Late Pleistocene and Holocene small mammal (Lipotyphla, Rodentia, Lagomorpha) remains from Medvezhyi Klyk Cave in the Southern Russian Far East

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ABSTRACT
Late Pleistocene-Holocene faunal complexes of small mammals (Lipotyphla, Rodentia, and Lagomorpha) from the Russian Far East are described for the first time. We used material from the Medvezhyi Klyk Cave, located in Southern Sikhote-Alin. The numerous fossil findings from the cave display a remarkable taxonomic diversity and high degree of preservation. AMS 14C dating used for determination of deposits age. The Holocene sediments were divided into three periods: Early, Middle, and Late. The Pleistocene deposits age was not exactly determined, but under approximately estimation it can reach 50–60 ka. Thirty-nine species were found, including one member of the extinct genus of arvicolins. There are six faunal complexes identified from the studied Late Pleistocene and Holocene deposits. In general, the faunal complexes characterized by the dominance of Craseomys rufocanus within rodents, Sorex caecutiens within lipotyphlans; and relatively stability composition of most number of the dominant, codominant and subdominant species. Accordingly, the faunal complexes were described by means of two determining criteria only: relative number of species; and presence or absence of certain species. The dominant species are eurytopic and so they cannot use for reconstruction of the paleoenvironment.

Key words: AMS 14C dating, Holocene, Lagomorpha, Late Pleistocene, Lipotyphla, Micromammals, Rodentia, Russian Far East

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INTRODUCTION

The modern mammalian fauna of the south part of Russian Far East is heterogeneous, with co-existing representatives of two different groups: Eastern Siberian species group from coniferous forests (= taiga); and Manchurian–Chinese species group from steppes, forest steppes, and deciduous forests. This explains the large number of taxa (almost 30% of the total assemblage) which exists on either northern or southern limits of their habitats (Oleinikov 2009). It was mentioned previously (Bromley 1974) that northern mammal species actively penetrate into areas with vegetation of the southern type, while the southern mammals do not migrate into the northern biomes. The distribution of the members from each group (Eastern Siberian and Manchurian–Chinese) is related to both the current geographical position and the natural environmental change through time.

The southern Sikhote-Alin Mountains belong to the Far Eastern (Manchurian) vegetation province of conifer-broadleaved and oak forests, with sub-oceanic moderately cool and wet climate (e.g. see Suslov 1961). The total number of trees and shrubs exceeds 200 species. The most common trees are Korean pine (Pinus koraiensis), Manchurian nut-tree (Juglans

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mandshurica), elm (Ulmus glabra), Manchurian ash (Fraxinus mandshurica), and Mongolian oak (Quercus mongolica) (e.g. see Kuzmin 2006).

The forming of modern biogeographical patterns of extant small mammals in the Russian Far East is still not well understood, mainly due to the incompleteness of the Quaternary fossil records in Palaeartic East Asia. As a result, the information of the Late Pleistocene and Holocene micromammal fauna in this region is fragmentary. Until now, the best-studied Late Pleistocene and Holocene small mammal faunas are known from Northeast China (Jin and Kawamura 1996), and Japan (Kawamura 1988, 1989, 2010; Kawamura and Nakagawa 2009); along with limited data from the Korean Peninsula (Park 1988). The preliminary data from Bliznets Cave in the southern Sikhote-Alin Mountains have been published by Alekseeva (1986), Tiunov et al. (1992), and Nesterenko et al. (2002). Data of small mammals from Geographicheskogo Obchshchestva Cave are more fragmentary (Ovodov 1977).Kirillova and Tesakov (2008) published preliminary data from Late Pleistocene deposits of Sakhalin.

The cave-well of Medvezhyi Klyk (Bear Fang) represents the most complete records of Late Pleistocene and Holocene micromammals from the Russian Far East currently available, and it might be the best-preserved assemblage of small mammals in the entire Northeast Asia including North China, Japan, Korea, and the Russian Far East. To date, some studies based on material from the Medvezhyi Klyk Cave have already been conducted for certain groups of animals – Mollusca (Prozorova et al. 2006), Chiroptera (Tiunov 2016), Lemmini (Tiunov and Panasenko 2010). Preliminary work was made using a material Lipotyphla, Rodentia, and Lagomorpha (Panasenko and Tiunov 2010). A new species of Mimomys Forsyth-Major, 1902 (Rodentia: Cricetidae) was described by Tiunov et al. (2016). The analysis of the age variability of the white-toothed shrews (Panasenko and Kholin 2011) and brown-toothed shrews (Panasenko and Kholin 2013; Omelko and Kholin 2017) was done. In this paper results of AMS-dating, finds of small mammals as well as previously published data are comprehensively analyzed to determine the age of sediments and to identify of the faunal complexes of small mammals from the Late Pleistocene and Holocene of the Southern Sikhote-Alin. This is the original study in the mentioned terms, and it is important for our understanding of the small mammal assemblages development while Northeast Asia.

Description and taphonomy of the Medvezhyi Klyk Cave

The Medvezhyi Klyk Cave is located in the southern part of the Sikhote-Alin Mountains (Demin et al. 1980; Bersenev 1989; Tiunov and Panasenko 2007) in the Lozovyi (former name – Chandalaz) Ridge. It is situated in the Primorskiy Territory of the Russian Federation, ca. 90 km east of the city of Vladivostok (Figs 1, 2A). The geographic coordinates of the cave are 43°01.72′N, 133°01.38′E; and the elevation is 465 m asl. (Baltic Sea datum). The entrance to the cave is on the northern flank of a watershed ridge (Fig. 2B). It has a fissure shape (1 to 0.55 m) that extends to the NW and looks upwards, in the form of vertical shaft created by karstic processes. The initial depth (from the entrance to the bottom) is 17.4 m. After a pit 5.4 m deep was excavated by our team (Fig. 3), the total depth extends to 22.8 m. A brief description of the lithological layers is given in the caption to Figure 3.

Medvezhyi Klyk Cave was a natural trap for animals due to its shaft-like shape. Animals that lived in the vicinity of the cave fell inside it occasionally; they were not able to get out of it because of steep walls and died of starvation, and afterwards buried on the bottom of cave. Mainly mammals and other animals that lived in the vicinity of cave appear in the cave deposits. However, since also bones of fish and mammal species who did not live nearby (water shrew Neomys fodiens (Pennant, 1771); and rodents – Myospalax psilurus Milne-Edwards, 1874 and Tscherskia triton (de Winton, 1899)) were found, we assume as another factor of bone accumulation the activity of predatory birds (such as Strigiformes and Falconiformes) who were hunting outside of the cave’s area. They might have rested in the cave. Some bones have traces of chemical weathering such as etching (due to its digestion by predatory birds). This also testifies in favor of predatory birds’ participation in the accumulation of bones at the Medvezhyi Klyk Cave. On the other hand, bones with weathered surface are quite rare. Currently, there are no niche suitable for resting birds over the cave (Fig. 2B), and there are no fresh traces of bird activity. We do not know what shape of the inlet at the cave was earlier, as far as it was convenient for birds, but we assume that the role of birds in the formation of taphocenosis was secondary.
Fig. 1. Location of the Medvezhiy Klyk Cave.

