

UDK 565.796: 551.781.4

ROVNO AMBER ANT ASSAMBLAGE: BIAS TOWARD ARBOREAL STRATA OR SAMPLING EFFECT?

E. E. Perkovsky

Schmalhausen Institute of Zoology, NAS of Ukraine,
vul. B. Khmel'nitskogo, 15, Kyiv, 01030 Ukraine
E-mail: perkovsk@gmail.com

Rovno Amber Ant Assemblage: Bias Toward Arboreal Strata or Sampling Effect? Perkovsky, E. E. — In 2015 B. Guenard with co-authors indicated that the Rovno amber ant assemblage, as described by G. Dlussky and A. Rasnitsyn (2009), showed modest support for a bias towards arboreal origin comparing the Baltic and Bitterfeld assemblages, although it is not clear whether this reflects a sampling error or a signal of real deviation. Since 2009, the Rovno ant collection has now grown more than twice in volume which makes possible to check if the above inference about the essentially arboreal character of the assemblage is real or due to a sampling error. The comparison provided suggests in favour of the latter reason for the bias revealed by B. Guenard and co-authors. The new and larger data on the Rovno assemblage show that the share of non-arboreal ants is now well comparable with those concerning the Baltic and Bitterfeld assemblages. This holds true for the both total assemblages and subassemblages of worker ants only.

Key words: Eocene, community structure, Formicidae, fossils, genetic diversity, amber.

*This paper is a second in the series
of papers dedicated to memory
of Prof. Gennady Dlussky, who established
a new standard in palaeomyrmecology*

Modern ant assemblages were compared to the fossil assemblages of the Baltic, Bitterfeld, Rovno and Scandinavian amber deposits compiled by Dlussky and Rasnitsyn (2009) by Guenard et al. (2015).

Late Eocene amber assemblages in the paper of Dlussky and Rasnitsyn (2009) were represented by over 16,700 inclusions determined to the species level (respectively Baltic = 14,915, Bitterfeld = 1,039; Rovno = 501; and Scandinavian = 271).

To evaluate taphonomic biases in generic composition, Guenard et al. (2015) classified the extant genera known from the fossil records into one of the following categories: arboreal, epigaeic, hypogaeic, arboreal + epigaeic, epigaeic + hypogaeic, arboreal + epigaeic + hypogaeic (no genera were classified as arboreal + hypogaeic). Furthermore, they considered if the fossil specimens in each genus were known as worker (nonflying individual) or alate (flying gyne or male). This is an important distinction because many hypogaeic species are overrepresented by alate individuals trapped in resin during mating flights (Dlussky, Rasnitsyn, 2009).

The multinomial logistic regression analysis (Guenard et al., 2015) supports an epigaeic origin of the species richness across subfamilies when all fossil deposits sites are considered. The result is, however, slightly different when fossil assemblages are considered individually. While the Baltic amber and Bitterfeld ones relate more strongly to the epigaeic or epigaeic + hypogaeic origin, the Rovno amber assemblage appears biased towards the arboreal origin. Guenard et al. (2015) indicate that Rovno assemblage shows modest support for a bias towards arboreal origin, although it is unclear whether this reflects a sampling error or a signal of real deviation.

Table 1. Extant genera of ants in representative collections after Dlussky, Rasnitsyn (2009), interpreted ecologically after Guenard et al. (2015)

Ant genera	PIN-964	HMC	Rovno 2009
<i>Anonychomyrma</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Aphaenogaster</i>		epigaeic	epigaeic
<i>Camponotus</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Carebara</i>	hypogaecic	hypogaecic	hypogaecic
<i>Dolichoderus</i>	arboreal	arboreal	arboreal
<i>Formica</i>	epigaeic	epigaeic	epigaeic
<i>Gesomyrmex</i>	arboreal	arboreal	arboreal
<i>Gnamptogenys</i>		all#	all#
<i>Iridomyrmex</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Lasius</i>	epigaeic	epigaeic	epigaeic
<i>Monomorium</i>	epigaeic	epigaeic	epigaeic
<i>Myrmica</i>	epigaeic		
<i>Nylanderia</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Oecophylla</i>		arboreal	
<i>Plagiolepis</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Ponera</i>		epigaeic	epigaeic
<i>Prenolepis</i>	epigaeic+ arboreal	epigaeic+ arboreal	epigaeic+ arboreal
<i>Pseudolasius</i>		epigaeic	epigaeic
<i>Tapinoma</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Technomyrmex</i>		arboreal	
<i>Temnothorax</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Tetramorium</i>			epigaeic+ arboreal
<i>Tetraponera</i>	arboreal	arboreal	arboreal
Genera Σ	16	21	20
Epigaeic + Hypogaecic	31 %	33 %	35 %
Hypogaecic	6 %	5 %	5 %

