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# Changes in the fauna of bats in the south of the Russian Far East since the late Pleistocene

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ABSTRACT

The aim of the study was to identify changes in the fauna of bats during the late Pleistocene and Holocene in Southeast Russia, to utilize the results together with environmental data to disseminate modern analogues and reconstruct fossil environment. Fossil and subfossil lower jawbones of bats found in Medvezhyi Klyk cave deposits were identified by comparing morphology and surface features to modern species. The ecology and distribution of modern analogues are extrapolated to reconstruct the fossil environment. Fifteen bat species belonging to 6 genera were identified. Of the bat bone residues detected, the greatest number and the richest species composition formed approximately 40 ka BP in the lower layers of the cave sediments. In the layers formed in the Last Glacial Maximum period, the remains of only two species were found. The species diversity of bat bone residues gradually increased, reaching a maximum (7 species) in the layers corresponding to the optimum of the Holocene. At present, only single individuals of *Murina hilgendorfi* and *Plecotus ognevi* can occasionally be found hibernating in caves. Fossil remains of forest species are present in all layers of sediments, but occasionally, the remains of species of open landscapes not currently living in the territory appear as well. Studies have shown that during the warmer periods of the late Pleistocene and Holocene the species composition of bats in southern Primorye was expanded by southern thermophilic species that moved much farther north than previously thought. The presence of fauna of that time, including forest species that hunted mainly in open spaces, is indicative of the spread of savannah-like landscapes typical of the outskirts of the mammoth steppe. Changes in the species composition of bats occurring during the late Pleistocene and Holocene in southern Primorye adequately reflect the climate and landscape changes.



## 1. Introduction

The southern part of the Far Eastern region of Russia is characterized by increased diversity and the mixed nature of the fauna present, due to the peculiarities of geographical location, diversity of today's natural environment, and history of species expansion. The most significant changes in the distribution of animals relevant to the present occurred in the period of global climate changes in the late Pleistocene. There was a periodic offset of the area's fauna in the meridional direction on the eastern slopes of the Sikhote-Alin and throughout the entire Pleistocene refugium due to the humid climate (Krestov et al., 2009; Momohara et al., 2016). The unique features of that region may be elucidated by studying the history of faunal interchange directly in the local fossil record (Kim et al., 2015; Puzachenko et al., in press). The aim of this paper is to describe fossil and subfossil records of bat fauna in the Medvezhyi Klyk cave (43° 01′43 ″N, 133° 01′23″E) and, taking into account the environmental characteristics of particular species, to identify opportunities for the reconstruction of the paleogeographic condition and changes in the species composition of bats.

Of the 18 species of bats that presently live in the south of the Russian Far East (Tiunov, 2011), the majority are located on the southern or the northern limits. Fossil and subfossil findings of bats in the region are few. Most of these specimens are only defined to the genus (Ovodov, 1974, 1977). The most complete material was obtained from the Bliznetz cave location (Tiunov et al., 1992; Tiunov, 1997).

## 2. Materials and methods

The samples investigated in this study comprises subfossil and fossil teeth originating from the Medvezhyi Klyk cave deposits, situated in the central part of the Lozovyi mountain range (spurs of

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the mountain system of Sikhote-Alin, Primorskyi Krai, Russia) (see Fig. 1). The entrance (2.0 × 0.55 m) is located on the crest of the watershed in the northern part of the ridge at an altitude of 465 m above sea level. The cave is a vertical cavity of karst origin that is 17.4 m deep. The bottom of the cave is shaped like an elongated oval, 5.3 m in length and 1.3 m in width. The area of the excavation was 1.0 × 0.5 m. The 13 lithological layers recognized in the Medvezhyi Klyk cave compose a total excavation depth of 5.3 m (Panasenko and Tiunov, 2010; Tiunov et al., 2016). Sediments were selected during excavation with a conditional horizon of 5–10 cm. The sediment samples taken in the field were screen-washed with 1.0 mm mesh size for microvertebrates. Location layers 1, 2, 3, 5, 7, 9, 11, 12, and 13 were horizontal, and fossil material was not mixed. The material of the layers (6, 7, 8, 9) with an inclined position (see Fig. 2) has been merged in the analysis. According to the radiocarbon dating of a humerus of a brown bear found in layer 7 (1.08–1.18 m), the estimated age of this layer is 13,790–14,200 years (GIN-13479) (Tiunov et al., 2016). Estimates for the other layers range from 7000 to 45,000 years BP. The accumulation of the bone remains of bats is probably the result of both natural mortality of animals during hibernation, and the result of birds of prey making their nests in the proximal part of the cave. The fossil remains do not show major morphological and/or morphometric differences from living species.

