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Analysis of Changes in Morphology of Head Capsule of *Formica lemani* Bondroit, 1917 in West Siberia in the Last One Thousand Years with the Methods of Geometrical Morphometry

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Abstract—The methods of geometric morphometry were used when comparing recent and subfossil ants *Formica lemani* in West Siberia, revealing clear morphological changes in the structure of head capsule that happened in the last several hundreds of years and were related not to taphonomic but to morphogenetic reconstructions. The rate of microevolutionary changes was revealed to be unexpectedly high, since only in several hundreds of years the degree of divergence of recent and subfossil ants approximated to the subspecies level.

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The ants of the *Formica fusca* group are the species widely distributed in the forest biocenoses in Eurasia. It is a large group of close, often confused species with one-color black or brown body [1]. The morphology of these species changed little since early Oligocene, when the group first appeared in paleontological chronicle. The Baltic amber provides the species *F. flori* Mayr., which is very similar to the modern *F. fusca* and *F. lemani* and is likely to be an ancestor of the whole group [1]. We can suppose that during this period of time certain morphological changes had to happen, since the adaptive radiation of the group species took place as they adapted to the forest, bog, meadow-steppe and even tundra biocenoses.

In the alluvial deposits and peat bogs in the Urals and West Siberia that are several thousands years old there are rather numerous remains of ants representing the genera *Camponotus*, *Formica*, *Lasius*, *Leptothorax*, *Myrmica* [2, 3]. In these deposits the ants are preserved as odd body fragments, because after death the soft tissues of the ants decay, and the insects' bodies disintegrate into separate chitin pieces. The fragments that are best-preserved and can be recognized as belonging to ants include head capsules, fragments of thorax, scapes. The head capsules provide the best material for more detailed identification, with the representatives of *Formica* being identified up to subgenus and even group of species. Further strict identification is usually impossible, since the modern taxonomy of the Formica is built primarily on the signs of hair on different body parts, and the ants lose their hairs and setae as they turn to fossil.

Nevertheless, we can suppose that in the course of the last several thousands years the ant fauna has not changed significantly, and as fossils we find the same species that inhabit the same places today. This gives us unique chance to compare the fossil and live ants and to follow possible changes in morphology of some structures during this time.

In this work we made an attempt to compare the morphology of head capsules of the fossil black Formica who lived relatively recently, no more than 1–2 thousand years ago, on the territory of West Siberia and of the modern *F. lemani* Bondroit that are widely distributed there. With a great degree of confidence we can suppose that subfossil ants also belong to this species. Since the time between these samples is relatively short, we could suppose that morphological changes would be insignificant in this case, too. To register even the tiniest but stable changes in the form of head capsule of ants we used the methods of geometrical morphometry [4–7]. It is well-known that geometrical morphometry allows one to get rid of size component and to study the form of biological objects as it is [6]. Earlier these methods were used for this group of animals for studying the morphology of wings of the sexual individuals of the ants, including paleontological material [8, 9].

MATERIAL AND METHODS

The subfossil material was collected in August, 1988, by A. V. Borodin on the right bank of the Kul'-egan River (left tributary of the Ob in its middle course). The site of collection is located at 60°25′N, 75°50′E. The total of 8 samples were taken from this cut, primarily from its middle and lower parts. The sample taken from its middle part (sample 2 from a depth of 3.90–4.10 m) is dated with radiocarbon method as 21 815 ± 225 years (SO AN-6837).

The sample 1, from which the fragments of ants' bodies were extracted, was taken in the upper part of 7.5-meter cut, 10 cm from the surface of the peat layer located directly under moss sod. The total of 365 individuals of the insects were extracted from the sample, 122 belonging to Formicoidea (33%, the total number of the ants in the sample as related to other groups) with the species of the genus *Myrmica* prevailing. The species composition of the ants found in this sample fully corresponds to the modern state of entomocomplexes inhabiting the studied territory. Analysis of the species composition helps to reconstruct the flood plain communities with developed tree-shrub vegetation and highly moistened soil (probably, due to small water bodies like crescent lakes). This can be proved by the significant number of fragments of small water beetles of the genus *Hydroporus*. A relative abundance of the leaf beetles *Plateumaris sericea* indicates developed near-water vegetation, the flea beetles of the subfamily Alticinae are related to willows, and the weevils *Notaris aethiops*, with the near water species of the sedge. The presence of tree vegetation in the burying places is shown by the founds of *Dromius quadraticollis*, the weevils *Pissodes pini* and *Anthonomus varians*.

We can suppose that the layer from which the sample was taken formed in the last several hundreds years when the climate was completely identical with the modern one. The changes could be only of succession character, related to the changes in the river course and corresponding kind of flood plain (riverbed, terrace, etc.).