Table 2. Extant genera of ants in representative collections (new data, Perkovsky, 2016), interpreted ecologically after Guenard et al. (2015)

Ant genera	Baltic 2016	Bitterfeld 2016	Rovno 2016
<i>Acanthomyrmex</i>	epigaeic		
<i>Amblyopone</i>	hypogaecic		
<i>Aphaenogaster</i>	epigaeic	epigaeic	epigaeic
<i>Camponotus</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Carebara</i>	hypogaecic	hypogaecic	hypogaecic
<i>Crematogaster</i>	epigaeic + arboreal		epigaeic + arboreal
<i>Cryptopone</i>			hypogaecic
<i>Dolichoderus</i>	arboreal	arboreal	arboreal
<i>Formica</i>	epigaeic	epigaeic	epigaeic
<i>Gesomyrmex</i>	arboreal	arboreal	arboreal
<i>Gnamptogenys</i>	all	all	all
<i>Hypoponera</i>	hypogaecic	hypogaecic	hypogaecic
<i>Lasius</i>	epigaeic	epigaeic	epigaeic
<i>Liometopum</i>	epigaeic		
<i>Meranoplus</i>	epigaeic		
<i>Monomorium</i>	epigaeic	epigaeic	epigaeic
<i>Myrmica</i>	epigaeic	epigaeic	epigaeic
<i>Nylanderia</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Oecophylla</i>	arboreal	arboreal	
<i>Pachycondyla</i>	all	all	all
<i>Plagiolepis</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Platythyrea</i>	arboreal		
<i>Ponera</i>	epigaeic	epigaeic	epigaeic
<i>Prenolepis</i>	epigaeic+ arboreal	epigaeic+ arboreal	epigaeic+ arboreal
<i>Pristomyrmex</i>		epigaeic	
<i>Proceratium</i>	hypogaecic		hypogaecic
<i>Pseudolasius</i>	epigaeic	epigaeic	epigaeic
<i>Stenamma</i>	hypogaecic		
<i>Tapinoma</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Temnothorax</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Tetramorium</i>	epigaeic + arboreal		
<i>Tetraponera</i>	arboreal	arboreal	arboreal
<i>Vollenhovia</i>	epigaeic + arboreal		epigaeic + arboreal
Genera Σ	32	22	24
Epigaeic + Hypogaecic	44 %	46 %	46 %
Hypogaecic	16 %	9.5 %	17 %

Table 3. Extant genera of ants in representative collections (new data), interpreted ecologically after Guenard et al. (2015): worker ants only

Workers	Baltic 2016	Bitterfeld 2016	Rovno 2016
<i>Acanthomyrmex</i>	epigaeic		
<i>Amblyopone</i>	hypogaecic		
<i>Aphaenogaster</i>	epigaeic	epigaeic	epigaeic
<i>Camponotus</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Carebara</i>	hypogaecic	hypogaecic	hypogaecic
<i>Crematogaster</i>	epigaeic + arboreal		
<i>Dolichoderus</i>	arboreal	arboreal	arboreal
<i>Formica</i>	epigaeic	epigaeic	epigaeic
<i>Gesomyrmex</i>	arboreal	arboreal	arboreal
<i>Gnamptogenys</i>		all	
<i>Hypoponera</i>	hypogaecic		
<i>Lasius</i>	epigaeic	epigaeic	epigaeic
<i>Liometopum</i>	epigaeic		
<i>Meranoplus</i>	epigaeic		
<i>Monomorium</i>	epigaeic	epigaeic	epigaeic
<i>Myrmica</i>	epigaeic	epigaeic	epigaeic
<i>Nylanderia</i>		epigaeic + arboreal	
<i>Oecophylla</i>	arboreal	arboreal	
<i>Plagiolepis</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Platythyrea</i>	arboreal		
<i>Prenolepis</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Pseudolasius</i>	epigaeic	epigaeic	epigaeic
<i>Tapinoma</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Temnothorax</i>	epigaeic + arboreal	epigaeic + arboreal	epigaeic + arboreal
<i>Tetramorium</i>	epigaeic + arboreal		
<i>Tetraponera</i>	arboreal	arboreal	arboreal
<i>Vollenhovia</i>	epigaeic + arboreal		epigaeic + arboreal
Genera Σ	25	18	16
Epigaeic + Hypogaecic	44 %	43 %	44 %
Hypogaecic	12 %	5.5 %	6 %