Fig. 2. Landscapes around Medvezhiy Klyk Cave: A – northeastern part of Lozovyi Ridge; B – view on the ridge from northeast to southwest. Arrow show at entrance of Medvezhiy Klyk Cave.
Fig. 3. Cross-section of the pit in Medvezhiy Klyk Cave. A – cross-section of the SW wall; B – cross-section of the NE wall. Lithological layers: 1 – clay and humus; 2 – thick humus; 3 – stones with humified loam fill; 4 – humified loam with scree and large amount of small bones; 5 – loam with scree, large amount of bones and snail shells; 6 – loam with large scree and lumps; 7 – loam with rare lumps; 8 – loam; 9 – loam with large scree and lumps; 10 – heavy loam; 11a – loam with numerous scree, stones, and lumps, with many hollows; 11b – loam, boundary between layers 11a and 11b is determined by colour; 12 – re-deposited cave sediments which came from above during the excavation of lump concentration, to the bottom become lumps with hollows, upper boundary is unclear; 13a – loam with small amount of scree; 13b – layer is determined on the basis of faunal composition (see text). Horizontal and vertical scales are the same.
Table 1. Number of micromammal remains from the Medvezhyi Klyk Cave.

| Taxa                                             | Layers          |
|--------------------------------------------------|-----------------|
|                                                  | 13b 13a (12)a   |
| Sorex mirabilis Ognev, 1937                      | 14 3 18 11      |
| S. roboratus Hollister, 1913                     | 8 37 33 33      |
| S. ex gr. unguiculatus-isodon                    | 128 257 308     |
| S. daphaenodon Thomas, 1907                      | 0 3 4 3         |
| S. tundrensis Merriam, 1900                      | 3 2 0 3         |
| S. caecutiens Laxmann, 1788                      | 243 496 675     |
| S. gracilimus Thomas, 1907                       | 6 1 5 3         |
| S. minutissimus Zimmermann, 1780                 | 152 217 176     |
| Neomys fodiens (Pennant, 1771)                   | 0 1 1 0         |
| Crocidura shantungensis Miller, 1901             | 2 9 105 48      |
| C. lasiura Dobson, 1890                          | 7 11 31 11      |
| Crocidura sp.                                    | 1 1 0 0         |
| Mogera spp.                                      | 9 6 8 12        |
| Talpidae gen. sp.                                | 0 1 1 0         |
| Sciurus vulgaris Linnaeus, 1758                   | 0 0 0 1         |
| Pteromys volans (Linnaeus, 1758)                 | 3 6 0 1         |
| Tamias sibiricus (Laxmann, 1769)                 | 65 69 134       |
| Apodemus peninsulare Thomas, 1906                 | 7 8 47 15       |
| A. agrarius (Pallas, 1771)                       | 2 0 10 2        |
| Apodemus spp.                                    | 19 32 98 52     |
| Rattus norvegicus Berkenhout, 1769                | 0 0 12 0        |
| Taxa                                         | Layers |
|----------------------------------------------|--------|
|                                              | 13b    | 13a   | (12)* | 11     | (9–10)* | 9      | (8–9)* | (7–8)* | 7      | (5–6)* | 5      | (3–4)* | 3      | (1–2)* |
| Micromys minutus (Pallas, 1771)              | 0      | 0     | 0      | 0      | 0       | 0      | 0      | 0      | 0      | 0      | 3      | 3      | 0      | 1      |
| Sicista caudata Thomas, 1907                 | 1      | 1     | 2      | 2      | 0       | 0      | 2      | 7      | 2      | 5      | 5      | 0      | 2      |
| Craseomys rufocanus (Sundevall, 1846)        | 137    | 243   | 488    | 427    | 76      | 157    | 107    | 586    | 499    | 438    | 1928   | 302    | 255    | 162    |
| Myodes rutilus (Pallas, 1778)                | 32     | 91    | 81     | 70     | 29      | 49     | 22     | 185    | 81     | 36     | 53     | 19     | 16     | 7      |
| Alexandromys fortis (Buchner, 1889)          | 0      | 0     | 21     | 23     | 0       | 0      | 6      | 16     | 1      | 8      | 27     | 9      | 18     | 5      |
| Alexandromys cl. maximowiczii                | 4      | 3     | 64     | 95     | 6       | 21     | 49     | 64     | 8      | 13     | 22     | 1      | 10     | 3      |
| Alexandromys cl. oeconomus                   | 0      | 0     | 5      | 3      | 0       | 0      | 0      | 3      | 0      | 0      | 1      | 0      | 0      | 0      |
| Alexandromys cl. mongolicus                  | 0      | 1     | 1      | 2      | 0       | 0      | 0      | 6      | 0      | 0      | 0      | 0      | 0      | 0      |
| Mimomys chandolensis Tiunov, Golenishchev et Voyta, 2016 | 0      | 0     | 0     | 1      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      |
| Myopus schisticolor (Lilljeborg, 1844)       | 4      | 7     | 24     | 33     | 12      | 16     | 2      | 16     | 11     | 3      | 1      | 1      | 3      | 0      |
| Lemmus amurensis Vinogradov, 1924            | 5      | 1     | 31     | 11     | 5       | 15     | 1      | 13     | 4      | 1      | 3      | 0      | 0      | 0      |
| Lemmini                                      | 28     | 34    | 23     | 81     | 23      | 45     | 11     | 87     | 28     | 14     | 10     | 3      | 2      | 4      |
| Myospalax psilurus Milne-Edwards, 1874       | 0      | 1     | 1      | 2      | 0       | 4      | 0      | 15     | 3      | 0      | 1      | 1      | 0      | 2      |
| Tscherskia triton (de Winton, 1899)          | 0      | 0     | 0      | 0      | 0       | 0      | 0      | 0      | 0      | 0      | 1      | 0      | 0      | 1      |
| Lepus spp.                                   | 0      | 0     | 2      | 0      | 2       | 0      | 2      | 1      | 1      | 6      | 1      | 0      | 0      |
| Ochotona hyperborea Pallas, 1811             | 9      | 26    | 28     | 27     | 5       | 20     | 19     | 52     | 26     | 5      | 11     | 3      | 4      | 3      |
| Total                                        | 889    | 1568  | 2435   | 2260   | 473     | 861    | 541    | 2538   | 1404   | 970    | 3978   | 858    | 661    | 426    |

Note: * – Numbers in brackets correspond to mixed layers.
Abiotic factors such as rockfall and flash floods were possible formed the mixing deposits in some levels of the cave. Burrowing activity of animals as a mixing factor of deposits seems unlikely because the falling animals fast died without food. The cave acted as a natural trap, and animals had no access to cave’s exit. The cave deposits contain very high concentration of bones. It was connected with a low rate of formation of terrigenous sediments in the cave.