The species composition of the groups of insects from the middle and lower parts of the cut (samples 2-8) basically differ from the entomocomplex represented in the sample 1. They are dominated by the Arctic (*Curtonotus alpinus*, *Pterostichus sublaevis*, *P. vermiculosus*, *Tachinus* cf. *arcticus*) and Arctic-boreal (*Pterostichus* (*Cryobius*) cf. *pinguedineus*, *P. tareumiut*, *Hemitrichapion tscernovi*, *Morychus* cf. *viridis*) species indicating harsh climate similar to the natural conditions of the modern south tundra or forest-tundra.

For comparison we used the sampling of the ants *F. lemani* taken in 2007 in the vicinity of the town of Khanty-Mansiysk in the nature park "Samarovskii Chugas" on the island B.Chukhtinskii in the floodplain of the Ob. This sampling is the closest one from what we have both in geographical location and natural conditions of the ants' habitats. The ants were collected in the soil traps on a secondary meadow at the edge of the mixed birch-pine forest with Siberian pine.

The total of 8 head capsules of the subfossil ants of the genus *Formica* with sufficient degree of preservance and 21 head capsule of the modern ants *Formica lemani* Bondroit, 1917, were measured. The head capsules of the ants were mounted on the object-plate with the back of the heads down. This method of fixing unifies all subsequent measures of the head. The ants' heads were photographed with Panasonic Lumix FZ7 (close-up regime, ×7 image expansion) placed on the binocular microscope MBS-10 (×4 image expansion). The obtained images were processed and digitized with TPSdig screen digitizer software [10]. The landmarks were placed in homologous joints of clearly determined morphological structures and parts of the head capsules, including clypeus, frontal plate, eyes and ocelli. The landmarks were put on the left half of the image of head capsule two times each. On the horizontally turned copies of the images the landmarks were put again on their left sides, to characterize the changeability in its mirror reflection. The landmarks were put twice on each of the sides of the head capsule in order to estimate the value of systematic error. The situation scheme of 11 homologous marks on the ants' heads is given in Fig. 1. The preliminary comparison of the changeability of the shape of head capsule in its left and right sides did not reveal significant differences between them, and the material for the both sides of the head capsule was pooled. The centroid size characterizing the object size was calculated as square root from the sum of squares of distances from the landmarks to the geometric center of the image.

The Procrustes analysis and calculation of individual relative warps (RW) were conducted with the help of the TPS [10–12] and PAST 1.90 [13] software. The canonical analysis was conducted in CVAGen6o, and two-factor multivariate variance analysis MANOVA, in Manovaboard, the two programs being part of Integrated Morphometric Package (IMP) [14]. For statistical estimation the bootstrap method based on 100 repeated replicas was used.

RESULTS AND DISCUSSION

MANOVA II of partial warps (PW) of the shape of head capsule of the ants was preliminary conducted considering the factor "time of collection" with two

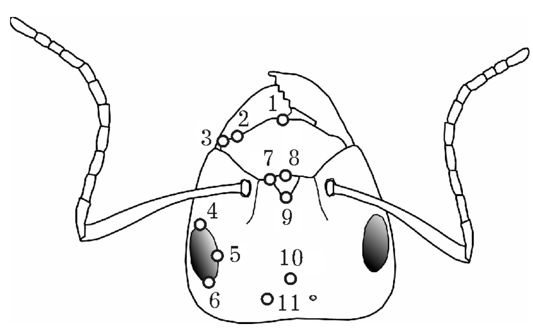

Fig. 1. Scheme of arrangement of the landmarks (1–11) on the head capsule of the ants *Formica lemani*.

grades (subfossil and recent individuals) and the factor "repeated landmark putting" (two repeats in each sampling). The conducted analysis with the use of bootstrap revealed significant intergroup differences in the first factor "time of collection" (F = 115.94; $d.f.1$ = 18; $d.f.2$ = 2070; p < 0.01) and absence of significant differences in the second factor (F = 0.10; $d.f.1$ = 18; $d.f.2$ = 2070; p = 0.95) as well as interaction of the two factors (F = 0.10; $d.f.1$ = 18; $d.f.2$ = 2070; p = 1.00). The share of intergroup differences in the first factor is 50.26% of the explained dispersion, in the second, 0.12%. Thus, between the subfossil and modern samplings of the ants significant differences are revealed in the shape of head capsule, which exceed random differences conditioned by the repeated landmarking manifold.

