

Community Structure in the Amber Forest: Study of the Arthropod Syninclusion in the Rovno Amber (Late Eocene of Ukraine)

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Abstract: Arthropodan syninclusions in the Late Eocene Rovno amber were examined using χ^2 to reveal correlation of the component groups (some taxa of Diptera, ants, aphids, and mites) supposedly indicative of the biocoenotic relationships in the ancient amber forest. Three tightly correlated groups were identified, representing a putative aerial plankton guild (Chironomidae + Ceratopogonidae) and two tree-trunk guilds, one of which (Dolichopodidae + *Germaraphis*) is possibly connected to more open or/and more hygrophilous habitats than the other (*Sciara* zone Diptera + “*Acarus*” *rhombus*). The ants were not linked with any of the above components.

Key words: syninclusion, Rovno amber, Eocene, synecology, amber forest biocoenosis, Diptera, Formicidae, *Germaraphis*, “*Acarus*” *rhombus*

1 Introduction

Since the seminal publication by Jan Koteja (1989) there is a growing awareness that syninclusion analysis is an important tool to reveal the structure of biocenoses of ancient amber forests (Kutscher and Koteja, 2000; Sontag, 2003; Perkovsky, 2006, 2007a, b, 2008a, b, 2009a, b, 2010; Perrichot and Girard, 2009; Weitschat, 2009; Wichard, 2009). The present study is intended to make the next step in that direction using statistical analysis of syninclusion composition in the Rovno amber, a southern coeval analog of the famous Baltic amber (Perkovsky et al., 2007).

Recent studies have shown that inclusion composition is dependent on the weight fractions (size of pieces) of the amber (Perkovsky, 2009b, 2010). It was shown, for instance, that specialized dendrobiont ants like *Ctenobethylus goepperti* (Mayr) make up a higher percentage of the ant assemblage in smaller amber pieces than in larger ones, and a lower percentage in the larger fraction, while the more generalistic (mainly herpetobiotic) *Lasius schiefferdeckeri* Mayr shows an opposite tendency. The larger the amber pieces, the higher are their chance to come from the tree trunk and not from the thinner branches. The above-mentioned trends suggest that *C. goepperti* was more prone to visit the tree crown than *L. schiefferdeckeri*, which were probably more confined to the trunk and maybe the thick branches.

Distribution of families of the order Diptera is found to be dependent on the weight fraction of amber as well (Tables 1, 2). Both tables show various patterns of that dependence, but most evident is a decreasing proportion of midges (Chironomidae) in

Table 1 Inclusion of Diptera in different weight fractions of the Rovno amber

Inclusia	< 1.5 g		1.5– 6.5 g		> 6.5 g	
	n	%	n	%	n	%
Chironomidae	684	38.3	895	34.0	452	30.3
Sciaridae	354	19.8	561	21.3	297	19.9
Dolichopodidae	222	12.4	335	12.7	184	12.3
Mycetophilidae s.l.	164	9.2	274	10.4	133	8.9
Ceratopogonidae	126	7.1	154	5.9	110	7.4
Cecidomyiidae	35	2.0	98	3.7	68	4.6
Psychodidae	29	1.6	61	2.3	64	4.3
Phoridae	62	3.5	94	3.6	48	3.2
Tipuloidea	44	2.5	84	3.2	74	5.0
Empididae	51	2.9	51	1.9	49	3.3
Rhagionidae	8	0.5	11	0.4	6	0.4
Scatopsidae	1	0.1	2	0.1	0	0.0
Simuliidae	4	0.2	5	0.2	3	0.2
Syrphidae	2	0.1	2	0.1	1	0.1
Mythicomyiidae	0		0	0	1	0.1
Chaoboridae	0		2	0.1	0	0
Dixidae	0		0	0	1	0.1
Mycetobiidae	0		2	0.1	1	0.1
Asilidae	1	0.1	1	0.1	0	0
Campichoetidae	0		1	0.1	0	0
<i>Sciara</i> zone Diptera	687	38.4	1172	44.5	684	45.9
<i>Sciara</i> zone Diptera: Chironomidae	1:1.0		1:0.76		1:0.66	
Total inclusia	1787		2633		1492	