**MATERIAL AND METHODS**

Excavations of the Medvezhyi Klyk Cave were conducted in 2005–2008 by scholars from the Laboratory of Theriology of the Federal Scientific Center of the East Asia Terrestrial Biodiversity (Vladivostok, Russia), along with members of the Vladivostok Speleological Club. The width of the pit ranges from 0.62 to 1 m, and the depth is 5.4 m (Fig. 3). The material was excavated in layers of 5–10 cm in thickness. Lithological units are given in figure 3. All recovered bone and teeth material was wet-sieved (mesh size 1 mm) in the field, and further work was conducted in the lab.

Numerous remains of mammals (insectivores, rodents, lagomorphs, chiropterans, carnivores and artiodactyls), birds, reptiles, amphibians and fish were found, along with shells of terrestrial gastropods and chitin insect fragments (Panasenko and Tiunov 2010). Taxonomic identification was performed for more than 19,862 remains (isolated teeth, mandibles, and crania) of lypotyphlans, rodents, and lagomorphs. Shrews were identified by mandibles; voles and lemmings were identified by first lower molar (m1); mice of *Apodemus* genus were identified by firs upper molar (M1); other rodents, hares and moles could be identified by any isolated teeth; pikas were identified by third lower premolar (p3).

The number of individuals (total number of individuals, TNI) was determined as the maximal amount of the skeletal elements of the same anatomical position (crania, mandibles, or isolated teeth) (Table 1). We did not count the minimal number of individuals (MNI) for whole material. But we performed the re-counting of MNI for 230 bones from the Layer 3 for estimation of the possible dissimilarities among methods, TNI and MNI. The difference between the two methods turned out to be very small, from 0.1% to 3.3%. The number of the rare species increased slightly, but the ratios for dominant, common, and rare species remains the same. Therefore, we accept TNI method of counting as a reliable.

The cave sediments represent by 13 lithological layers (Fig. 3), which excavated as a horizontal strata of fixed thickness. Several of lithological layers lay with tilting whereby a mixture of osteological material was occurred (these layers are indicated in Table 1). The mixed material did not analyze. Only unmixed faunal complexes from Layers 3, 5, 7, 9, 11, 13a, and 13b used for analysis (Table 1). Each layer (i.e., faunal complex) characterized by a list of in percentage (Table 2). There were five groups in material that differ in the species abundance. Accordingly Maleeva (1983) they were distinguished as follow: 1) very numerous or dominant species (more than 30% of the total frequency); 2) numerous or codominant species (10–29.9%); 3) common or subdominant species (1–9.9%); 4) rare species (0.2–0.9%); and 5) very rare species (less than 0.2%).

The percentage of species was calculated for all micromammals, and afterwards separately for lypotyphlans, rodents, and pikas. Combining the latter types makes sense because pikas are not numerous, and their analysis as separate group would not be representative; and also because pikas and rodents are very similar in terms of feeding habits. These circumstances allowed us to combine both groups. Some species cannot be certainly identified to species level, thus we used “open nomenclature”. The list of these taxa with short clarification presents in Appendix 1. Hares are animals of middle size, and we included them into this study to show the taxonomic diversity of fauna. Because hares were not identified up to the species level, they are not included in the faunal analysis, and therefore they do not bias the results of this work. In the use of the genera *Alexandromys* Ognev, 1914, *Myodes* Pallas, 1779, and *Craseomys* Miller, 1900, we follow Abramson and Lisovsky (2012). The differentiating features of the voles of the genus *Alexandromys* and the reliability of the species identification were considered earlier by Haring et al. (2015) and Voyta et al. (2019).

Differentiation of *Myopus schisticolor* (Lilljeborg, 1844) and *Lemmus amurensis* Vinogradov, 1924 are possible by morphometric parameters (Tiunov and Panasenko 2010), while the species overlap according to this feature. Therefore, examples that appear into the overlap zone stay identified only up to the tribe Lemmini. Therefore, we used all examples of the Lemmini tribe together for calculations charac-
Table 2. Percentage of micromammal taxa from the Medvezhyi Klyk Cave (non-mixed layers).

