

Late Pleistocene Taphocoenosis of Insects and Small Mammals from the Upper Reaches of the Ob River

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Abstract—A taphocoenosis including remains of insects and small mammals from the Quaternary deposits in the vicinity of the village of Kalistratikha (Altai Region, Russia) on the Ob River is revealed. The ¹⁴C dating of the deposits has shown 24.438 ± 0.350 ka. Insects are mostly represented by Coleoptera (59 species of 13 families) and dominated by species of Curculionidae, especially *Otiorhynchus*, and Carabidae. *Otiorhynchus ursus*, *O. altaicus*, and *O. unctuosus* are most abundant. The following 13 species are recorded in the Pleistocene deposits of Western Siberia for the first time: *Bembidion tibiale*, *B. gebleri*, *Pterostichus drescheri* (Carabidae), *Centorus rufipes* (Tenebrionidae), *Stephanocleonus ?grigorievi*, *Aulacobaris violaceomicans*, *Tychius albolineatus*, *Zaslavskypera conmaculata*, *Hypera misella*, *Limobius borealis*, *Chlorophanus tuvensis*, *Otiorhynchus unctuosus*, and *Mesagroicus piliferus* (Curculionidae). Small mammals are represented by a few fragments referred to as *Sorex* sp., *Allactaga* sp., *Spermophilus* cf. *erythrognys*, *Sicista* cf. *subtilis*, *Eolagurus* sp., *Lagurus* cf. *lagurus*, and *Microtus gregalis*. Small mammals and insects are typical of open landscapes, such as steppes and meadows; riparian insects also occur in the taphocoenosis. The modern geographical range of the majority of species of the steppe assemblage covers central Kazakhstan and adjacent areas; three species of the taphocoenosis are endemic to the mountain depressions of the Altai, Tuva, and northern Mongolia. The majority of meadow and riparian species are boreal–mountain. Judging from the composition of the taphocoenosis, the climate was drier and colder compared to the modern one, but warmer and more humid than during the succeeding Sartanian stadial. Prevailing landscapes were probably dry steppes with meadow and shrubby (osiers) vegetation in the lowered areas. Forests were absent or played a minor role (sparse trees might have been present).

Keywords: Insecta, Coleoptera, Mammalia, Quaternary, Karginian interstadial, Kalistratikha, Altai Region

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INTRODUCTION

Insect remains are characteristic of Quaternary deposits of northern territories, especially permafrost regions, and widely used for reconstructing natural conditions of the past (Nazarov, 1984; Coope and Lemdahl, 1995). In southern regions, chitin is preserved to a considerably lesser extent and insect localities are rare (Buckland and Coope, 1991). In particular, in the southeastern West Siberian Plain, Quaternary insects became known relatively recently, where they were recorded in alluvial deposits (Tsepelev et al., 2013; Tshernyshev et al., 2013; Gurina et al., 2016;

Legalov and Dudko, 2016; Zinovyev et al., 2016). Insect fragments are more frequently preserved in fine-texture matter, such as dark blue and gray clay and loam, with inclusions of plant detritus. In contrast to insects, bone remains occur in rough deposits and are particularly characteristic of cross-bedded sand.

In August, 2013, our team investigated Quaternary localities in the vicinity of the village of Kalistratikha on the Ob River, Altai Region. In the middle part of a steep, there is a horizontally bedded site with, where gray loams enclosing interbeds of alluvial plant detritus alternate with sand. In this site, a taphocoenosis including both insect chitin and small mammal bones

Table 1. Description of the section in the Kalistratikha locality

| Bed no. | Depth of bedding, m | Thickness, m | Description |
|---------|---------------------|--------------|--|
| 1 | 0.0–0.5 | 0.5 | Soil-plant bed |
| 2 | 0.5–10.3 | 9.8 | Alternating pale yellow dense sandy loams and loams with weak horizontal lamination |
| 3 | 15.3–21.0 | 10.7 | Grayish yellow dense loams homogeneous throughout the strata. A yellow brown loam interbed is in the lower part of the bed, at the boundary with the underlying bed. |
| 4 | 21.0–23.0 | 2 | Alternating gray dense loams and interbeds of alluvial detritus and medium-grained sand. Two clearings (I and II) are inside the bed at a distance of 6 meters. |
| 5 | 22.0–31.0 | 9 | Alternating coarse-grained sand and gray loams. The bed extends under the shore line |

Table 2. Description of the samples taken in the Kalistratikha locality

| Depth, m | Clearing no.–sample no. | Plant detritus | ¹⁴ C dating, ka | Insect remains | Bone remains | Notes |
|-------------|-------------------------|----------------|----------------------------|----------------|--------------|---|
| 21.02–21.05 | II–1 | + | – | 16 | – | Samples from interbeds of alluvial plant detritus |
| 21.2–21.2 | II–2 | + | – | 112 | – | |
| 21.25–21.35 | II–3 | + | – | 142 | – | |
| 21.45–21.55 | II–4 | + | – | 82 | – | |
| 21.65–21.75 | II–5 | + | – | 51 | – | |
| 22.5–22.8 | I–1 | + | 24.438 ± 0.350 | 28 | + | Sample from a lens of cross-bedded sands |

has been revealed. Thus, it became possible to perform paleofaunal analysis of insects and small mammals, which were buried synchronously.

The Kalistratikha locality first described by Pravoslavlev (1933) is particularly remarkable, providing most of the paleontological material, based on which the stratigraphic scheme of the Ob Steppe Plateau was developed (Panychev, 1979). Particular beds of the locality have yielded both spore–pollen and seed floras, mollusks, ostracods, and numerous bones small and large mammals (Pravoslavlev, 1933; Nikitin, 1935; Moskvitin, 1960; Maloletko, 1963; Zudin and Panychev, 1968; Panychev, 1979). Entomological material from this locality has not been known, except for one fragment of the beetle *Oodescelis polita* (Sturm, 1807) from a bed located much deeper than the taphocoenosis investigated by us (Pravoslavlev, 1933; Zudin and Panychev, 1968).

This bed is dated by the content of ¹⁴C in accompanying plant detritus as 24.438 ± 0.350 ka (SPb-1416); the calibrated age is 28.797–28.077 ka CalBP (calibration curve IntCal13, radiocarbon age range ± σ). This corresponds to the end of sea isotope stage MIS3 or the end of the Karginian interstadial. Earlier in the south of Western Siberia it was not known localities of insects of this age.