Note: *Sciara* zone Diptera include Tipuloidea, Sciaridae, Mycetophilidae s.l., Cecidomyiidae, Psychodidae, Phoridae.

larger pieces of amber, and the opposite trend displayed by the *Sciara* zone Diptera (after Larsson, 1978), namely: Tipuloidea, Sciaridae, Mycetophilidae s.l., Cecidomyiidae, Psychodidae, and Phoridae. This pattern is easily explained if the above hypothesis (that the higher weight fraction of the amber comes mainly from the lower part of the amber tree) is correct. As a generalization we can infer that small amber pieces occurred widely over the amber-

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producing tree and represent a better trap than larger pieces for aerial planktonic insects and other arthropods not confined to tree trunks or immediately above the forest floor. With this in mind, we undertook this analysis of amber inclusions with the intention to reveal significant deviations from randomness when various arthropod groups form syninclusions.

2 Methods

We analyzed the composition of arthropod inclusions in the Rovno amber collection kept at the Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, described in more detail by Perkovsky et al. (2007). All of the amber pieces studied originated from Pugach quarry in Klesov. When processed, amber loses about one-third of its original weight (see Perkovsky, 2009b, for details). Three sets were created for further analysis, based on the amber collection: (1) the weight fraction 2–5 g before preparation, which reached the range of 1.3–3.5 g after grinding and polishing, opaque pieces excluded (Table 3); (2) a subset of (1): smaller amber pieces containing wingless arthropods and/or wood fragments and so probably formed on the tree trunk and thick branches (unlike the rest of that fraction, which is supposed to come rather from the outer part of the tree crown, or nearby (Table 4); and (3) the weight fraction ≥ 4.5 g after preparation (Table 5).

More common taxa of the respective arthropod assemblages (those recorded for the three sets) were selected for analysis, with particular attention to the Diptera, the ants (family Formicidae, dominant species *Ctenobethylus goepperti* of the subfamily Dolichoderinae, and the subfamily Formicinae in set [3]), aphids considered to be common ant symbionts (genus *Germaraphis* Heie; see Perkovsky, 2010, for details), and the commonest amber mite “*Acarus*” *rhombus* Koch et Berendt, 1854.

Sets (1) and (2) were created to consider both empty pieces of amber and those bearing arthropod inclusions, unlike the third set (the high weight fraction) which was assembled before the goal of the present research was formulated. To compensate for this omission, the proportion of empty pieces was assessed, based on the Gdansk Representative Collection described by Sontag (2003), which is fortunately composed mainly of the weight fraction similar to our set (3): the minimum raw weight of amber pieces in set (3) (calculated from the minimum polished weight ≥ 4.5 g) is some 6.8 g as compared with the mean raw weight of the amber pieces indicated by Sontag as 11 g. The data by Sontag permits a calculation which indicates that the total number of the amber pieces there is 1.54× that for pieces with arthropod inclusions. That is why the figure of 851 amber pieces with arthropod inclusions, which comprise set (3), has been multiplied

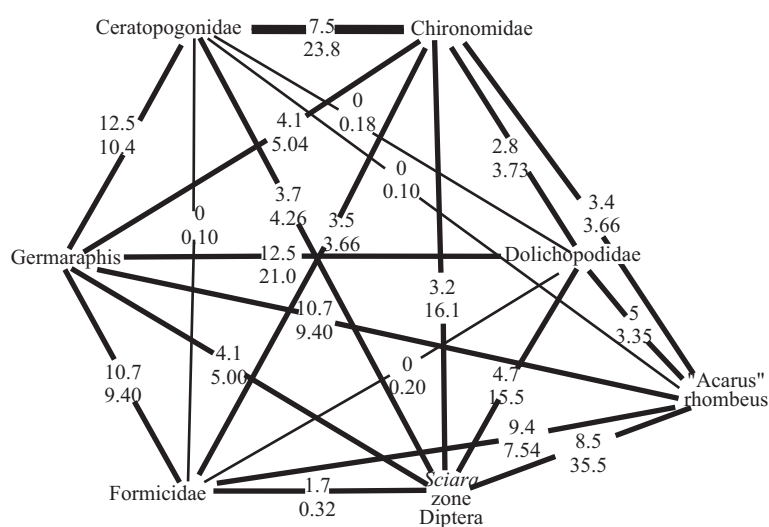


Fig. 1. Connections between component groups of Arthropoda syninclusions in smaller pieces of the Rovno amber (after Table 3).