| Taxa                                | Layers |
|-------------------------------------|--------|
|                                     | 13b    | 13a    | 11     | 9      | 7      | 5      | 3      |
| Sorex mirabilis                     | 1.6    | 0.2    | 0.5    | 0.0    | 0.1    | 0.9    | 2.0    |
| S. roboratus                        | 0.9    | 2.4    | 1.5    | 1.4    | 1.5    | 0.1    | 0.0    |
| S. ex gr. unguiculatus-isodon       | 14.4   | 16.4   | 15.7   | 19.2   | 8.2    | 6.2    | 6.5    |
| S. daphaenodon                      | 0.0    | 0.2    | 0.1    | 0.2    | 0.6    | 0.0    | 0.0    |
| S. tundrensis                       | 0.3    | 0.1    | 0.1    | 0.2    | 0.1    | 0.1    | 0.0    |
| S. caecutiens                       | 27.3   | 31.6   | 33.3   | 33.0   | 26.6   | 11.6   | 12.7   |
| S. gracillimus                      | 0.7    | 0.1    | 0.1    | 0.0    | 0.0    | 0.0    | 0.3    |
| S. minutissimus                     | 17.1   | 13.8   | 7.5    | 4.5    | 3.1    | 1.3    | 3.2    |
| Neomys fodiens                      | 0.0    | 0.1    | 0.0    | 0.0    | 0.0    | 0.1    | 0.0    |
| Crocidura shantungensis             | 0.2    | 0.6    | 2.2    | 0.0    | 3.0    | 10.7   | 12.1   |
| C. lasiura                          | 0.8    | 0.7    | 0.5    | 0.2    | 0.7    | 0.9    | 0.6    |
| Crocidura sp.                       | 0.1    | 0.1    | 0.0    | 0.0    | 0.0    | 0.0    | 0.0    |
| Mogera spp.                         | 1.0    | 0.4    | 0.6    | 0.1    | 0.0    | 0.2    | 0.6    |
| Talpidae gen. sp.                   | 0.0    | 0.0    | 0.0    | 0.0    | 0.0    | 0.0    | 0.0    |
| Sciurus vulgaris                     | 0.0    | 0.0    | 0.1    | 0.1    | 0.0    | 0.0    | 0.0    |
| Pteromys volans                     | 0.3    | 0.4    | 0.1    | 0.0    | 0.1    | 0.1    | 0.2    |
| Tamias sibiricus                    | 7.3    | 4.4    | 3.1    | 2.0    | 2.3    | 2.7    | 2.7    |
| Apodemus spp.                       | 3.1    | 2.6    | 3.2    | 0.8    | 6.1    | 13.0   | 12.6   |
| Rattus norvegicus                   | 0.0    | 0.0    | 0.0    | 0.0    | 0.0    | 0.2    | 0.0    |
| Micromys minutus                    | 0.0    | 0.0    | 0.0    | 0.0    | 0.0    | 0.1    | 0.0    |
| Sicista caudata                     | 0.1    | 0.1    | 0.1    | 0.0    | 0.5    | 0.1    | 0.0    |
| Craseomys rufocanus                 | 15.4   | 15.5   | 19.8   | 18.2   | 35.5   | 48.5   | 38.6   |
| Myodes rutilus                      | 3.6    | 5.8    | 3.2    | 5.7    | 5.8    | 1.3    | 2.4    |
| Alexandromys forcis                 | 0.0    | 0.0    | 1.1    | 0.0    | 0.1    | 0.7    | 2.7    |
| Alexandromys cf. maximowiczi        | 0.4    | 0.2    | 4.4    | 2.4    | 0.6    | 0.6    | 1.5    |
| Alexandromys cf. oeconomus          | 0.0    | 0.0    | 0.1    | 0.0    | 0.6    | < 0.1  | 0.0    |
| Alexandromys cf. mongolicus         | 0.0    | 0.1    | 0.1    | 0.0    | 0.0    | 0.0    | 0.0    |
| Mimomys chandolensis                | 0.0    | 0.0    | 0.1    | 0.0    | 0.0    | 0.0    | 0.0    |
| Lemmini                             | 4.2    | 2.7    | 5.8    | 8.8    | 3.1    | 0.4    | 0.8    |
| Myospalax psilurus                  | 0.0    | 0.1    | 0.1    | 0.5    | 0.2    | < 0.1  | 0.0    |
| Tscherckia triton                   | 0.0    | 0.0    | 0.0    | 0.0    | 0.0    | < 0.1  | 0.0    |
| Lepus spp.                          | 0.0    | 0.0    | 0.1    | 0.2    | 0.1    | 0.2    | 0.0    |
| Ochotona hyperborea                 | 1.0    | 1.7    | 1.3    | 2.3    | 1.9    | 0.3    | 0.6    |
teristics of the faunistic complexes. Differentiation of *Apodemus peninsulae* Thomas, 1906 and *Apodemus agrarius* (Pallas, 1771) is possible only for one tooth, which is not found in all fossil specimens. As a result, there are specimens defined to the species is less than specimens identified to the genus. In this regard, in the calculations, we also considered all members of the genus *Apodemus* Kaup, 1829 together.

One of the criteria to estimate the climatic conditions in the past is the relationship between “northern” and “southern” species and genera. We determined these groups based on their origin and their occurrence in modern habitats. The sub-division into “northern” and “southern” species is traditional for the modern fauna of this region (Matyushkin 1972; Bromley 1974), but it is not common for this kind of research, and usually for paleoecological analysis they are divided based on biotopic characteristics. However, for the Russian Far East it is not useful because all species are either forest or eurytopic dwellers. The list of the “northern” and “southern” taxa see in Appendix 2. The *S. ex gr. unguiculatus-isodon* and *Lepus* spp. are not clearly referable to either the group of northern or the group of southern taxa (“mixed assemblage”).

In 2010, six samples of mandibles with teeth (of bulk rodents) and isolated teeth (of two species, *Craseomys rufocanus* and *Miodes rutilus*) from layers 3, 5, 7, 9, and 11 were AMS 14C-dated. Three additional samples from layers 9, 11, and 13 were dated in 2011. Rodent limb bones were chosen for the second round of dating, to compare the results with the earlier data based on teeth. The AMS 14C dating was performed at the Arizona AMS Laboratory, following a routine protocol for bone material (Burr and Jull 2010; see also Ovodov et al. 2011). The Calib Rev 7.0.2 software was used for calibration of 14C dates (available at: http://calib.qub.ac.uk/calib/download/; see also Reimer et al. 2013) with ± 2 sigma uncertainties and rounded to ten year increments.

A conventional 14C date for the Medvezhyi Klyk Cave is available from the literature: from a brown bear bone in Layer 7 (depth 1.08–1.18 m): 12,140 ± 90 14C a BP (GIN-13479) (13,760–14,250 cal a BP) (Panasenko and Tiunov 2010).

Because no continuous sequences of terrestrial sediments, belong to the Middle and Late Pleistocene, were studied in the Russian Far East, we use the stratigraphic scheme by Korotky et al. (2005) as a basic source for comparison of our results with general paleoenvironmental situation in Primorye in the second part of the Late Pleistocene and in the Holocene. The stratigraphy developed by Korotky et al. (2005) was based on correlation of discontinuous sediment sections using mainly palynological data, and no reliable chronological framework for it was ever created. We are, therefore, fully aware of the shortfalls in Korotky et al.’s (2005) scheme, but consider it as a general source of paleoenvironmental information for the region under investigation. It does not contradict to general peculiarities of the Late Pleistocene climate of Northeast Asia known from the neighboring regions of Japan and China (e.g. Takahara and Kitagawa 2000; Late Cenozoic Climate... 2014).

**RESULTS**

**AMS 14C dating**

Eight AMS 14C values were generated for six specimens (Table 3). Two sets of dates were obtained for Layer 11. For the majority of samples, the collagen yield is generally acceptable, in the range of 3.2–6.8% weight of total bone (except for sample AA-90672). The carbon yield for collagen was also good, 23.0–42.6%. This suggests that the 14C ages are reliable (but see controversy for Layer 11). No collagen (or a very small amount, 0.3% of total bone) was extracted from the samples from Layer 9.

**Taxa of small mammals from the Cave**

Overall, 39 species of micromammals were determined (Table 1). This includes taxa that could not be identified to species level: *Sorex ex gr. unguiculatus-isodon*, *Crocidura* sp., *Talpidae gen. et sp. indet.*, *Alexandromys cf. maximowiczii*, *Alexandromys cf. mongolicus*, *Alexandromys cf. oeconomus* (see Appendix 1), and two groups that most probably consist of more than one species (*Mogera* spp. and *Lepus* spp.).