WORKING REGION, MATERIAL, AND METHODS

The locality is situated on the left bank of the Ob River, at the mouth of a nameless gully 1.2 km upstream from the village of Kalistratikha, Kalmanskii District, Altai Region, 52°58'06" N, 83°37'09" E. The beds with remains of insects and small mammals are found in the middle part of a 31-m-high steep. The section is described in Table 1. The material was sampled on August 12–14, 2013 by A.A. Gurina, R.Yu. Dudko, E.R. Dudko, E.V. Zinovyev, A.A. Legalov, and K.A. Tsepelev. One sample was taken from clearing I, Bed 4, at 22.1–22.4 m of depth. It contained fragments of insects, bone remains of small mammals, and plant detritus, which was used for radiocarbon dating. Five samples were taken in the interbeds of Bed 4 in clearing II (6 m left of clearing I); they contained plant detritus and insect fragments, 21.0–21.75 m of depth (Table 2).

The majority of researchers studying the section between the villages of Kalmanka and Kalistratikha recognized three members (or three formations). The upper member (Formation A after Pravoslavlev, 1933) is composed of yellowish brown porous loesslike loam with vague horizontal and wavy–oblique lamination (from 15–25 to 38 m thick). The second member (Formation B after Pravoslavlev, 1933) is complex

alluvial sandy–loamy (from 10–15 to 30 m thick), lacking loesslike deposits. The lower member (Formation C after Pravoslavlev, 1933) is mostly composed of dark brown dense sandy loam, with horizons of buried soils (2.5–8 m thick) (Pravoslavlev, 1933; Zudin and Panychev, 1968; Adamenko, 1974; Panychev, 1979; Russanov and Orlova, 2013). The stratigraphy of this section is considered in a number of studies, which provided several contradictory schemes, which assign the strata of the steppe plateau to Middle Quaternary deposits (Pravoslavlev, 1933; Maloletko, 1963; Arkhipov, 1971; Adamenko, 1974). The subsequently obtained ^{14}C dates of paleosols from the second member are 32.270 ± 0.500 ka (SOAN-396) and 31.000 ± 0.600 ka (MGU-203) contradict all previously developed schemes (Panychev, 1979; Russanov and Orlova, 2013). Bed 4 in our description, which has provided paleomaterial and plant detritus for dating, corresponds to the upper horizons of the second member. The date obtained by us is 24.438 ± 0.350 ka (SPb-1416), corroborating once again the relatively young age of these beds. This dating in general agrees with preservation and morphological characteristics of fossil remains of small mammals of specimens from sample I-1.

Sampling was performed following the technique described by Coope (1959) and supplemented by Gurina et al. (2016).

The abundance of insect species was estimated using the parameter N_{\min} , that is, the minimum number of individuals of a species equal to the maximum number of identified fragments of one type (for example, in coleopterans, the head capsules, pronota, left or right elytra).

RESULTS

Insects. The Kalistratikha locality has yielded 431 insect fragments representing four orders (Table 2), among which the overwhelming majority (98%) belong to the order Coleoptera in addition, there are individual specimens of Hymenoptera, bugs (Heteroptera), and Diptera. The samples taken at various depths differ in the concentration of subfossils. The most representative samples (112 and 142 fragments) come from samples II-2 and II-3 at 21.25–21.35 and 21.45–1.55 m of depth, respectively; they are most important for characteristics of the insect assemblage of the taphocoenosis (Table 2). Sample I-1 from the greatest depth (22.1–22.4 m) and earliest ^{14}C dating has provided only 28 insect fragments. Nevertheless, they include several stenotopic species, allowing the reconstruction of ecological conditions during the formation of these deposits and comparisons with reconstructions based on other samples.

The taphocoenosis contains at least 59 coleopteran forms of 13 families (Table 3); 29 of them are determined to species or species group; others, to genus or family. The estimates of the minimum number of indi-

viduals (N_{\min}) have shown that, in each sample, N_{\min} is from 12 to 55 specimens and 186 for the locality as a whole. The weevil family (Curculionidae) prevails in the taphocoenosis in the number of species (26 species, 44%) and, especially, in N_{\min} (102 specimens, 55%). The second position is occupied by ground beetles (Carabidae) represented by 18 species (31%) and 31 specimens (17%). The two families occur in all samples and almost always prevail; other families are represented by one or two species and a few specimens. An exception is provided by sample II-1 (poorest), which is dominated by Hydrophilidae fragments. At the generic level, the assemblage is dominated by *Otiorhynchus* (Curculionidae; six species, $N_{\min} = 62$) and *Bembidion* (Carabidae; six species, $N_{\min} = 14$). The most numerous species are *Otiorhynchus ursus*, *O. altaicus*, and *O. unctuosus*.

In the Pleistocene deposits of Western Siberia, 13 species are recorded for the first time: *Bembidion tibiale*, *B. gebleri*, *Pterostichus drescheri* (Carabidae), *Centorus rufipes* (Tenebrionidae), *Stephanocleonus ?grigorievi*, *Aulacobaris violaceomicans*, *Tychius albolineatus*, *Zaslavskypera conmaculata*, *Hypera misella*, *Limobius borealis*, *Chlorophanus tuvensis*, *Otiorhynchus unctuosus*, and *Mesagroicus piliferus* (Curculionidae).

Small mammals. Sample I-1 taken at a depth of 22.1–22.4 m contained 60 bone specimens of small mammals (isolated teeth, their fragments, and fragments of tooth rows). It is noteworthy that fragments are colored nonuniformly apparently because of taphonomic heterogeneity of enclosing matter, allowing the extent of redeposition of remains to be judged.

The following taxa are determined based on identifiable fragments (N_{\min}): *Sorex* sp. (1 specimen), *Allactaga* sp. (1), *Spermophilus* cf. *erythrogegens* (Brandt, 1841) (5), *Sicista* cf. *subtilis* (Pallas, 1773) (1), *Eolagurus* sp. (1), *Lagurus* cf. *lagurus* (Pallas, 1773) (3), and *Microtus gregalis* (Pallas, 1779) (4). The darkest (and probably earliest) specimens are determined as jerboa (*Allactaga* sp., 1 specimen) and susliks (*Spermophilus* cf. *erythrogegens*, 2 specimens). Most of the specimens belong to the regularly brown group and only one identifiable molar of the steppe lemming (*Lagurus* cf. *lagurus*) is light brown.

The relatively small sample size precludes relative dating based on the evolutionary level of reference forms of voles. The molar morphotypes of the steppe lemmings and narrow-skulled vole of the second group are characteristic of West Siberian faunas, beginning from the Middle–Late Neopleistocene boundary. The only lightest tooth of the steppe lemming is typical for Late Neopleistocene *Lagurus lagurus*. Judging from the molar dimensions, both steppe lemmings and narrow-skulled vole fall within the variation range of extinct and extant representatives.