Thin lines denote negative or no correlation, thick lines denote positive correlation, double lines denote the most significant ties. The figures at lines show: the upper one, relation between the actual and theoretical shares of the amber pieces containing a particular kind of syninclusion in the sample, the lower one, the respective χ^2 value; the lower figure is shown in bold when the value is above 3.84 and so the connection is significant at $P < 0.05$.

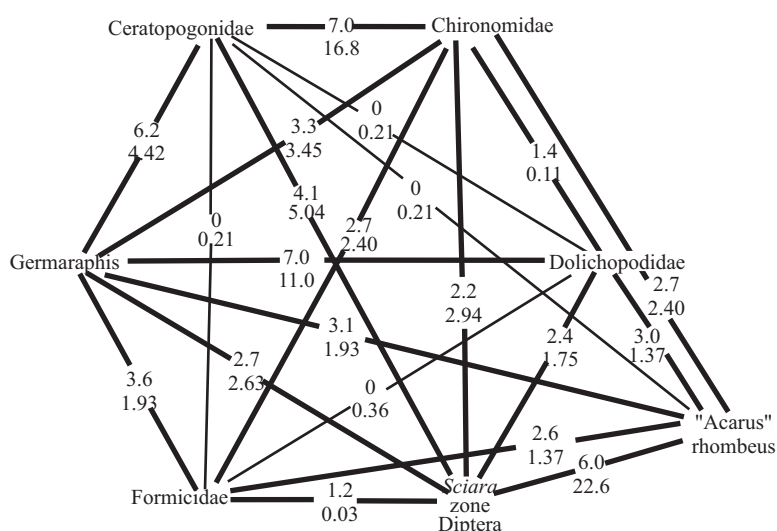


Fig. 2. Connections between component groups of Arthropoda in syninclusions in smaller pieces of the Rovno amber with wingless arthropods and/or wood fragments (after Table 4). Lines and figures as on Fig. 1.

in the proportion of 1.5 to get the restored total size of the sample as 1276 amber pieces.

Column “n” in Tables 3–5 gives the number of pieces of amber with inclusions/syninclusions of a respective kind (as indicated in the column “Inclusia”). The column “actual share” shows the respective figures in column “n” divided by the total number of amber pieces considered (Table 3: 1339; Table 4: 426; Table 5: 1276; see above for explanation of the last figure). The column “theoretical share” represents the actual shares of the components (the taxa forming the syninclusion) multiplied together. The column “actual / theor. share” indicates how the components of

the syninclusion are connected to each other: they are positively correlated when the respective figure is greater than 1 (and the more so the higher the figure), they are negatively correlated when the figure is less than 1, and they are independent when the value is equal to 1. The statistical significance of the correlation between the components of the amber arthropod assemblage was assessed using the χ^2 test, which indicates the significance of coincidence of events. The χ^2 calculation is described in statistical textbooks and in available software like Statistica 6.0 and above (Statistica 6.0, 2010). The critical values of χ^2 are as follows. When χ^2 is equal to or greater than 3.84, the probability of the occasional coincidence of the events is less than one in 20 ($P < 0.05$), and the difference between the actual and theoretical value can be considered as significant. When χ^2 is equal to or greater than 6.63, then the probability of occasional coincidence of events is less than one in 200 ($P < 0.005$), and the difference between the actual and theoretical value is termed highly significant.