Bat remains are housed in the collection of the Institute of Biology and Soil Science, Russian Academy of Sciences in Vladivostok.

## 3. Results and discussion

There were 4715 fragments of the axial skull and lower jaws of 15 species of bats found. In analysing the results, only the lower jaw fragments of bats, which prevailed in the cave sediments, were considered. From 3544 lower jaw fragments, 2990 were identified to match a species (see Table 1).

The greatest number and the richest species composition of bat bone remains were found in the lower layer (13–11) deposits at depths ranging from 5.4 m to 2.53 m. According to preliminary estimates, the age of these layers corresponds to the to the marine oxygen isotope stage (MIS) 3. The fragments of skulls and lower jaws found were identified as belonging to the following species: *Rhinolophus nippon, Plecotus ognevi, Myotis rufoniger, M. petax, M. macrodactylus, M. bombinus, M. frater, M. gracilis, M. ikonnikovi, Hypsugo alashanicus, Eptesicus nilssonii, Murina hilgendorfi, Murina ussuriensis, Murina* sp.

Deposits accumulated in layers 9–10 probably date to the Last Glacial Maximum, approximately 18–20 ka BP. These layers revealed a minimal amount of bat bone remains belonging to *Plecotus ognevi* and *Murina hilgendorfi*. Currently, these two species are the most common hibernating in the caves south of the Primorsky Territory, even in small, relatively cool caves (Tiunov, 1985).

Species diversity of bat bone residues in more recent layers gradually increased, reaching a maximum in layer 5, formed during the Holocene optimum of approximately 7 ka BP (from 0.49 m to 0.95 m). In this layer, the fossil remains of *Plecotus ognevi, M. bombinus, M. frater, M. ikonnikovi, Hypsugo alashanicus, Eptesicus pachyomus, and Murina hilgendorfi* were discovered.

Presently, single individuals of *Murina hilgendorfi* and *Plecotus ognevi* are only occasionally found hibernating in caves.

Bone remains of *Murina hilgendorfi* were the most numerous and were found in all deposit layers. The relative amount of their bone depositions in a layer varied from 40 to 100% (see Fig. 3). In a layer, the mean relative abundance was 66%. It is obvious that this species existed at least 40 thousand years ago, and is now present in all of the Primorye territory (Tiunov, 1985), dominating and hibernating in caves. Considering that this is a typical forest species, it is clear that it has a continuous presence in forest landscapes, even in times of climatic maxima.

*Plecotus ognevi* is also a forest species. With regards to the number of fossil remains in depositions before Last Glacial