Figure 2 shows the results of canonical discriminant analysis of relative warps (RW) characterizing the changeability of the shape of had capsule of the ants. The figure indicates clear difference between the polygons of the samplings of subfossil and modern ants. We should note that the shift of the polygons after repeated classifications in both groups is quite small and is of random character. The reliability of discrimination of subfossil and recent ants is 100%. When making cross-validation, the share of accurately identified objects is 98.28% (only one of the sides of a head capsule in the sampling of subfossil ants was close in its characteristics to the recent individuals). It is also interesting that the estimation of the relation between individual size of centroid (proportional to the general size of the objects) and the values of the first two canonical variables did not reveal any significant coefficients of correlation. No significant correlation was revealed between the centroid size and Procrustes distances from reference point (Pierson correlation coefficient r = –0.087; Z = –0.647; p = 0.741). This indicates that the found morphological changes are not related to the ant size but reflect the change in proportions and shape of the head capsule, i.e., are related to the morphogenetic changes.

The obtained result is unexpected, since the samplings are divided by a relatively short period of time, probably, only several hundreds years. Evidently, this period of time is still significant for ants, and certain morphogenetic changes (including directional) can take place. It is also possible that these changes are related to those happening in nature and climate. As we have mentioned, in the lower layers of the cut there was found an entomocomplex typical of tundra biocenoses. The warming of the climate and formation of the forests resulted in, first, introduction of the forest ant species and, second, their adaptation to the new harsher environment. This adaptation could include morphological changes that we found.

It is interesting to examine in details the changes in the head capsule of the ants. Figure 3 shows the averaged configurations of the left half of the head capsule of subfossil (a) and recent (b) ants with visible differences.

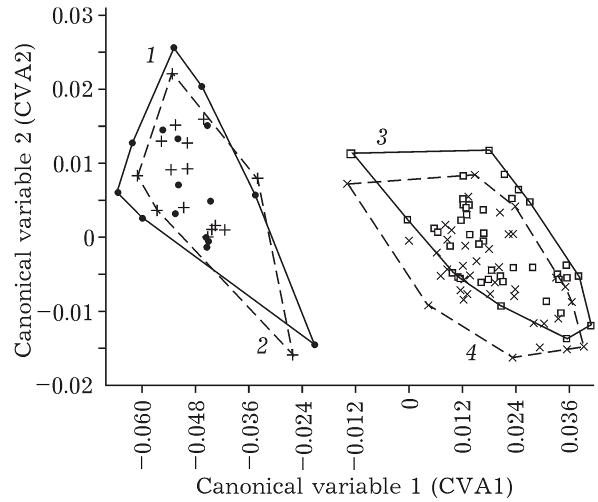

Fig. 2. Results of the canonical analysis of relative warps (RW) of the head capsule of the subfossil (*1*, *2*) and recent (*3*, *4*) ants *F.lemani* (allochronous samplings with repeated arrangement of the landmarks are given in hatch).

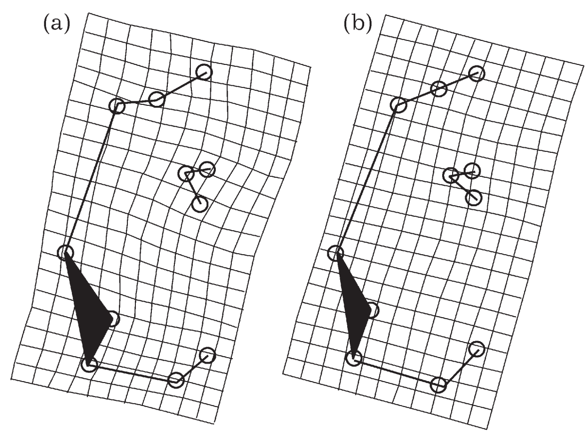

Fig. 3. Comparison of configurations of the head capsule of subfossil (*a*) and recent (*b*) ants *F. lemani* with regard to the first two canonical variables.

The observed differences can be divided into two groups. The first group features wider head and more dorsal location of the eye in the subfossil forms. This group can be partially related to the deformation due to flattening the ants' head as a result of burying. The head capsule is shaped so that when it is pressed it is deformed in width rather than in length. However, we should note that the thickness of the higher layers (about 10 cm) is not big enough to cause significant deformation.

The second group of differences is clearly not related to the postmortem deformations. It concerns a different shape of clypeus, wider, with more expressed edge flexure, higher frontal plate, and shorter distance between the central and side ocelli. These changes being summarized, the modern ants have longer back part of the head and shorter and narrower face part. The reasons for these changes remain unclear and demand a separate thorough study.

Nevertheless, we can conclude that the head capsule of *F. lemani* in the last several hundreds of years with changing climate and biota in West Siberia acquired morphological changes not related to the postmortem deformations. These changes help to accurately diagnose the recent and subfossil ants. The scale of secular changeability that we observe show that the rate of morphogenetic changes is unexpectedly high as the species settles in the north, and in only several hundreds of years it resulted in the subspecies level of divergence of the compared allochronous groups of ants.

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