weighing above 6 g, forms a syninclusion with Chironomidae and Polycentropodidae (Table 2). Similarly in the Kalandyk collection of the Baltic amber, two *Physohelea* specimens are found, one of them representing *Ph. obtusa* female found together with a caddis fly in an amber piece of 8.35 g weight (E. Sontag and R. Szadziewski, pers. comm., 2011). The genus is limited now to a lake-rich area between 41°S and 43°S from Chiloé till Nahuel Huapi (Grogan and Wirth, 1979). The above records indicate that *Physohelea* Grogan and Wirth, 1979 could be connected with larger water bodies as early as since the Eocene.

Conclusion

The research carried out reveals that using subordinate taxa of a major group instead of the latter taken as a whole may change considerably a general pattern of relations in the past biocenosis. We replaced the family Ceratopogonidae as represented in the arthropod assemblage of the Late Eocene Rovno amber with its constituent genera and

genus groups. Unlike the previous results (Perkovsky et al., 2010a, 2012) a pleiad of the air plankton insect breaks up into several groups (Chironomidae, *Culicoides* + Trichoptera, *Ceratopogon* group). Rather unexpectedly, a ‘*Sciara* zone’ pleiad disintegrates as well into several groups including Sciaridae, Phoridae + female *Forcipomyia*, and the central pleiad with Cecidomyiidae, Mycetophilidae, and three genera/genus groups of biting midges. Still more unexpected is that some former participants of the ‘*Sciara* zone’ pleiad becomes more distant from their former ‘companions’ than the trunk visitor group does: this concerns Phoridae and even Sciaridae itself. An evident inference is that the structure of biocenoses, equally past and present, is highly complicated, and every attempt to decipher it reveals a new and different pattern depending on the method and approach. The syninclusion analysis appears as a promising method, even though one of many of them.

Acknowledgements

Ryszard Szadziewski and Elzbieta Sontag of Gdańsk University, Poland, made us possible to know and use unpublished information about syninclusia in the Kalandyk collection of the Baltic amber kept at the Gdańsk University. S.I. Melnitsky (St. Petersburg State University, Russia) permits using unpublished data on caddis flies in the Rovno amber. We are thankful to I.A. Shamshev and Z.A. Fedotova (All-Russian Research Institute of Biological Plant Protection, St. Petersburg-Pushkin, Russia) for helpful suggestions on empids and gall midges of Rovno amber. Dr. Art Borkent (Salmon Arm, Canada) kindly made a number of important suggestions to the manuscript.

The study is supported for EEP by the Paleontological Society International Research Program (PalSIRP) Sepkoski Grant for 2012, for APR by RFBR Grant # 12-04-01177 and the Presidium RAS Program “Origin of biosphere and evolution of the geo-biological systems”.

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