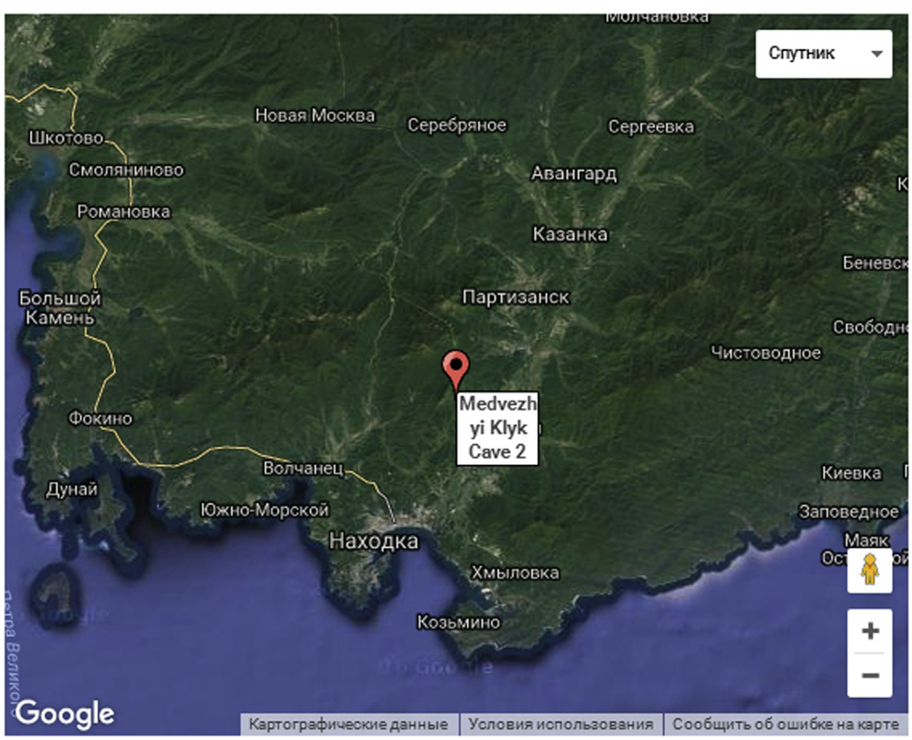


**Fig. 1.** Location of the Medvezhyi Klyk cave.

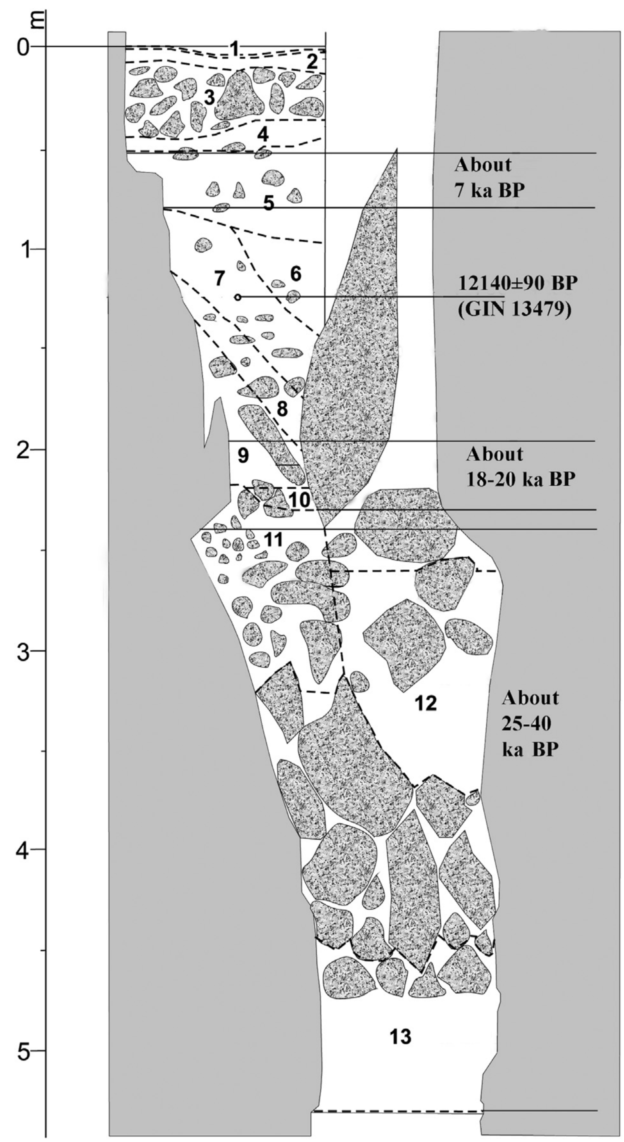


**Fig. 2.** Cross-section of the pit in Medvezhyi Klyk cave.

Maximum and after the Holocene optimum, this species is second to *Murina hilgendorfi*. The fossil remains of a species of the genus *Myotis* were also periodically found in the depositions. All 6 species of *Myotis* occurring now in the Primorye and found in the cave deposits are forest species. Their bone remains are entirely absent only in the uppermost layers of the deposits, and in the layers that were formed during the Last Glacial Maximum. Their absence in the upper layers of the deposits is probably due to changes in the morphology of the cave. The presence of a high number of large stones in layer 3 is apparently due to the collapse of the grotto at the entrance. The changed microclimate of the cave does not meet the hibernation conditions of species in this genus. The modern cave morphology also does not meet the conditions for living birds of prey.

*Eptesicus nilssonii* is also a forest species and is the most common bat species in the north of the Russian Far East. In Primorye, this species is known to the area only from a single catch in the northern region in the mid-1960s. Before and after the Last Glacial Maximum, this species had the second or third highest number of bone remains in the cave sediments. Above the level of the Last Glacial Maximum, the relative amount of bone remains of *Eptesicus nilssonii* gradually reduced.

All *Murina* species are forest species. *Murina* sp. have also been previously found in the lower layers of the Bliznetz cave deposits (Tiunov, 1997). Judging by the size of the lower jaw, this species occupies an intermediate position between *Murina hilgendorfi* and the small species tubular-billed aurata group.

In addition to forest species in cave sediments, bone remains of thermophilic species of bats that live in open and semi-open landscapes were found, such as *Rhinolophus nippon*, *Myotis rufoniger*, *Hypsugo alashanicus* and *Eptesicus pachyomus*.