**Characteristics of the faunal complexes**

**Layer 13.** A distinctive feature of the fauna of small mammals from Layer 13 is the maximum amount lipotyphlans remains (up to 66%; Fig. 4). Moreover, most findings (about 90% of all lipotyphlans remains) belonged to three taxa – *S. caecutiens*, *S. minutissimus* and *S. ex gr. unguiculatus-isodon*.
(Figs 5, 6). All other species are rare or very rare. *Craseomus rufocanus* is dominant; *T. sibiricus* and *M. rutilus* are codominant; and Lemmini, *O. hyperborea*, *A. fortis*, *A. maximowiczii*, *Alexandromys* ex gr. *maximowiczii* are subdominant (Fig. 7) in the rodents.

Also, a specific characteristic of the faunal complex is the extremely high number of *S. minutissimus*, up to 17.2%. Moreover, in the lipotyphlans its participation is 26.5%. This species is Holarctic and it habitat from southeastern Sweden in the east to Alaska in the west (Dolgov 1985; Hope et al. 2010). At present this species is rare, its quality is 0.4–4.3% in shrew associations (Dolgov 1985). Fossil *S. minutissimus* is found outside its modern area – in Western and Eastern Europe, and Caucasus (e.g. Rzebik-Kowalska 1998, 2000; Zaitsev and Osipova 2004). This species is represented by single or few finds in all Quaternary locations.

Another feature of Layer 13 is the maximum number of taxa non identify to species, three of them (*Crocidura* sp., Talpidae gen. sp., *Alexandromys* cf. *maximowiczii*) are not found in the upper layers.

The originality of the faunal complex is complemented by a significant number of southern species – thirteen, their rate reaches 23% (Fig. 8). *Sorex caecutiens* is dominant; *S. minutissimus*, *S. ex gr. unguiculatus-isodon*, *C. rufocanus* are codominant; *T. sibiricus*, *M. rutilus*, *Apodemus* spp., Lemmini, *O. hyperborea* are subdominant in the small mammal faunal complex of Layer 13 (Fig. 5).

Two sublayers were identified in Layer 13 based on small lithological differences – 13a and 13b (Fig. 3). The study of quantitative and qualitative characteristics of the fauna of the sublayers revealed some of their features. Thus, *S. daphaenodon*, *N. fodiens*, *Mogera* spp., Talpidae gen. sp., *M. psilurus*, *Alexandromys* cf. *mongolicus* were found (although rare) in the Sublayer 13a while these taxa are absent in the Sublayer 13b. *Sorex roboratus* is subdominant in the Sublayer 13a while it is rare in the Sublayer 13b. *Sorex mirabilis* is subdominant in the Sublayer 13b, while it is rare in the Sublayer 13a. There is no dominant in the Sublayer 13b, the most numerous is *S. caecutiens*, but its number is 27.4% corresponding to the codominant. This may indicate that the sublayers accumulated in different conditions, although this difference, apparently, was not large.

**Layer 11.** The distinctive characteristic of the small mammal faunal complex of Layer 11 is the high-

| Field No. | Lab. No (AA-) | Layer | Depth, cm | Material | Date, 14C a BP | Calendar age, cal a BP | δ¹³C, ‰ | Collagen yield, % | Carbon yield, % |
|-----------|--------------|-------|-----------|----------|---------------|------------------------|--------|-----------------|-----------------|
| KL01      | 90668        | 3     | 13–18     | teeth and mandibles | 2.140 ± 35 | 2.000–2.300 | -21.0 | 5.8             | 34.0            |
| KL02      | 90669        | 5     | 63–68     | teeth and mandibles | 5.070 ± 40 | 5.730–5.910 | -20.7 | 6.8             | 34.0            |
| KL03      | 90670        | 7     | 93–98     | teeth and mandibles | 9.730 ± 70 | 10.790–11.260 | -21.0 | 4.0             | 34.0            |
| KL04      | 90671        | 9     | 207–215   | teeth and mandibles | –       | –         | –0.3  | 6.0             |                 |
| KL05      | 90672        | 11    | 253–263   | teeth and mandibles | 33.170 ± 950 | 35.210–39,540 | -20.4 | 0.5             | 23.0            |
| KL06      | 90673        | 11    | 283–288   | teeth and mandibles | 11.880 ± 70 | 13.490–13,950 | -20.9 | 4.6             | 33.0            |
| KL09      | 98290        |      |           | bones            | 16.480 ± 200 | 19.410–20,410 | -21.1 | 3.9             | 38.1            |
| KL10      | 98291        | 13    | 535–540   | bones            | > 41.100 | > 44.630 | -19.7 | 4.0             | 41.4            |
Fig. 4. The relationship between remains of lipotyphlans, rodents and lagomorphs in Medvezhyi Klyk Cave during the Late Pleistocene and Holocene.

Fig. 5. The relative abundance of the most numerous taxa in different strata of Medvezhyi Klyk Cave.
est amount of *C. rufocanu*s (19.5%) and *C. shantungensis* (2.2%), the lowest amount of *M. rutilus* (3.2%) among the Pleistocene layers (Fig. 5), while amount of *A. maximowiczcii* (3.5%) is the highest not only in the Pleistocene, but also in the Holocene. *Mimomys chandolensis* was described from this layer (Tiunov et al. 2016). *Sorex caecutiens* continues to dominate; *C. rufocanu*s, *S. ex gr. unguiculatus-isodon* are codominant in the small mammal faunal complex of Layer 11. Subdominant taxa becoming more numerous they are *S. minutissimus*, Lemmini, *A. maximowiczcii*, *M. rutilus*, *T. sibiricus*, *Apodemus* spp., *C. shantungensis*, *S. roboratus*, *O. hyperborea*, *A. fortis*.

Lipotyphlans also predominate over rodents and lagomorphs in the faunal complex of Layer 11 (Fig. 4). *Sorex caecutiens* is dominant among lipotyphlans; *S. ex gr. unguiculatus-isodon* and *S. minutissimus* are codominant although the amount of the latter is twice less compared with the previous Layer 13 (Fig. 6). Only one subdominant species there is *C. shantungensis*. *Craseomys rufocanu*s dominates among rodents (Fig. 7). There are no codominant species; subdominant species are the same as in the small mammal faunal complex of Layer 11 with addition of *Alexandromys cf. oeconomicus*.

There are a maximum number of southern taxa in Layer 11 (14; Fig. 8A), their number is maximum among the Pleistocene layers (27%; Fig. 8B).