Table 3. Species composition and abundance of insect fragments in the Kalistratikha taphocoenosis

| No. | Species | Clearing no.—sample no. | | | | | | N_{\min} , sum |
|-------------------|---|--|-----------|-----------|-----------|-----------|-----------|---------------------|
| | | I-1 | II-1 | II-2 | II-3 | II-4 | II-5 | |
| | | N_{\min} /number of heads—pronota—elytra—other fragments | | | | | | |
| Coleoptera | | | | | | | | |
| Carabidae | | | | | | | | |
| 1 | <i>Nebria cf. nivalis</i> (Paykull, 1798) | — | — | — | 1/0-0-1-0 | — | — | 1 |
| 2 | <i>Elaphrus</i> sp. | — | — | 1/1-0-0-0 | — | — | — | 1 |
| 3 | <i>Clivina fossor</i> (Linnaeus, 1758) | — | — | — | 2/2-0-0-0 | — | 2/0-1-2-0 | 4 |
| 4 | <i>Bembidion</i> (<i>Notaphus</i>) sp. | — | 1/0-1-2-0 | — | 1/1-0-0-0 | — | 1/0-1-0-0 | 3 |
| 5 | <i>B. (Eupetedromus)</i> sp. | — | — | — | 1/0-0-1-0 | — | — | 1 |
| 6 | <i>B. (Bembidionetolitzkya) tibiale</i> (Duftschmid, 1812) | — | — | — | 1/0-0-2-0 | — | — | 1 |
| 7 | <i>B. (Plataphus) ? gebleri persuasum</i> Netolitzky, 1938 | — | — | — | — | 1/0-0-1-0 | — | 1 |
| 8 | <i>B. (Ocydromus sensu lato)</i> sp. | — | — | — | 2/0-2-0-0 | — | — | 2 |
| 9 | <i>B. (?Pamirium)</i> sp. | — | — | — | 1/0-0-1-0 | — | — | 1 |
| — | <i>Bembidion</i> spp. | — | 1/0-1-0-0 | 1/0-1-0-0 | 2/0-1-2-0 | — | 1/1-0-0-1 | 5 |
| 10 | <i>Poecilus (Derus) cf. hanhaicus</i> (Tschitschérine, 1894) | — | — | 1/0-0-1-0 | — | — | — | 1 |
| 11 | <i>P. (Derus)</i> sp. | — | — | 2/0-2-0-0 | — | — | — | 2 |
| 12 | <i>Pterostichus (Plectes) drescheri</i> (Fischer von Waldheim, 1817) | — | — | 1/0-0-1-0 | — | — | — | 1 |
| 13 | <i>P. (Eosteropus) maurusiacus</i> (Mannerheim, 1825) | 1/0-1-0-0 | — | — | — | — | — | 1 |
| 14 | <i>Pterostichus</i> sp. | — | — | — | — | 1/1-0-0-0 | — | 1 |
| 15 | <i>Amara</i> sp. | — | — | — | 1/0-0-1-0 | — | — | 1 |
| 16 | <i>Curtonotus</i> sp. | — | — | — | — | 1/0-0-2-0 | — | 1 |
| 17 | <i>Harpalus</i> sp. | — | — | — | 1/0-0-1-0 | — | — | 1 |
| 18 | <i>Cymindis</i> sp. | — | — | 1/0-1-0-0 | — | — | — | 1 |
| — | gen. sp. | 1/0-1-0-0 | — | 1/0-0-0-3 | 3/3-0-1-5 | 1/0-0-2-3 | 1/0-0-1-4 | 7 |
| Dytiscidae | | | | | | | | |
| 19 | gen. sp. | — | — | — | — | 1/0-0-0-1 | — | 1 |
| Hydrophilidae | | | | | | | | |
| 20 | gen. sp. | — | 3/0-0-5-0 | — | 4/0-0-5-0 | — | 2/0-0-3-0 | 9 |

Table 3. (Contd.)

| No. | Species | Clearing no.—sample no. | | | | | | N_{\min} , sum |
|---------------|---|--|-----------|-----------|-----------|-----------|-----------|---------------------|
| | | I-1 | II-1 | II-2 | II-3 | II-4 | II-5 | |
| | | N_{\min} /number of heads—pronota—elytra—other fragments | | | | | | |
| Helophoridae | | | | | | | | |
| 21 | <i>Helophorus</i> sp. 1 | | | | | 1/0-0-1-0 | | 1 |
| 22 | <i>Helophorus</i> sp. 2 | | | | | 1/0-0-1-0 | | 1 |
| Silphidae | | | | | | | | |
| 23 | <i>Aclypea bicarinata</i> (Gebler, 1830) | 1/0-1-1-0 | — | — | — | — | — | 1 |
| 24 | gen. sp. | 2/2-1-0-0 | — | — | 1/0-1-0-1 | 1/0-0-1-0 | — | 4 |
| Staphylinidae | | | | | | | | |
| 25 | gen. sp. | — | — | — | — | 4/4-0-0-0 | — | 4 |
| Scarabaeidae | | | | | | | | |
| 26 | <i>Aegialia</i> sp. | — | — | — | — | — | 1/0-1-0-0 | 1 |
| 27 | <i>Aphodius</i> sp. | — | — | 2/0-2-0-0 | 3/0-0-5-0 | — | 1/1-0-1-0 | 6 |
| — | gen. sp. | — | — | — | 1/0-0-1-0 | — | — | 1 |
| Byrridae | | | | | | | | |
| 28 | <i>Porcinolus murinus</i> (Fabricius, 1794) | — | — | 1/0-0-1-0 | — | — | — | 1 |
| Elateridae | | | | | | | | |
| 29 | <i>Negastrius?</i> sp. | — | — | — | 1/0-0-1-0 | — | 1/0-0-1-0 | 2 |
| 30 | <i>Hypnoidus</i> sp. | — | — | 1/0-0-1-0 | — | 1/0-0-1-0 | 1/0-0-1-0 | 3 |
| — | gen. sp. | — | — | 1/0-1-0-1 | 1/0-0-1-0 | 1/0-0-0-1 | — | 3 |
| Tenebrionidae | | | | | | | | |
| 31 | <i>Centorus rufipes</i> (Gebler, 1833) | — | 1/0-1-0-0 | 1/0-1-0-0 | — | 1/0-1-0-0 | — | 3 |
| Chrysomelidae | | | | | | | | |
| 32 | <i>Psylliodes</i> sp. | — | — | — | 2/0-0-2-0 | — | — | 2 |
| 33 | <i>Prasocuris?</i> sp. | — | — | — | — | — | 1/0-0-1-0 | 1 |
| — | gen. sp. | — | — | — | — | 3/0-1-5-0 | — | 3 |
| Brentidae | | | | | | | | |
| 34 | Apioninae gen. sp. | — | — | 1/0-0-1-0 | — | — | — | 1 |
| Curculionidae | | | | | | | | |
| 35 | <i>Tournotaris bimaculata</i> (Fabricius, 1792) | — | — | 3/1-3-2-2 | 1/0-1-2-3 | — | — | 4 |
| 36 | <i>Notaris aethiops</i> (Fabricius, 1793) | — | — | 1/0-0-1-0 | 1/1-0-0-0 | — | — | 2 |
| 37 | <i>Bagous</i> sp. | — | 1/0-0-1-0 | — | — | 1/1-0-0-0 | — | 2 |
| 38 | <i>Stephanocleonus ?grigorievi</i> Suvo-rov, 1915 | 1/0-0-2-0 | — | — | — | — | — | 1 |