Bone remains of *Eptesicus pachyomus* in the Russian Far East were found for the first time. The nearest locality where this species is present is in the northeastern province of Heilongjiang in China (Smith and Xie, 2008). Previously, this species identified as *E. serotinus*. *E. serotinus* is now regarded a species occurring in Europe and in western and central Asia, while in southern and eastern Asia, it is replaced by a sister species, *E. pachyomus*, and in southern Mediterranean by *E. isabellinus* (Juste et al., 2013).

It is important to note that from the Last Glacial Maximum to the maximum of the Holocene optimum, the number of bone remains of *Hypsugo alashanicus* is second after *Murina hilgendorfi*. Currently, this species is found in Primorye only in the summer and behaves like a typical synanthropic species. However, we have found a significant amount of this species in caves in the provinces of Heilongjiang and Jilin in northeastern China.

*Rhinolophus nippon* and *Myotis rufoniger* are not currently found in the Far East of Russia. Their nearest habitats are located in Northeast China's Heilongjiang Province and the Korean Peninsula (Zhang et al., 2009; Csorba et al., 2014). Previously, fossil remains of these two species were found in Holocene sediments in the Bliznetz cave (Tiunov et al., 1992), located 2 km away in a straight line from the Medvezhyi Klyk cave. Bone remains of *M. rufoniger* were previously identified as belonging to *M. formosus*, dwelling farther south. These two species are closely related, and the independence of the species was only confirmed in recent years (Csorba et al., 2014). Recent studies have also shown, that the contemporarily considered widely distributed bat *R. ferrumequinum* comprises two species, the West Palaearctic *R. ferrumequinum* and East Palaearctic and Oriental *R. nippon* Temminck, 1835 (Benda and Vallo, 2012).

The absence of deposits of *Rhinolophus nippon* and *Myotis rufoniger* fossil remains in the layers corresponding to the optimum of the Holocene can be attributed to the structural features of the Medvezhyi Klyk cave. Even with the probable previous presence of a grotto at the entrance, which struck this cave later than the Bliznetz caves, it is not an optimal place for bat hibernation.