**Layer 9.** The distinctive characteristics of the small mammal faunal complex of Layer 9 are the maximum number of Lemmini (5.5%), *S. ex gr. unguiculatus-isodon* (19.9%) and the minimum amount of *Apodemus* spp. (0.7%). The dominant here is still *S. caecutiens*, reaching in this layer its maximum (34.3%; Fig. 5). Codominant continue to be *S. ex gr. unguiculatus-isodon* and *C. rufocanu*s. Subdominant here are *M. rutilus*, Lemmini, *S. minutissimus*, *Alexandromys cf. maximowiczcii*, *O. hyperborea*, *T. sibiricus*, *S. roboratus*. The total number of taxa is minimal compared to other layers (19).

Lipotyphlans prevail over rodents and lagomorphs in the faunal complex (Fig. 5). *Sorex caecutiens* dominates among lipotyphlans, its number becomes maximum for the Pleistocene layers. The group *S. ex gr. unguiculatus-isodon* here reaches its maximum amount (32.5%; Fig. 6), and it should also be attributed to the dominants. Only two subdominant species remain present here – *S. minutissimus* and *S. roboratus*. *Craseomys rufocanu*s stays the dominant among rodents (Fig. 7); *M. rutilus* and *Lemmini* are codominant; and *Alexandromys cf. maximowiczcii*, *O. hyperborea*, *T. sibiricus*, *Apodemus* spp., *M. psilurus* are subdominant. And only three rare taxa left – *Lepus* spp. and *S. vulgaris*.

Only five southern species present here (the minimum value, both for the Pleistocene layers and for the Holocene), however, their numbers are quite high at 21%, which is comparable to this indicator in Layer 13 (Fig. 8).

**Layer 7.** *Craseomys rufocanu*s begins to dominate in the of small mammal faunal complex of Layer 7 (Fig. 7). Only one species *S. caecutiens* is numerous. *Sorex ex gr. Unguiculatus-isodon*, *M. rutilus*, *Apodemus* spp., *S. minutissimus*, *C. shantungensis*, *T. sibiricus*, Lemmini, *A. maximowiczcii*, *O. hyperborea*, *S. roboratus* are subdominant species and quite numerous. Among small mammals, rodents begin to predominate over lipotyphlans (54% and 44%, respectively, Fig. 4). Among lipotyphlans *S. caecutiens* stays the dominant; its amount reaches a maximum value of 60.7% (Fig. 6) in the Layer 7. *Sorex ex gr. unguiculatus-isodon* is codominant; *S. minutissimus*, *C. shantungensis*, *S. roboratus*, *C. lasiura*, *S. daphaenodon* are subdominant. *Craseomys rufocanu*s remains the dominant among the rodents (Fig. 7), one species *M. rutilus* is codominant, and the subdominants ones are the same as in the previous layer list and *A. fortis* and *Alexandromys cf. oeconomicus*.

There, the number of southern species increase (as compared with layer 9) to eight, the northern ones remains eleven, while the number of southern species has increased significantly (up to 45%) and almost equal to the number of northern ones (Fig. 8).

**Layer 5.** In the small mammal faunal complex of the Layer 5, *C. rufocanu*s is also dominant (Fig. 5). There are two codominant species (*S. caecutiens* and *C. shantungensis*). Subdominant taxa here include *Apodemus* spp., *S. ex gr. unguiculatus-isodon*, *T. sibiricus*, *M. rutilus*, *S. minutissimus*, *A. fortis*.

Number of rodents became significantly larger than in the Pleistocene layers in the Layer 5 (66%; Fig. 4). Among lipotyphlans, along with *S. caecutiens* (36.5%), the second dominant appears *C. shantungensis* (33.5%; Fig. 6). Currently, *C. shantungensis* is rare in the shrew associations in the Russian Far East (Nesterenko 1999). *Sorex ex gr. unguiculatus-isodon* is codominant in Layer 5; *S. minutissimus*, *S. mirabilis* and *C. lasiura* are subdominant. Among rodents, *C. rufocanu*s becomes the absolute monodominant, reaching its maximum value in this layer (75.3%:
Fig. 6. The relative abundance of the dominant shrew species during the Late Pleistocene and Holocene strata of Medvezhyi Klyk Cave.

Fig. 7. The relative abundance of the dominant rodent species during the Late Pleistocene and Holocene strata of Medvezhyi Klyk Cave.
Fig. 7). *Apodemus* spp. is codominant; only two species *T. sibiricus*, *A. fortis* are subdominant.

**Layer 3.** The small mammal faunal complex of Layer 3 is very similar to the complex of Layer 5. *Craseomus rufocanus* is also dominant here. *Sorex caecutiens* and *C. shantungensis* are numerous also too (Fig. 5). *Sorex mirabilis* is added to the list of subdominants from the previous layer. *Sorex roboratus*, *S. tundrensis*, *M. psilurus*, and *S. caudata* disappeared.

Rodents predominate over lipotyphlans (58% and 41%, respectively; Fig. 4). Among the lipotyphlans dominants, codominant and subdominant taxa stay the same and in the same sequence as in the previous layer, only one change is added (*Mogera* spp.). Among the rodents, the dominant and numerous species stay the same; the composition of common taxa partially changes and consists of *T. sibiricus*, *M. rutilus*, *A. fortis*, *A. maximowiczii*, Lemmini, *O. hyperboreaean* (Fig. 7).

Number of northern species decrease by one compared with Layer 5, but their amount increases to 25%, southern ones decrease by three, their numbers decrease insignificantly to 68% (Fig. 8).

**DISCUSSION**

**AMS 14C dating and age of Medvezhiy Klyk Cave sediments**

**Layer 13.** The result of AMS 14C dating for Layer 13 (> 44.630 cal a BP; Table 3) can be considered as approximate. The faunal complex of Layer 13 could be formed in a quite warm or temperate climate because of number and rate of south species is rather high. In addition, thermophilic species of bats *Rhinolophus nippon* Temminck, 1835 and *Myotis rufoniger* (Tomes, 1858) were found here (Tiunov 2016). Possibly they are live in one of the warm stages of MIS 3, corresponding to the Chernoruchye stage according to regional scale (Korotkiy et al. 2005). However, now there is not enough data to make final conclusions regarding the age of Layer 13.