Table 3. (Contd.)

| No. | Species | Clearing no.—sample no. | | | | | | N_{\min} , sum |
|-----|--|--|-----------|-----------|-----------|-----------|-----------|---------------------|
| | | I-1 | II-1 | II-2 | II-3 | II-4 | II-5 | |
| | | N_{\min} /number of heads—pronota—elytra—other fragments | | | | | | |
| 39 | <i>Asproparthenis</i> sp. | 1/0-1-0-0 | — | — | — | — | — | 1 |
| 40 | Cleonini gen. sp. | — | — | 3/0-3-1-0 | 1/0-1-0-1 | — | — | 4 |
| 41 | <i>Aulacobaris viola-</i> <i>ceomicans</i> (F. Solari, 1904) | — | — | 1/0-1-0-0 | — | — | — | 1 |
| 42 | Ceutorhynchini gen. sp. | — | — | 1/0-0-1-0 | — | — | — | 1 |
| 43 | <i>Isochnus flagel-</i> <i>lum</i> (Erichson, 1902) | — | — | — | — | 1/0-0-1-0 | 1/0-0-2-0 | 2 |
| 44 | <i>Tychius albolinea-</i> <i>tus</i> Motschulsky, 1859 | — | — | — | — | 1/0-0-0-2 | — | 1 |
| 45 | <i>Tychius alexii</i> (Korotyaev, 1991) | — | — | — | — | 1/0-0-2-0 | — | 1 |
| — | <i>Tychius</i> sp. | — | — | 1/0-1-0-0 | — | — | — | 1 |
| 46 | <i>Eremochorus</i> sp. | — | — | 1/0-1-0-0 | — | — | — | 1 |
| 47 | <i>Zaslavskypera</i> <i>conmaculata</i> (Herbst, 1795) | — | — | — | — | 1/0-0-1-0 | — | 1 |
| 48 | <i>Hypera misella</i> (Faust, 1882) | — | — | — | 1/1-1-0-0 | — | — | 1 |
| 49 | <i>Hypera</i> sp. | 1/0-1-0-0 | — | 1/0-1-0-0 | 1/0-0-0-1 | — | — | 3 |
| 50 | <i>Limobius borealis</i> (Paykull, 1792) | — | — | 1/0-1-0-0 | — | — | — | 1 |
| 51 | <i>Trichalophus</i> <i>maeklini</i> (Faust, 1890) | — | — | 1/0-0-1-0 | — | — | — | 1 |
| 52 | <i>Sitona</i> sp. | — | — | 2/1-2-1-0 | — | — | — | 2 |
| 53 | <i>Chlorophanus</i> <i>tuvensis</i> Korotyaev, 1992 | — | — | — | — | 1/0-0-2-0 | — | 1 |
| 54 | <i>Phyllobius</i> <i>viridiaeris</i> (Laicharting, 1781) | — | — | — | — | 1/1-0-0-0 | — | 1 |
| — | <i>Phyllobius</i> sp. | — | — | 1/0-0-1-0 | — | 2/0-0-4-0 | — | 3 |
| 55 | <i>Otiiorhynchus</i> <i>politus</i> Gyllenhal, 1834 | — | 1/1-0-0-0 | 1/0-1-0-0 | 1/1-0-1-0 | 2/0-0-3-0 | — | 5 |
| 56 | <i>O. unctuosus</i> Germar, 1824 | 1/1-0-0-0 | — | 1/0-1-0-0 | 4/4-3-2-5 | 2/0-1-3-1 | — | 8 |
| 57 | <i>O. pullus</i> Gyllen- hal, 1834 | — | — | 2/0-1-3-0 | 3/0-3-1-0 | — | 1/0-0-2-0 | 6 |

Table 3. (Contd.)

| No. | Species | Clearing no.—sample no. | | | | | | N_{\min} , sum |
|--------------------|--|--|-------------|----------------|----------------|--------------|--------------|---------------------|
| | | I–1 | II–1 | II–2 | II–3 | II–4 | II–5 | |
| | | N_{\min} /number of heads—pronota—elytra—other fragments | | | | | | |
| 58 | <i>O. ursus</i> Gebler, 1844 (= <i>kasachstanicus</i> Arnoldi, 1964) | — | — | 5/0–0–8–0 | 5/0–0–9–0 | 1/0–0–2–0 | 1/0–0–2–0 | 12 |
| 59 | <i>O. altaicus</i> Strierlin, 1861 (= <i>karkaralensis</i> Bajtenov, 1974) | 3/0–0–3–0 | — | — | 1/0–0–1–0 | 1/0–0–1–0 | — | 5 |
| — | <i>O. ursus</i> + <i>O. altaicus</i> | 3/2–3–0–1 | 1/1–0–0–0 | 16/9–16–0–4 | 15/4–15–0–0 | 4/0–4–0–1 | 1/0–0–0–1 | 40 |
| 60 | <i>Otiiorhynchus</i> sp. | — | — | 1/0–1–0–3 | — | 1/0–0–1–5 | 1/0–0–1–4 | 3 |
| 61 | <i>Mesagroicus piliferus</i> (Boheman, 1833) | — | 1/1–0–0–0 | 1/1–1–0–0 | — | — | — | 2 |
| — | Curculionidae gen. sp. | 1/1–1–2–0 | — | 3/0–3–0–3 | 1/0–1–2–4 | 2/0–0–3–6 | 1/0–0–0–1 | 8 |
| — | Coleoptera indet. | 1/0–0–2–0 | 2/0–0–2–0 | 1/1–0–2–8 | 4/3–1–7–20 | 2/1–1–4–4 | 1/0–0–1–15 | 11 |
| Coleoptera, sum | | 14/6–10–10–1 | 12/3–3–10–0 | 52/14–45–26–24 | 55/20–30–50–40 | 39/8–8–41–24 | 14/2–3–18–26 | 186 |
| Heteroptera | | | | | | | | |
| Heteroptera indet. | | 1/1–0–0–0 | — | 1/1–1–0–0 | 1/0–1–0–0 | — | — | 3 |
| Diptera | | | | | | | | |
| Diptera indet. | | — | — | 1/0–0–0–1 | — | — | 1/0–0–0–1 | 2 |
| Hymenoptera | | | | | | | | |
| Hymenoptera indet. | | — | — | — | 1/0–0–0–1 | 1/0–0–0–1 | 1/1–0–0–0 | 3 |
| Insecta | | | | | | | | |
| Insecta indet. | | 0–0–0–2 | — | 0–0–0–10 | 0–0–0–45 | 0–0–0–9 | 0–0–0–8 | ? |