3 Results

Table 3 shows the connections between arthropod groups as revealed in the analysis of syninclusion composition in the smaller Rovno amber of the weight fraction 2–5 g before preparation, or 1.3–3.5 g after preparation (Fig. 1). The table and figure show that most connections are positive (values well above 1), which form a continuum embracing all groups involved. However, the statistically highly significant connections ($P < 0.005$) form three separate pairs: Chironomidae + Ceratopogonidae, Dolichopodidae + *Germaraphis*, and *Sciara* zone Diptera + *Acarus*, and the lone family Formicidae.

Table 4 and Fig. 2 show a similar pattern with the same three pairs of closely correlated groups with the highly significant connections ($P < 0.005$). Again they leave the ants isolated.

Table 5 and Fig. 3 present a similar, though more complicated picture. Again, the positive connections (those with the actual share distinctly higher than the theoretical one) embrace all of the groups considered, but the statistically highly significant positive connections ($P < 0.005$) join only two groups of Chironomidae + *Germaraphis* + Dolichopodidae, and *Sciara* zone Diptera + “*Acarus*”, isolated groups, again with the ants left alone, even though this time they are divided into isolated Formicinae and *C. goepperti*. Alternatively, when relying on a lower level of significance ($P < 0.05$), the only change is that Formicinae joins the group *Sciara* zone Diptera + “*Acarus*” whilst *Ctenobethylus* *goepperti* remains isolated.”

4 Discussion

The results obtained are consistent (reproduced in three different analyses) but quite unexpected. The point is not that the results show no significant correlation between ants and their

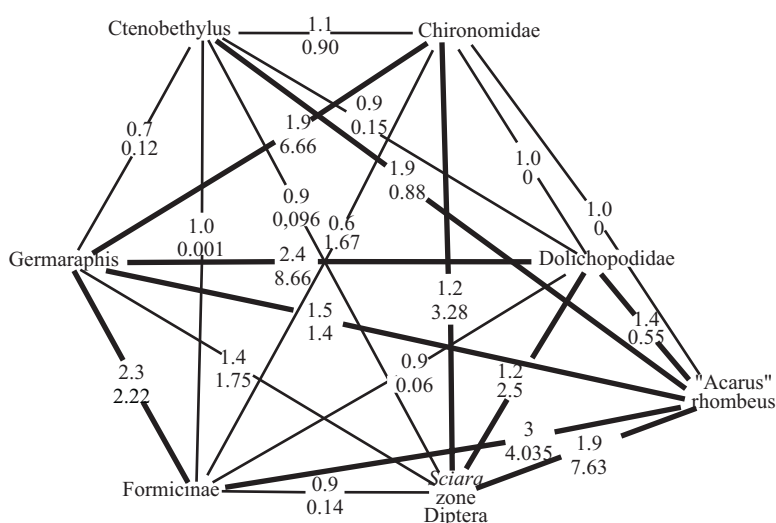


Fig. 3. Connections between component groups of Arthropoda in syninclusion in larger pieces of the Rovno amber (after Table 5). Lines and figures as on Fig. 1.

Table 2 Diptera in the Rovno amber of three weight fractions counted by the amber pieces with inclusion of respective families (irrespective of number of inclusion per piece)

Inclusia	< 1.5 g		1.5–6.5 g		> 6.5 g	
	n	%	n	%	n	%
Chironomidae	507	39.2	497	39.3	180	42.9
Sciaridae	255	19.7	326	25.8	113	27.0
Dolichopodidae	201	15.6	256	20.2	115	27.5
Mycetophilidae s.l.	140	10.8	214	16.9	76	18.1
Ceratopogonidae	105	8.1	108	8.5	57	13.6
Cecidomyiidae	35	2.7	86	6.8	47	11.2
Psychodidae	29	2.3	46	3.6	38	9.1
Tipuloidea	41	3.2	75	5.9	57	13.6
Phoridae	57	4.4	61	4.8	23	5.5
Empididae s. l.	49	3.9	48	3.8	30	7.2
<i>Sciara</i> zone Diptera	522	40.2	642	50.8	264	63.0
<i>Sciara</i> zone Diptera: Chironomidae	1:0.97		1:0.77		1:0.68	
Total amber pieces	1293		1265		419	