**Layer 11.** Two sets of dates were obtained for Layer 11. The dates of 13,490–13,950 cal a BP and 19,410–20,410 cal a BP (Table 3), obtained for the lower part of this layer, refer to the periods of the Late Pleistocene with a cold climate. The period 15–13 ka, corresponding to the boundary of MIS 1–2, is also characterized by a cold climate. At that time in the Southern Sikhote-Alin birch-larch and light forests were growing, tundra was typical for highlands (Korotkiy et al. 2005). The period 20–18 ka (MIS 2) is the peak of the Last Glacial Maximum (LGM). But faunal complex of this layer is characterized by large number and high abundance of southern species and presence thermophilic species of bats *R. nippon* and *M. rufoniger* (Tiunov 2016), as well as the thermophilic soil mollusk *Strobilops coreana* Pilsbry, 1927 (Przororova et al. 2006). Therefore, these climatic conditions are contrary to the faunistic data.

The dates obtained for the upper part of this layer showed a more ancient age (35,210–39,540 cal a BP; > 44,170 cal a BP; Table 3). This value like with the dating from Layer 13. The species composition and the ratio of small mammals in Layers 13 and 11 differ significantly, this suggests that they were formed at different times, and since Layer 13 lies deeper than
its age is older. These dates are not clear. But judging by the faunal complex, Layer 11 could be formed in one of the warm stages of MIS 3. Thus, the formation of Layer 13, apparently, occurred at one of the stages of beginning of MIS 3 (perhaps 60–50 ka), and the formation of Layer 11 – at one of the stages of the middle or end of MIS 3 (perhaps 45–35 ka). For this time (39–33 ka) the complex of large mammals from the Geographicheskogo Obshchestva Cave also located in the Southern Sikhote-Alin is well studied (Ovodov 1977; Kuzmin et al. 2001; Baryshnikov 2014, 2015a, 2015b, 2016).

Fig. 9. The age-depth profile for calibrated ages of the Medvezhyi Klyk Cave strata (see Table 3). Black circle is the conventional ^14C date, and gray circles are AMS ^14C dates.

Most likely, this inversion of the dating of two horizons (depths of 253–263 cm and 283–288 cm) in Layer 11 occurred due to impurities of the younger material into the lower horizon (depths of 283–288 cm). This could happen due to the displacement of the upper layers of the ground as a result of the fall of a huge block (Fig. 3) and the further movement of the ground along the formed voids with water flows or under the influence of gravity. The homogeneity of the species composition and the ratio of species within Layer 11 suggests that the impurities were relatively small and did not affect the faunal characteristics of the sediments. The organoleptic characteristics (color, presence of dendrites, hygroscopicity) of the bones inside Layer 11 are also quite homogeneous, so it isn't much mixing in the entire layer, but only minor impurities, which nonetheless influenced the results of radiocarbon dating.

Layer 9. AMS ^14C dating is not received for this layer (Table 3). The time of formation of this layer can only be determined indirectly based on the results of the dating of the overlying and underlying layers (Fig. 9). Despite the uncertainty with specific dates, the faunal complex indicates that the formation of Layer 9 could occur in MIS 2. In Layer 9, bone remains of only one species of bats were found, while in Layers 11 and 13, 12 and 14 species were found respectively (Tiunov 2016). That is, judging by the fauna, it was quite a cold time.

According to paleogeographic reconstructions, the climatic minimum 20–18 thousand years ago in the territory of the Southern Sikhote-Alin was accompanied by a decrease in average annual temperatures by 8–9° C and a decrease in precipitation to 400–500 mm. At that time, undifferentiated landscapes with a predominance of birch-larch forests and light forests were widespread there, areas of mountain tundras expanded, and lowland marshes became widespread (Korotky et al. 2005). Almost all the species found could live in such landscape-climatic conditions (and now live in more northern territories with similar conditions).
For the upper layers of the Madvezyi Klyk Cave (3, 5, and 7), AMS $^{14}$C dating showed values of the Late, Middle, and Early Holocene, respectively (Table 3), this corresponds to MIS 1. Their occurrence and faunal complexes are consistent with these results.

Layer 7. The AMS $^{14}$C dating (10,790–11,260 cal a BP; Table 3) was obtained for this layer, this age corresponds to the very beginning of the Holocene. Judging by the paleogeographic data for the South Far East, the climate at the beginning of the Holocene was cool and dry (Korotky et al. 2005). Structure of the faunal complex of this layer conforms to these conditions.

Layer 5. According to AMS $^{14}$C dating (5910–5730 cal a BP; Table 3) Layer 5 corresponds to the average Holocene (Holocene Optimum). The average annual temperatures of this time exceeded the current ones by 3–5 °C. The vegetation consisted of deciduous forests with thermophilic elements such as ash, elm, and birch (Korotky et al. 2005). It was a wet period with strong summer monsoons. Pine-deciduous forests were widely distributed on the eastern coast of Primorskiy Territory (Razjigaeva et al. 2018).

Layer 3. AMS $^{14}$C dating of this layer (2300–2000 cal a BP; Table 3) indicates that it was formed in the Late Holocene. At this time, the main type of vegetation was deciduous forests with an admixture of Korean pine; the climate was similar to modern with some fluctuations (Korotky et al. 2005). On the eastern coast of Primorye, the climate was cool in 2200–1750 cal a BP (Razjigaeva et al. 2018). At the Shkotovskoye Plateau (South Sikhote-Alin), almost at the same time (2250–2015 cal a BP), a brief warming was idicated (Razjigaeva et al. 2017).

**Changes of faunal complexes during Late Pleistocene and Holocene in South Sikhote-Alin**

Pleistocene fauna of small mammals has common features. There is domination of lipotyphlans over rodents, northern species over southern ones (as a percentage), the dominance of $S$. caecutiens not only among lipotyphlans, but among all small mammals, a high rate of $S$. ex gr. unguiculatus-isodon (14.5–20%), relatively low rate of $C$. rufocanus (15.3–19.5%), which takes second and even third place in Pleistocene faunal complexes. The predominance of lipotyphlans over rodents with lagomorphs in the faunal complexes of small mammals is not typical. Usually, rodents significantly predominate over lipotyphlans in other regions, for example in Ural (for example, Fadeeva and Smirnov 2008). In this case, this cannot be explained by taphonomy reasons, since the situation changes in the Holocene layers (Fig. 4). The complex of landscape-climatic conditions probably influeneced the ratio of lipotyphlans and rodents.

The fauna of the Early Holocene can be characterized as transitional from the Pleistocene to the Holocene. It is almost the same number of “northern” and “southern” species (Fig. 8A). There is still some similarity with the Pleistocene faunal complexes is the high abundance of $S$. caecutiens (26.5% among small mammals). Similarity with Holocene faunal complexes is in the predominance of rodents over lipotyphlans (Fig. 4), a significant increase in the number of $C$. rufocanus among both rodents (Fig. 7) and among all small mammal taxa (Fig. 5).