DISCUSSION

Ecological preferences of species from the Kalistratikha taphocoenosis are rather diverse, involving steppe, meadow, riparian, aquatic, and solonchak (saline land) coleopteran assemblages. The steppe assemblage apparently includes xerophilous and mesoxerophilous species characteristic of various steppe types: *Poecilus hanhaicus*, *P. (Derus)* sp., *Aclypea bicarinata*, *Porcinolus murinus*, *Stephanocleonus grigorievi*, *Tychius albolineatus*, *T. alexii*, *Eremochorus* sp., *Otiiorhynchus altaicus*, *O. ursus*, *O. pullus*, *O. unctuosus*, and *Mesagroicus piliferus*. Many of them have been recorded in the Late Pleistocene deposits of the southern and middle parts of the West Siberian Plain, for which cryoarid conditions are reconstructed: *Poecilus hanhaicus*, *P. (Derus)* sp., *Aclypea bicarinata*, *Porcinolus murinus*, *Otiiorhynchus*

altaicus, *O. ursus*, and *O. pullus* (Zinovyev, 2011; Tshernyshev et al., 2013; Legalov et al., 2016; Zinovyev et al., 2016). *Tychius albolineatus*, *T. alexii*, *Mesagroicus piliferus*, and *Otiiorhynchus unctuosus* are only known from “warm” steppes of the regions with a continental (not sharply continental) climate. Species of the genus *Eremochorus* are more typical for semi-deserts and deserts; only a few representatives occur in steppes.

Several species are mostly typical of meadow habitats; *Otiiorhynchus politus*, *Trichalophus maeklini*, *Zaslavskypera conmaculata*, *Hypera misella*, and *Limobius borealis* are characteristic of meadows in the taiga zone and Alpine meadows of mountains. *Phyllobius viridiaeris* is confined to meadows and meadow steppes in the southern forest zone and forest–steppe zone.

The assemblage connected with various humid habitats is rather diverse and numerous, including reophilic species inhabiting banks of rapid streams (*Nebria nivalis*, *Bembidion tibiale*, *B. gebleri*) and stagnatophiles dwelling at the shore line of stagnant and slowly flowing water bodies (*Bembidion (Notaphus) sp.*, *B. (Eupetedomus) sp.*, *B. (Pamirium) sp.*, *Bagous sp.*, and possibly *Elaphrus sp.*). Two species, *Isochnus flagellum* and *Chlorophanus tuvensis*, develop on willows and mostly occur in river valleys. *Tournotaris bimaculata* and *Notaris aethiops* are characteristic of hygrophytic meadows and marshes. The aquatic assemblage includes hydrophiles (Hydrophilidae) and two species of the genus *Helophorus*. Finally, *Centorus rufipes* is an obligatory halophile inhabiting the shores of salty lakes. Apparently, this ecological group is also represented by *Asproparthenis sp.*, since the majority of species of this genus are halophiles.

Obligatory forest species have not been revealed in the taphocoenosis. However, *Pterostichus drescheri* and *P. maurusiacus* are species characteristic of taiga, but the first in the Altai–Sayany mountains is also characteristic of high-mountain meadows (Dudko and Zinchenko, 2009) and the second is usual in floodplains, penetrating along the river valleys into the forest–steppe zone (Dudko and Lyubchansky, 2002). Tundra species also occur, but rare. The most cryophilic species is *Notaris aethiops*, which is characteristic of zonal and mountain tundras, but penetrate deep into the taiga zone along humid (marshy) habitats and rarely occurs in forest–steppe (Legalov and Opanasenko, 2000).

The ecological beetle groups are distributed more or less uniformly in samples from different depths. Sample I-1 (deepest, dated) is distinguished by the absence of meadow species. This may be connected with the taphonomic factors and (or) drier climate. Unfortunately, the low density of chitin in this sample prevents high-quality analysis. Sample II-1 (least deep) is also somewhat impoverished, containing predominantly aquatic and riparian beetles. Other samples contain all coleopteran ecological assemblages, suggesting that there were constant conditions during the formation of the bed and uniform taphocoenosis.

Based on ecological preferences of insects from the Kalistratikha locality, dry and moderately cold conditions are reconstructed for the time of the formation of the taphocoenosis. Steppes were probably prevailing landscapes. In the most humidified habitats (lowlands, river valleys), there was meadow vegetation. In the floodplains willows occurred. The presence of forest vegetation is improbable.

All identified small mammal taxa could dwell in arid conditions resembling that of the modern steppe and semidesert zones. *Eolagurus luteus* is characteristic of xerophytic and xeromesophytic grassy communities, including wormwoods, which do not exclude the presence of halophytic communities. *Lagurus*

lagurus is characteristic of xerophytic and xeromesophytic herb communities, including grasses. *M. gregalis* allows the reconstruction of a wide range of habitats from xerophytic to mesophytic grassy communities, mainly herbs and grasses (Markova et al., 2017). Individual teeth of rodents, which may be redeposited, judging from their preservation, and belong the same set of taxa and, hence, do not change ecological interpretation.

Modern distribution of species. Comparisons of modern and past geographical ranges belong to the main methods for reconstruction of the faunogenesis. The modern ranges of the majority of Palearctic coleopteran species are rather completely understood, whereas the data on the Pleistocene concern only some territories (mainly northern) and a few species (which were abundant in the Pleistocene, having strong chitin and identified based on available fragments). In this connection, new finds of species in the region are very important. In addition, the analysis of modern distribution of the species represented in the taphocoenosis supplement the data of ecological analysis on natural conditions.

The modern ranges of the majority of species from the Kalistratikha locality concern only the Upper Ob Region or even located beyond this area. Only a few species occur here in the optimum of the range and are rather common. These are polyzonal *Clivina fossor*, *Tournotaris bimaculata*, *Zaslavskypera conmaculata*, and *Phyllobius viridiaeris* and steppe *Otiorhynchus unctuosus*.