symbiotic aphids, the connections which appeared so apparent from our previous analyses conducted with different tools (see Introduction), but that the patterns revealed are so similar in spite of the fact that they are based on samples that are formed supposedly in different habitats of the crown vs. trunk of the amber tree (Table 3 and Fig. 1 vs. Tables 4, 5 and Figs. 2, 3, respectively; see above). Nevertheless, we consider these results as reasonable and important. Our proposal is that the best way to inquire about past biocoenotic relationships based on syninclusion analysis is to discover the links in a different and more strictly comparative way. As a result, the most spectacular and interesting links, which result from a purposeful search, such as those between ants and their symbiotic aphids, do not necessarily appear as the strongest under the present version of the syninclusion analysis. Correct or not, the above hypothesis deserves further testing by application of the proposed syninclusion analysis to more diverse material representing different taxa and different ambers.

The results obtained allow (syn-)ecological inferences as well. Of the three regularly retrieved groupings, the one embracing Chironomidae and Ceratopogonidae is the most apparent as the

Table 3 Inclusion composition of the Rovno amber, weight fraction 2–5 g before preparation (see text for further explanations)

Inclusia	<i>n</i>	Actual share	Theor. share	Actual/theoret. share	χ^2
With inclusia	363	0.27110			
With syninclusia	138	0.10306			
Chironomidae	65	0.04854			
Ceratopogonidae	11	0.00822			
Dolichopodidae	22	0.01643			
<i>Sciara</i> zone Diptera	65	0.04854			
Formicidae	12	0.00896			
<i>Germaraphis</i>	10	0.00746			
" <i>Acarus</i> "	12	0.00896			
Chironomidae + Ceratopogonidae	4	0.0030	0.0004	7.5:123.841	
Chironomidae + Dolichopodidae	3	0.0022	0.0008	2.8:1 3.735	
Chironomidae + <i>Sciara</i> zone Diptera	10	0.0075	0.0024	3.2:116.140	
Chironomidae + Formicidae	2	0.0015	0.0004	3.5:1 3.658	
Chironomidae + <i>Germaraphis</i>	2	0.0015	0.0004	4.1:1 5.039	
Chironomidae + " <i>Acarus</i> "	2	0.0015	0.0004	3.4:1 3.658	
Ceratopogonidae+Dolichopodidae	0	0	0.0001	0 0.185	
Ceratopogonidae+ <i>Sciara</i> zone Diptera	2	0.0015	0.0004	3.7:1 4.265	
Ceratopogonidae + Formicidae	0	0	0.0001	0 0.100	
Ceratopogonidae + <i>Germaraphis</i>	1	0.0007	0.0001	12.5:110.418	
Ceratopogonidae + " <i>Acarus</i> "	0	0	0.0001	0 0.100	
Dolichopodidae+ <i>Sciara</i> zone Diptera	5	0.0037	0.0008	4.7:115.470	
Dolichopodidae+ Formicidae	0	0	0.0001	0 0.202	
Dolichopodidae+ <i>Germaraphis</i>	2	0.0015	0.0001	12.5:121.010	
Dolichopodidae+ " <i>Acarus</i> "	1	0.0007	0.0001	5.0:1 3.354	
<i>Sciara</i> zone Diptera + Formicidae	1	0.0007	0.0004	1.7:1 0.317	
<i>Sciara</i> zone Diptera + <i>Germaraphis</i>	2	0.0015	0.0004	4.1:1 5.004	
<i>Sciara</i> zone Diptera + " <i>Acarus</i> "	5	0.0037	0.0004	8.5:135.527	
Formicidae + <i>Germaraphis</i>	1	0.0007	0.0001	10.7:1 9.402	
Formicidae + " <i>Acarus</i> "	1	0.0007	0.0001	9.4:1 7.541	
<i>Germaraphis</i> + " <i>Acarus</i> "	1	0.0007	0.0001	10.7:1 9.402	
Empty	976	0.728			
Total amber pieces	1339				