The Holocene is characterized by the predominance of the southern species over the northern ones, and of the rodents over the lipotyphlans, and $C$. rufocanus becomes dominant both among the rodents and among all small mammal taxa.

The faunal complexes of the Middle and Late Holocene turned out to be very similar. Craseomys rufocanus became an absolute dominant among rodents (Fig. 7). Two dominant species are $S$. caecutiens and $C$. shantungensis among the lipotyphlans (Fig. 6). The presence of two dominants among lipotyphlans in the Holocene is also observed on materials from other caves of the Southern Sikhote-Alin (Omelko 2018).

Eleven species from the list (among them are dominant, codominant and subdominant) are found throughout the whole time from the Late Pleistocene to Holocene, nine of them reach the present day on this territory. Another eight species (there are subdominant and rare among them, only $C$. shantungensis is codominant) are absent only in a one layer. Thus, the dominant, codominant and subdominant species practically does not change during the considered period of time. Dominants not changed inside rodents and lipotyphlans. This is very different from other regions of Northern Eurasia, where one fauna is replaced by another, for example, in the Urals (e.g. Smirnov et al. 1990, 2014) and in Europe (e.g. Musil 1992; Markova et al. 2008; Aaris-Sørensen 2009; Ponomarev et al. 2013). Dominant species are eurytopic therefore
they are not indicative for vegetation, landscape and climate reconstructions. Certain non-numerous species (subdominant, rare and very rare) are added or disappear in faunal complexes in some periods. As a result, throughout the considered time, a fairly homogeneous fauna is observed.

When analyzing material from the south of the Far East, we have to operate with only two parameters: the relative number of species and the presence or absence of certain species. The absence of reference species or fauna, undoubtedly, complicates the dating of sediments. And the similarity of the Middle and Late Holocene faunas is such that they cannot be distinguished even by these parameters.

CONCLUSION

As a result of AMS $^{14}$C dating and analysis of the remains of small mammals from the Medvezhyi Klyk Cave, it was possible to divide the Holocene into Early, Middle and Late. The age of the Pleistocene sediments has been established only tentatively; additional studies are needed in order to obtain more accurate data.

Analysis of the small mammal finds on the one hand shows some of the features of the certain layers, as well as the Holocene and Pleistocene faunas as a whole. These differences are mainly in the ratio of the number of southern and northern species; lipotyphlans and rodents; dominant species within small mammals in whole. On the other hand, there are features of the fauna that do not change throughout the entire time under consideration (from the Late Pleistocene to the Late Holocene) this is the dominance of $C. rufocanus$ within rodents, $S. caecutiens$ within lipotyphlans; and relative stability composition of most number of the dominant, codominant and subdominant species. Apparently, such homogeneity of the fauna for a long time is characteristic for small mammals of the Southern Sikhote-Alin.

Thus result of analyzes displayed two criteria for the determination small mammal faunal complexes in the South Far East: relative number of species; and presence or absence of certain species. The absence of reference species, undoubtedly, complicates the dating of sediments. And the similarity of the Middle and Late Holocene faunas is such that they cannot be distinguished even by these parameters.

Since the data obtained are the first not only for the South Sikhote-Alin, but also for the whole of Northeast Asia, there is nothing to compare them with. New locations and findings will help to establish which features of the faunal complexes are individual for a given location, and which are common to the region. Taking into account the amount of material from the Medvezhyi Klyk Cave and the duration of sediment accumulation time, we assume that the main features of the faunal complexes are regional.

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APPENDIX 1. The list of taxa under “open nomenclature” with remarks

Lipotyphla: Soricidae

*Sorex* ex gr. *unguiculatus-isodon*

Remark: The distinction between *S. unguiculatus* and *S. isodon* is based on the cranial characteristics. Material from the Medvezhiy Klyk Cave represented by mandibles. Species determination with using of the mandibular characteristics has not yet been developed. Thus, for the analyses we used mixed material of *S. unguiculatus* and *S. isodon*.

*Crocidura* sp.

Remark: This taxon includes mandibles of white-toothed shrew (*Crocidurinae: Crocidura*) which are intermediate in size between *C. laisiura* and *C. shantungensis*. Because here the size is the main criterion for the species determination, all intermediate forms are distinguished as a possible separate species even though there is not enough material to describe them as new species.

Rodentia: Cricetidae

*Alexandromys* cf. *maximowiczii*

Remark: This taxon contained the isolated teeth that possibly belonged to *A. maximowiczii* (Schrenck, 1859) and *A. middendorfii* (Poljakov, 1881) accordingly previously results by Voyta et al. (2013).
**Alexandromys cf. mongolicus**

Remark: This taxon includes isolated teeth distinguishable smaller than teeth of middle-sized (A. maximowiczii, A. oeconomus (Pallas, 1776), A. middendorfii) and large-sized (A. fortis) species. These teeth differ from teeth A. mongolicus in the slightly large measures, and shape of an occlusal surface of m1 anteroconid.

**Alexandromys cf. oeconomus**

Remark: The most teeth with “economus-like” fusion between dentine islets of anteroconid cap and lingual triangle T5 included in this taxon. They displayed non-typical shape of m1 anteroconid, which possible can be identified as extinct morphotypes of the m1 of A. oeconomus (at least).

**Lagomorpha: Leporidae**

**Lepus spp.**

Remark: The remains of hares are doing not be identify to the species level. We have to take in account the presence of two species – L. timidus Linnaeus, 1758 and L. mandshuricus Radde, 1861 – which exist in the neighboring territories today.

**APPENDIX 2. A list of “northern” and “southern” taxa of Far East of Russia and adjacent territories**

**Northern taxa:**

Lipotyphla: Soricidae – Sorex isodon, S. caecutiens, S. minutissimus, S. tundrensis, S. daphaenodon, S. roboratus, and Neomys fodiens
Rodentia: Sciuridae – Tamias sibiricus, Pteromys volans, and Sciurus vulgaris
Rodentia: Muridae – Micromys minutus
Rodentia: Cricetidae – Myodes rutilus, Alexandromys maximowiczii, A. oeconomus, A. mongolicus, Lemmus amurensis, and Myopus schisticolor
Lagomorpha: Ochotonidae – Ochotona hyperborea

**Southern taxa:**

Lipotyphla: Talpidae – Mogera
Lipotyphla: Soricidae – Sorex mirabilis, S. gracilimus, S. unguiculatus, Crocidura lasiura, and C. shantungensis
Rodentia: Cricetidae – Alexandromys fortis, Myospalax psilurus, Tscherskia triton, and Craseomys rufocanus
Rodentia: Muridae – Apodemus peninsulae, A. agrarius, and Rattus norvegicus
Rodentia: Sminthidae – Sicista caudata