Almost all species of the taphocoenosis confined ecologically to floodplains, meadows, and forests have boreomountain ranges (Fig. 1). They are more or less widespread in northern Eurasia, covering the taiga and (or) tundra zones; in the south, they only occur in mountain regions, in particular, in the Altai Mountains. In the southern West Siberian Plain, these species are absent (*Nebria cf. nivalis*, *Trichalophus maeklini*) or represented by individual records in the coldest habitats in the floodplain or slopes of northern exposition at the foothills (*Pterostichus drescheri*, *P. maurusiacus*, *Notaris aethiops*, *Isochnus flagellum*, *Otiorhynchus politus*) (Legalov and Opanasenko, 2000; Dudko and Lyubchansky, 2002). The optimum of the ranges of boreomountain species is in the taiga zone; thus, these species are confined to cool and moderately humid conditions.

Steppe and halophilic species occur in the arid regions within the steppe zone, frequently penetrating into the forest–steppe and (or) semidesert zones. In the Kalistratikha locality, three species widespread over the entire steppe zone of Eurasia: *Porcinolus murinus*, *Centorus rufipes*, and *Tychius albolineatus*. In the east, they occur up to southern Transbaikalia (and the third species is even recorded up to the southern Far East of Russia), but absent in the steppes of north-eastern Siberia. *Mesagroicus piliferus* has a somewhat

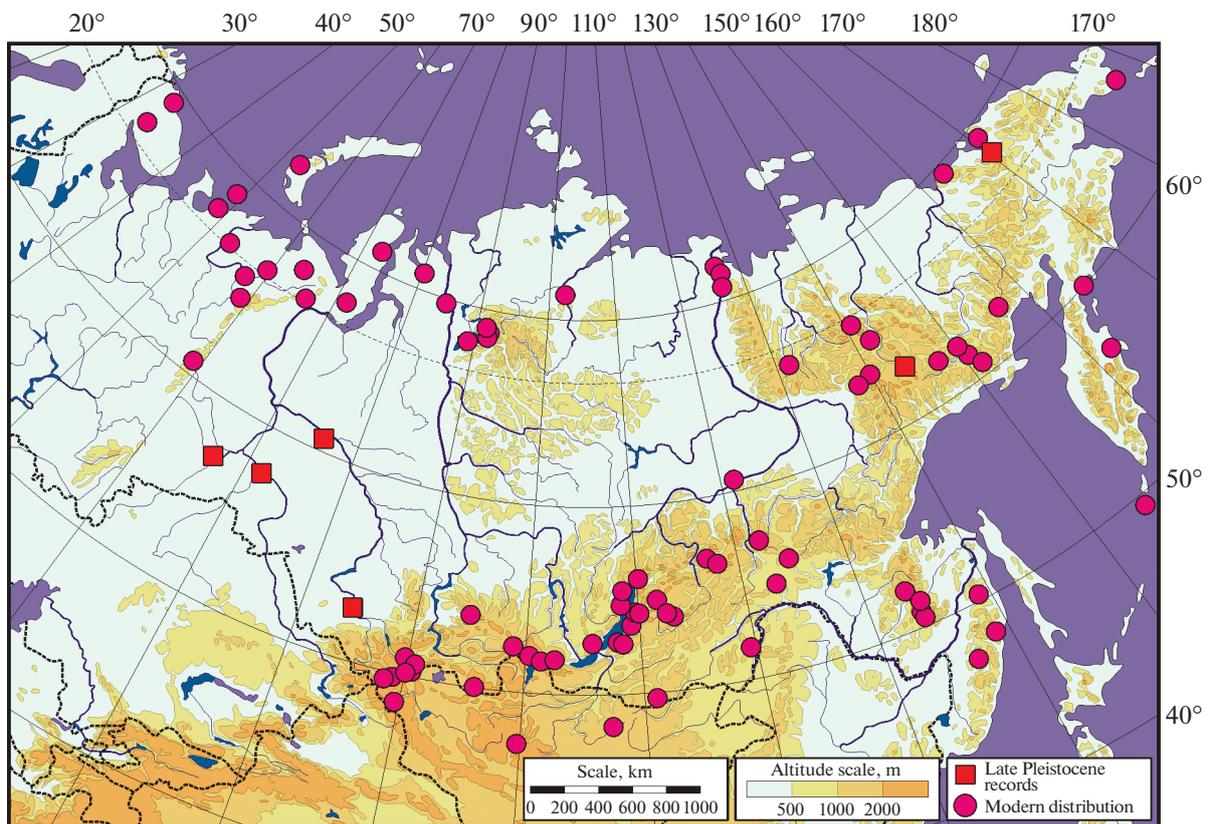


Fig. 1. Late Pleistocene and modern ranges of species of the *Nebria nivalis* group.

narrower range extending from Eastern Europe to foothills of the western Altai Mountains. The next group of species with the Kazakhstan type of the geographical range includes many species, some of which are among most abundant taxa of the taphocoenosis: *Otiorhynchus altaicus*, *O. ursus*, *O. pullus*, *Tychius alexii*, and *Aclypea bicarinata*. These species occur in steppes of central Kazakhstan and (or) the western Altai Mountains; some reach the southeast of European Russia and (or) southern Western Siberia; for more detail, see Nikolaev and Koz'minykh (2002), Borisov et al. (2014), and Legalov et al. (2016). The participation of these species in the taphocoenosis is evidence of a rather dry climate. In addition, species ranges of some of them are completely confined to the regions with a warm climate, where the mean winter and summer temperatures are close to the modern (for Kalistratikha) ones or even warmer (*Otiorhynchus altaicus*, *O. ursus*, *Tychius alexii*, *Aclypea bicarinata*). However, as has previously been shown, at present, these species do not realize their entire potential ranges. In other words, they can (and possibly prefer) develop under colder conditions, but adjacent cold regions (the taiga zone of Western Siberia, the southern Urals, and western Altai) have a humid climate and, hence, are unsuitable for arid species (Zinov'yev et al., 2016).

A separate group is composed of steppe mountain species, such as *Poecilus* cf. *hanhaicus*, *Stephanocleonus grigorievi*, and *Chlorophanus tuvensis*. They have local ranges in intermountain depressions of the southeastern Altai Mountains, Tuva, and northern Mongolia (Fig. 2). It is frequently believed that species endemic to mountain depressions were formed in these depressions due to weak migration ability and isolation. However, the presence of such species in Quaternary plain deposits at a distance of hundreds of kilometers from their modern ranges cast doubt on their weak migration ability and, hence, on the center of speciation. Apparently, another important cause of the localness of geographical ranges is the stenotopy of species, confinement to certain conditions characteristic of intermountain depressions. Thus, climatic conditions in the intermountain depressions of the southeast Altai Mountains, Tuva, and northern Mongolia are probably close to that of the upper reaches of the Ob River at the time of the formation of the taphocoenosis from Kalistratikha.