Table 4 Inclusion composition of the Rovno amber, weight fraction 2–5 g before preparation (see text for further explanations): only amber pieces with inclusions of wingless arthropods and/or wood fragments

Inclusia	<i>n</i>	Actual share	Theor. share	Actual/theoret. share	χ^2
With arthropods inclusia	219	0.5141			
Chironomidae	26	0.0610			
Ceratopogonidae	7	0.0164			
Dolichopodidae	12	0.0282			
<i>Sciara</i> zone Diptera	30	0.0704			
Formicidae	12	0.0282			
<i>Germaraphis</i>	10	0.0235			
" <i>Acarus</i> "	12	0.0282			
Chironomidae + Ceratopogonidae	3	0.0070	0.0010	7.0:116.776	
Chironomidae + Dolichopodidae	1	0.0023	0.0017	1.4:1 0.108	
Chironomidae + <i>Sciara</i> zone Diptera	4	0.0094	0.0043	2.2:1 2.944	
Chironomidae + Formicidae	2	0.0047	0.0017	2.7:1 2.404	
Chironomidae + <i>Germaraphis</i>	2	0.0047	0.0014	3.3:1 3.451	
Chironomidae + " <i>Acarus</i> "	2	0.0047	0.0017	2.7:1 2.404	
Ceratopogonidae + Dolichopodidae	0	0	0.0005	0 0.206	
Ceratopogonidae+ <i>Sciara</i> zone Diptera	2	0.0047	0.0012	4.1:1 5.039	
Ceratopogonidae + Formicidae	0	0	0.0004	0 0.206	
Ceratopogonidae + <i>Germaraphis</i>	1	0.0023	0.0004	6.2:1 4.425	
Ceratopogonidae + " <i>Acarus</i> "	0	0	0.0005	0 0.206	
Dolichopodidae + <i>Sciara</i> zone Diptera	2	0.0047	0.0020	2.4:1 1.747	
Dolichopodidae + Formicidae	0	0	0.0008	0 0.358	
Dolichopodidae + <i>Germaraphis</i>	2	0.0047	0.0007	7.0:111.045	
Dolichopodidae + " <i>Acarus</i> "	1	0.0023	0.0008	3:1 1.373	
<i>Sciara</i> zone Diptera + Formicidae	1	0.0023	0.0020	1.2:1 0.031	
<i>Sciara</i> zone Diptera + <i>Germaraphis</i>	2	0.0047	0.0017	2.7:1 2.626	
<i>Sciara</i> zone Diptera + " <i>Acarus</i> "	5	0.0117	0.00198	6:122.613	
Formicidae + <i>Germaraphis</i>	1	0.0023	0.0007	3.6:1 1.930	
Formicidae + " <i>Acarus</i> "	1	0.0023	0.0008	3:1 1.373	
<i>Germaraphis</i> + " <i>Acarus</i> "	1	0.0025	0.0008	3.1:1 1.930	
Total amber pieces	426				

Table 5 Inclusion composition of the Rovno amber, weight fraction ≥ 4.5 g after preparation (see text for further explanations)