It is thought that the south of the Russian Far East remained relatively mild during the Last Glacial Maximum compared to the northern regions. Different forest vegetation had been present in all periods of the late Pleistocene and Holocene (Korotky et al., 2005). This is also evidenced by the presence of the cave deposits of the fossil remains of *Murina hilgendorfi* in all layers. At the same time, it seemed that signs of significant afforestation in the area appear only approximately 900–800 years ago, before the dominant type of vegetation was forest-steppe (Verkhovskaya, 1990). A wider distribution of the open landscapes in the south of the Primorye Territory in the late Pleistocene and Holocene were also evidenced by 5 species of grey voles found in all layers of sediments of the cave (now one species lives there) (Voyta et al., 2011) and a report of zokor fossil remains at locations currently in the typical forest zone of southern Primorye (Tiunov, 2014).

Open landscapes were likely not dominant but were widespread, at least in the valleys and the southern slopes of the mountains. Despite the relatively milder temperatures, species distribution would still have been affected by the climatic

**Table 1**
The number of identified bat lower jaws in lithological layers of the Medvezhyi Klyk cave deposits.

| Species | Lithological layers | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 3-4 | 5 | 5-6-7 | 7 | 6-7 | 6-7-8 | 7-8-9 | 8-9 | 9 | 9-10 | 11 | 12 | 13 |
| *Rhinolophus nippon* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 14 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0.3 | 2.3 |
| *Myotis rufoniger* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 2 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 1.1 | 0.3 |
| *Myotis petax* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 2 | 7 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.0 | 0.6 | 1.1 |
| *Myotis macrodactylus* | 0 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 6 | 6 | 2 |
| | 0 | 0 | 0.6 | 2.5 | 0 | 0 | 3.4 | 1.3 | 0 | 2.2 | 0 | 0 | 0 | 1.0 | 1.7 | 0.3 |
| *Myotis bombinus* | 0 | 0 | 2 | 1 | 5 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 13 | 2 | 10 |
| | 0 | 0 | 0.6 | 1.2 | 6.2 | 0 | 0 | 0 | 0 | 4.4 | 0 | 0 | 0 | 2.2 | 0.6 | 1.6 |
| *Myotis gracilis* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 27 | 8 | 17 |
| | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4.6 | 2.2 | 2.8 |
| *Myotis ikonnikovi* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 18 | 4 | 20 |
| | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 6.7 | 0 | 0 | 3.1 | 1.1 | 3.2 |
| *Myotis frater* | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 6 |
| | 0 | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0.6 | 1.0 |
| *Plecotus ognevi* | 4 | 3 | 42 | 14 | 80 | 3 | 4 | 5 | 2 | 5 | 4 | 0 | 2 | 158 | 88 | 162 |
| | 22.2 | 15.8 | 14.6 | 17.3 | 11.2 | 3.3 | 13.8 | 6.6 | 5.7 | 11.1 | 26.7 | 0 | 22.2 | 26.8 | 24.6 | 26.3 |
| *Hypsugo alashanicus* | 2 | 0 | 20 | 8 | 132 | 16 | 8 | 17 | 3 | 9 | 1 | 0 | 0 | 10 | 19 | 3 |
| | 11.1 | 0 | 7.0 | 9.9 | 18.4 | 17.8 | 27.6 | 22.4 | 8.6 | 20.0 | 6.7 | 0 | 0 | 1.7 | 5.3 | 0.5 |
| *Amblyotus nilssonii* | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 10 | 2 | 2 | 3 | 0 | 0 | 57 | 20 | 69 |
| | 0 | 0 | 0.6 | 1.2 | 0 | 1.1 | 3.4 | 13.2 | 5.7 | 4.4 | 20.0 | 0 | 0 | 9.7 | 5.6 | 11.2 |
| *Eptesicus pachyomus* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Murina ussuriensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 |
| *Murina* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0.6 |
| *Murina hilgendorfi* | 12 | 16 | 219 | 55 | 493 | 70 | 15 | 43 | 28 | 26 | 6 | 7 | 7 | 284 | 201 | 299 |
| | 66.7 | 84.2 | 76.3 | 67.9 | 68.8 | 77.8 | 51.7 | 56.6 | 80.0 | 57.8 | 40.0 | 100 | 77.8 | 48.2 | 56.1 | 48.5 |
| Number of lower jaws identified to species | 18 | 19 | 287 | 81 | 716 | 90 | 29 | 76 | 35 | 45 | 15 | 7 | 9 | 589 | 358 | 616 |
| Number of non- identified lower jaws | 5 | 0 | 24 | 3 | 118 | 15 | 4 | 10 | 10 | 13 | 11 | 16 | 8 | 98 | 59 | 160 |
| Total | 23 | 19 | 311 | 84 | 834 | 105 | 33 | 86 | 45 | 58 | 26 | 23 | 17 | 687 | 417 | 776 |