An unusual feature is co-occurrence of two ground beetle species of the genus *Bembidion* from the subgenera *Bembidionetolitzkya* and *Plataphus*. Almost all species of these subgenera occur on pebble river banks and, consequently, their ranges are connected with mountain ranges. Species of *Bembidionetolitzkya*

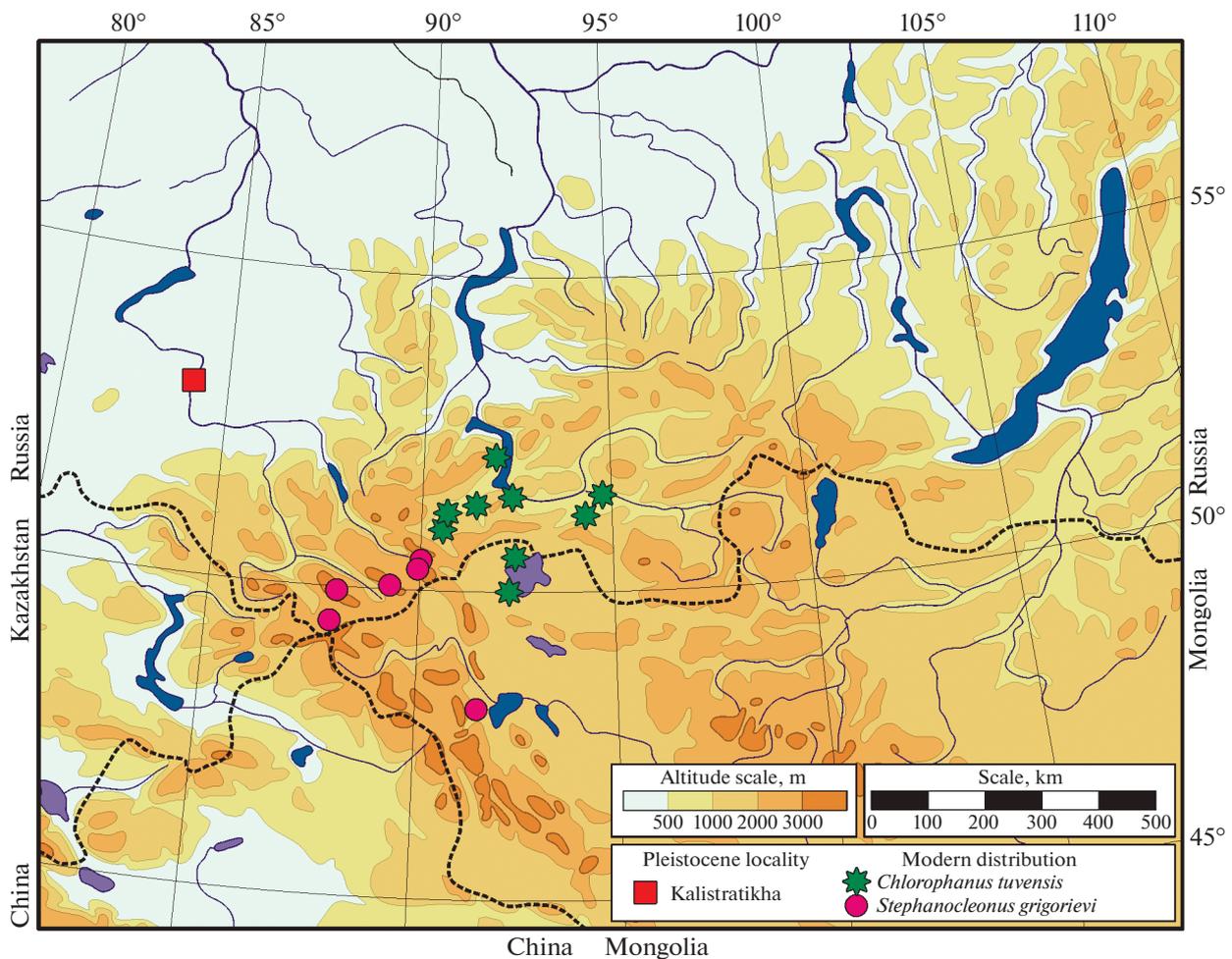


Fig. 2. Late Pleistocene and modern ranges of *Stephanocleonus grigorievi* and *Chlorophanus tuvensis*.

occur in mountains of Europe, western and Central Asia, and the Caucasus and Himalayas (Marggi et al., 2003). The majority of species of *Plataphus* occur in the mountains of Siberia, Far Eastern Russia, eastern Asia, North America, and the Tibet–Himalaya Mountains; and only one species, *B. prasinum* (Duftschmid, 1812), is recorded in northern and Central Europe (Marggi et al., 2003; Bousquet, 2012). Thus, the ranges of these subgenera overlap only in the Himalayas and northern Europe. In the Kalistratikha locality, *B. (Bembidionetolitzkya) tibiale* is recorded; the modern range of this species covers the mountains of Europe, western Asia (Turkey), and the Caucasus. The species occurs on pebble river banks in the medium-high and low mountains, but often penetrates into foothills (Belousov and Sokolov, 1994; Hürka, 1996). *B. (Plataphus) gebleri* (Gebler, 1833) is widespread in the mountains of southern and Eastern Siberia, the Far East, and North America (Marggi et al., 2003; Bousquet, 2012). Unexpectedly, an elytron of this species found in Kalistratikha corresponds to the Far East subspecies *B. g. persuasum*, which has a

transversely striated microsculpture. Thus, representatives of this ecological group, which is confined to mountains, in Pleistocene conditions could have gone down onto the plain and probably had considerably wider ranges. In the southern West Siberian Plain, representatives of both western (*Bembidionetolitzkya*) and eastern (*Plataphus*) groups co-occurred.

Another example of the eastern range is provided by *Hypera misella*, the modern range of which covers humid areas of the Altai–Sayany mountain ranges and, separately, the Far East of Russia (Legalov, 2010).

Comparison with other Pleistocene localities. The insect assemblage from the Kalistratikha locality is generally similar to other known Late Pleistocene faunas of the south and partly middle part of the West Siberian Plain and Urals. In the southern West Siberian Plain, two Late Pleistocene insect assemblages have been described; both are younger (Sartanian) than the Kalistratikha locality: Bun’kovo on the Chik River is dated $^{14}\text{C} = 11.550 \pm 125$ ka (Zinovyev et al., 2016) and Dubrovino on the Ob River, $^{14}\text{C} = 19.444 \pm$