Inclusia	<i>n</i>	Actual share	Theor. share	Actual/theoret. share	χ^2
Chironomidae	295	0.2312			
Dolichopodidae	175	0.1371			
<i>Sciara</i> zone Diptera	431	0.3378			
Formicinae	49	0.0384			
<i>Ctenobethylus</i>	51	0.0400			
<i>Germaraphis</i>	34	0.0266			
" <i>Acarus</i> "	26	0.0204			
Chironomidae + Dolichopodidae	41	0.0321	0.03169	1.0:1 0.007	
Chironomidae + <i>Sciara</i> zone Diptera	117	0.0917	0.07810	1.2:1 3.278	
Chironomidae + Formicinae	7	0.0055	0.00888	0.6:1 1.672	
Chironomidae + <i>Ctenobethylus</i>	13	0.0102	0.00925	1.1:1 0.090	
Chironomidae + <i>Germaraphis</i>	15	0.0118	0.00615	1.9:1 6.664	
Chironomidae + " <i>Acarus</i> "	6	0.0047	0.00472	1.0:1 0.001	
Dolichopodidae+ <i>Sciara</i> zone Diptera	71	0.0556	0.04631	1.2:1 2.499	
Dolichopodidae + Formicinae	6	0.0047	0.00526	0.9:1 0.062	
Dolichopodidae + <i>Ctenobethylus</i>	6	0.0047	0.00548	0.9:1 0.149	
Dolichopodidae + <i>Germaraphis</i>	11	0.0086	0.00364	2.4:1 8.656	
Dolichopodidae + " <i>Acarus</i> "	5	0.0039	0.00280	1.4:1 0.553	
<i>Sciara</i> zone Diptera + Formicinae	15	0.0118	0.01297	0.9:1 0.143	
<i>Sciara</i> zone Diptera + <i>Ctenobethylus</i>	16	0.0125	0.01351	0.9:1 0.096	
<i>Sciara</i> zone Diptera + <i>Germaraphis</i>	16	0.0125	0.00899	1.4:1 1.752	
<i>Sciara</i> zone Diptera + " <i>Acarus</i> "	17	0.0133	0.00689	1.9:1 7.628	
Formicinae + <i>Ctenobethylus</i>	2	0.0016	0.00154	1.0:1 0.001	
Formicinae + <i>Germaraphis</i>	3	0.0023	0.00102	2.3:1 2.216	
Formicinae + " <i>Acarus</i> "	3	0.0023	0.00078	2.9:14.0353	
<i>Ctenobethylus</i> + <i>Germaraphis</i>	1	0.0008	0.00106	0.7:1 0.116	
<i>Ctenobethylus</i> + " <i>Acarus</i> "	2	0.0016	0.00082	1.9:1 0.876	
<i>Germaraphis</i> + " <i>Acarus</i> "	1	0.0008	0.00054	1.5:1 0.141	
Total amber pieces	1276				

aerial plankton subset of the amber forest community. The other two groupings: Dolichopodidae + *Germaraphis*, and *Sciara* zone Diptera + "*Acarus*", both probably represent the amber tree-trunk (and possibly the above-forest-floor) guilds, for the following reasons. Dolichopodid flies are well known for their habit of resting on tree trunks. *Germaraphis* aphids have a close living analogue *Stomaphis* Walker, which is known to be tended by ants of the genera *Lasius* F. and *Liometopum* Mayr in bark crevices low on tree trunks (Perkovsky, 2010). *Sciara* zone Diptera live mainly on fungi in the leaf litter, under the bark of trees, etc. The amber mite "*Acarus*" *rhombeus* Koch and Berendt, 1854 is considered to be a very unusual representative of Astigmata belonging to none of the extant families (E.Sidorchuk and P. Klimov, in prep.). However, the ecological difference between these two groupings is a puzzle, unless a hint from the midges is taken seriously. It was already mentioned that Chironomidae enters the group of Dolichopodidae + *Germaraphis* in one of our samples, even if the significance of connection of the midges to *Germaraphis* is lower than the others in that grouping (cf. Table 5 and Fig. 3). Midges are a part of the aerial plankton guild and, at the same time, they are known to be generally hygrophilous insects. These features make it possible to propose, very tentatively, that the pair Dolichopodidae + *Germaraphis*, as compared with the *Sciara* zone Diptera + "*Acarus*", might represent either a more hygrophilous variety of the tree-trunk guild, or connected to a more open landscape (with sparse trees), or both. Hopefully, planned future research will resolve these puzzles".

5 Conclusion

The present study of the composition of the inclusion assemblages in the Rovno amber using syninclusion analysis has brought unexpected but significant results. Their significance is primarily because the approach used herein has resulted in a different pattern compared with those produced by more customary approaches, and so it highlights the subject in a different way. In particular, the syninclusion analysis has revealed the existence of three tight groups of dwellers of the Rovno amber forest, which might represent three different guilds of the past biocenosis.

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