Upper line – the number of species lower jaw in a layer; lower line – proportion of the total number of certain species lower jaws in a layer.

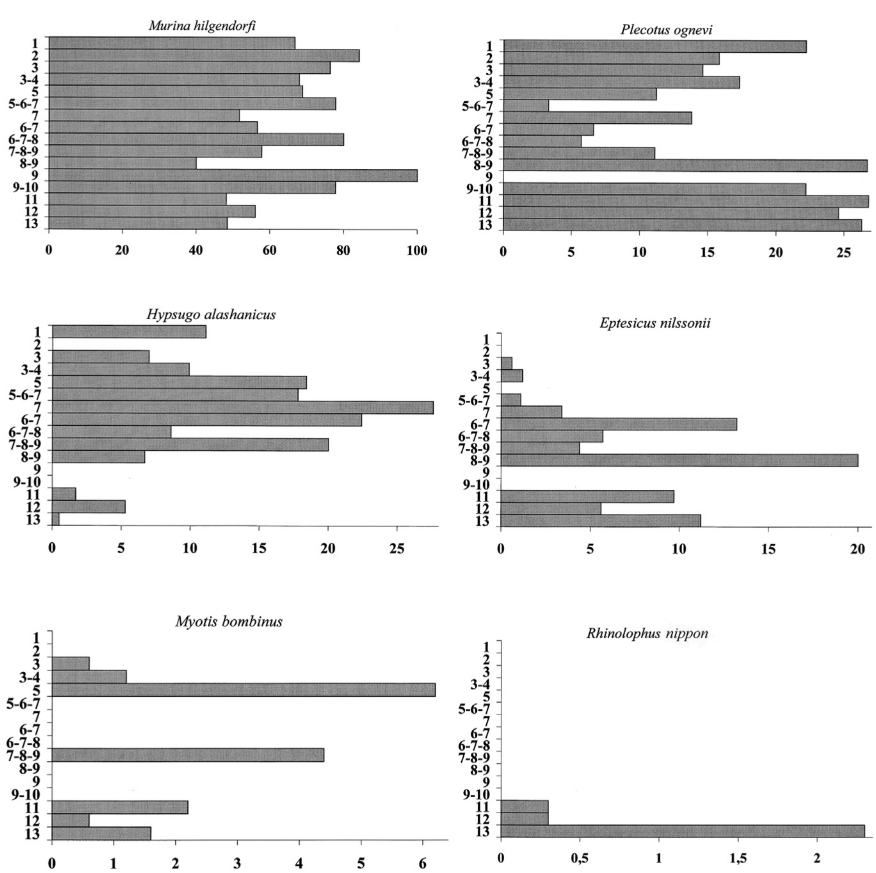


**Fig. 3.** Distribution of bat remains (lower jaws) in Medvezhyi Klyk cave deposits. Vertical – lithological layers; horizontal – the percentage remains in every layer.

oscillations but would have had the potential to persist in pockets of relatively stable micro-ecosystems during glacial periods (Krestov et al., 2009; Flanders et al., 2011).

Thus, during the warmer periods of the late Pleistocene and Holocene, bat species composition in southern Primorye expanded due to southern thermophilic species that moved much further north than previously thought (Tong, 2007). The presence of fauna at that time that were forest species and species that hunt mainly in open spaces shows the distribution of savannah-like landscapes typical of the outskirts of the mammoth steppe. Changes in the species composition of bats occurring during the late Pleistocene and Holocene in southern Primorye adequately reflect the climate and landscape changes.

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