Table 4. Comparison of Late Pleistocene insect assemblages of Western Siberia and the Urals

| Character | Locality | | | | |
|-------------------------|--|-----------------------------------|-----------------------------------|------------------------------------|----|
| | Nikitino | Dubrovino | Bun'kovo | Kalistratikha | |
| Reference | Stefanovsky et al., 2002; Zinovyev, 2011; Legalov et al., 2016 | Gurina et al., in press | Zinovyev et al., 2016 | This paper | |
| Coordinates | 57°34' N, 63°17' E | 55°27'07" N, 83°15'18" E | 55°03'46" N, 82°29'50" E | 52°58'06" N, 83°37'09" E | |
| ¹⁴ C age, ka | 24.480 ± 0.550 (SOAN-4537) | 19.444 ± 0.150 (SPb-1417) | 11.550 ± 0.125 (SOAN-8806) | 24.438 ± 0.350 (SPb-1416) | |
| Number of species | Total | 69 | 93 | 64 | |
| | Curculionidae | 19 | 34 | 27 | |
| | Carabidae | 33 | 33 | 21 | 18 |
| | <i>Otiorhynchus</i> | 3 | 10 | 9 | 5 |
| | <i>Stephanocleonus</i> | 2 | 5 | 8 | 1 |
| % based on N_{\min} | Curculionidae | 46 | 72 | 67 | 55 |
| | Carabidae | 35 | 14 | 18 | 17 |
| | <i>Otiorhynchus</i> | 20 | 55 | 49 | 33 |
| Dominant species | <i>Otiorhynchus karkaralensis</i> | <i>Otiorhynchus karkaralensis</i> | <i>Otiorhynchus karkaralensis</i> | <i>Otiorhynchus kasachstanicus</i> | |

0.150 ka (Gurina et al., in press). In the middle part of the West Siberian Plain, there is the Nikitino insect locality on the Kirga River, which is thoroughly investigated and contemporaneous with Kalistratikha (Stefanovsky et al., 2002; Zinovyev, 2011; Legalov et al., 2016). The taxonomic compositions of these localities are compared in Table 4; in all localities, weevils, particularly the genus *Otiorhynchus*, prevail. Such faunas are conditionally referred to as the *Otiorhynchus* type (Zinovyev, 2011); their index species are some members of the genus *Otiorhynchus* belonging to the Central Kazakhstan Assemblage and usually dominated by *Otiorhynchus altaicus* (Legalov et al., 2016). *Otiorhynchus*-type faunas are characteristic of the Late Pleistocene deposits of the southern West Siberian Plain and Urals and are analogous.

The taxonomic compositions of insect assemblages from Kalistratikha and other localities of the south and middle part of Western Siberia differ only slightly (Table 4). The Kalistratikha assemblage is dominated by *Otiorhynchus ursus*, while in Bun'kovo, Dubrovino, and Nikitino, *O. altaicus* prevail. In addition, the genus *Stephanocleonus* is represented in Kalistratikha by only one species. The taphocoenosis from Kalistratikha is distinguished to a greater extent by the ecological composition and geographical ranges of species. In particular, Nikitino, Dubrovino, and Bun'kovo localities have two insect species assemblages which are absent in Kalistratikha. The tundra assemblage, including species of the subgenus *Cryobius* of the genus *Pterostichus*, *Diacheila polita* (Faldermann,

1835), *Lepyrus nordenskioldi* Faust, 1885, and *Otiorhynchus arcticus* (Fabricius, 1780), is characteristic of zonal and mountain tundras. The tundra-steppe assemblage, including *Cymindis arctica* Kryzhanovsky et Emetz, 1979, *Poecilus ravus* (Lutshnik, 1922), *Stephanocleonus foveifrons* Chevrolat, 1873, *S. eruditus* Faust, 1890, and *Coniocleonus astragali* Ter-Minassian et Korotyayev, 1977, is characteristic of the regions with a cold and dry climate (northeastern Siberia and northern Transbaikalia). On the contrary, although the Kalistratikha assemblage is dominated by arid species, it also has an association characteristic of humid regions, such as the northern and western Altai Mountains, Kuznetsk Alatau, and Western Sayan Mountains (*Pterostichus drescheri*, *P. maurusiacus*, *Hypera misella*, *Trichalophus maeklini*). In Bun'kovo, these species have not been recorded; in Nikitino and Dubrovino, they are extremely rare.

Thus, the insect assemblage from the Kalistratikha locality is generally similar to other Late Karginian and Sartanian entomofaunas of the southern part of the West Siberian Plain (*Otiorhynchus*-type faunas of cold forestless steppes) and differs from them in the absence of typical tundra species and in the presence of boreal humid species. The above data suggest, that at the end of the Karginian Time (terminal MIS3), the climate in the Upper Ob Region was relatively dry and cold compared to the modern climate, although it was warmer and more humid than in the succeeding Sartanian stadial, which agrees with the data on the Pre-Altai Plain (Panychev, 1979).

CONCLUSIONS

In the taphocoenosis of the Kalistratikha locality, a rich insect assemblage (62 species) composed mostly of the coleopteran families Curculionidae and Carabidae and accompanied by a small mammal assemblage of seven species is revealed.

The taphocoenosis is dominated by *Otiorhynchus ursus*, which is characteristic in the modern fauna of dry steppes of central Kazakhstan. Other insect species from the Kalistratikha locality vary in ecological characteristics; the steppe assemblage prevails here; riparian and meadow species are also abundant, whereas aquatic and halophilic species are marked as rare and obligatory forest species are absent. Stenotopic species of small mammals (*Eolagurus luteus*, *Lagurus lagurus*) of the taphocoenosis are characteristic of open grassy communities, such as modern steppes with abundant overground phytomass.

The modern fauna of the Upper Ob Region is only characterized by a few coleopteran species recorded in the Kalistratikha taphocoenosis. The modern ranges of the majority of steppe species cover central Kazakhstan and adjacent areas; some species are widespread in the steppe zone, reaching southern Transbaikalia. Species endemic to steppe intermountain depressions of the Altai–Sayany Mountains (*Poecilus* cf. *hanhai-cus*, *Stephanocleonus grigorievi*, *Chlorophanus tuvensis*) are also recorded. Most of the meadow and riparian species have boreomountain ranges and occur in the taiga zone and forest belt of mountains of southern Siberia. Several species characteristic of the regions with a humid boreal climate are recorded in the taphocoenosis (*Pterostichus drescheri*, *P. maurusiacus*, *Hypera misella*, *Trichalophus maeklini*). The insect assemblage of the Kalistratikha taphocoenosis is similar to other Late Pleistocene assemblages from southern and partly central parts of the West Siberian Plain (which are tentatively named *Otiorhynchus*-type faunas), but it is distinguished by the absence of a tundra species association and presence of humid species.

Based on entomological data, the climate of the region at the end of the Karginian time is reconstructed as relatively dry and cold compared to the modern one, but warmer and more humid than in the succeeding Sartanian stadial. Prevailing landscapes were probably dry steppes, complicated in depressions by meadow and shrubby (willow) vegetation. Forests were absent or played a minor role. The small sample size of small mammals precludes a detailed reconstruction of environments. Nevertheless, the mammal composition, like insects, suggests that there were open dry landscapes.

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