The present note is aimed to check the possibility of sampling error and particularly the effect of sample size. Instead of collections of strikingly different size, the assemblages have been selected comparable in that respect (table 1). These are the Baltic amber collection PIN-964 (Paleontological Institute, Russian Academy of Sciences, Moscow, 435 specimens identified to the genus level in 2009), and HMC (Humboldt Museum, Berlin, Germany) for the Bitterfeldian amber (680 specimens identified to the genus level) (Dlussky, Rasnitsyn, 2009), both comparable in size with the I. I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine (SIZK) collection of the Rovno amber (507 specimens identified to the genus level by 2009). The SIZK collections experienced considerable growth since 2009 (up to 1143 specimens identified to the genus level), whilst only correction of identification of some taxa concerned the other collections. This makes possible to assess the effect of the collection growth on the ecological structure of the ant assemblage (tables 2–4).

Conclusions

Dlussky and Rasnitsyn (2009) demonstrated that any accurate comparison of amber faunas based on the composition of rare species they include is impossible, because, in most cases, such species are represented by only a few individuals, and their absence in a particular amber type is likely to be an effect of the small sample size. All hypogaecic ants studied by Dlussky consist 0.8 % from 5111 studied ants (their workers — 0.3 %), epigaeic ants (without *Formica* and *Lasius*) — 1.3 % (their workers — 1.1 %). Only six hypogaecic and epigaeic genera are represented in Late Eocene amber by more than three workers, all other genera are very rare; so, it is no wonder that all species from extant genera indicated as new for Rovno amber (Perkovsky, 2016) appear hypogaecic (four species) or epigaeic (two species). That is why testing the two hypotheses had an expectable result. The new and larger data on the Rovno assemblage show that the share of non-arboreal ants is now well comparable

Table 4. Comparison of data in tables 1–3

All ants	Assemblages		
	Baltic 2009	Bitterfeld 2009	Rovno 2009
Epi+Hypo	43 %	40 %	35 %
Hypo	18 %	8 %	5 %
Genera Σ	28	25	20
All ants	Baltic 2016	Bitterfeld 2016	Rovno 2016
Epi+Hypo	44 %	46 %	46 %
Hypo	16 %	9.5 %	17 %
Genera Σ	32	22	24
Workers	Baltic 2009	Bitterfeld 2009	Rovno 2009
Epi+Hypo	37.5 %	32 %	35 %
Hypo	12.5 %	4.5 %	6 %
Genera Σ	24	22	17
Workers	Baltic 2016	Bitterfeld 2016	Rovno 2016
Epi+Hypo	44 %	39 %	44 %
Hypo	12 %	5.5 %	6 %
Genera Σ	25	18	16

with those concerning the Baltic and Bitterfeld assemblages. This holds true for the both total assemblages and for subassemblages of worker ants only (table 4).

The author is sincerely grateful to A. P. Rasnitsyn (Paleontological Institute, Moscow) for the helpful advice and discussion of the manuscript, to A. G. Radchenko (SIZK) for discussion of the ecology of some hypogaean ants.

References

- Dlussky, G. M., Rasnitsyn, A. P. 2009. Ants (Insecta: Vespida: Formicidae) in the Upper Eocene amber of Central and Eastern Europe. *Paleontological Journal*, **43** (9), 1024–1042.
- Guenard, B., Perrichot, V., Economo, E. P. 2015. Integration of global fossil and modern biodiversity data reveals dynamism and stasis in ant macroecological patterns. *Journal of Biogeography* (2015), **42** (12), 2302–2312. DOI: <http://dx.doi.org/10.1111/jbi.12614>
- Perkovsky, E. E. 2016. Tropical and Holarctic ants in Late Eocene ambers. *Vestnik Zoologii*, **50** (2), 111–122.

Received 02 June 2016

Accepted 15 June 2016