Late Quaternary shrews (Mammalia: Soricomorpha) from Priamurye according to data from Koridornaya Cave

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Research Article

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Abstract

During excavations in Koridornaya Cave (Pompeevskiy Ridge, Jewish Autonomous Oblast, Russia) in 2017–2018, for the first time in Priamurye (Outer Manchuria), numerous bone remains of Late Quaternary mammals were recovered. The purpose of this work was to determine the species list of shrews of that time and to estimate their abundance. In the deposits of Koridornaya Cave, 890 cranial remains of shrews (Soricidae) were found belonging to 11 species from four genera: Sorex, Neomys, Berenemdia, and Crocidura. The formation time of the deposits corresponds to the Karginsky interstadial (MIS 3), and the upper part of the deposits contains Holocene (MIS 1) material. Pleistocene communities of shrews of the Pompeevskiy Ridge included modern inhabitants of this territory (S. caecutiens, S. isodon, S. unguiculatus, S. daphaenodon, S. roboratus, S. minutissimus, N. fodiens, and C. lasiura) and S. tundrensis; C. ex gr. suaveolens appeared in the Holocene. Sorex gracilissimus, which currently lives here, either was absent in Late Pleistocene communities or was extremely rare. The dominant species in the communities of that time was S. caecutiens, just as in the Southern Sikhote-Alin (Late Pleistocene to Holocene) and in most of modern communities of shrews in the south of the Russian Far East.

Introduction

In recent years, a lot of new data were obtained about mammals of the Russian Far East from the second half of the Late Pleistocene and Holocene. Rodent species new to science have been described: Petaturista tetyukhensis Tiunov et Gimranov, 2020 (Tiunov & Gimranov, 2020) and Mimomys chandolensis Tiunov, Golenishchev et Volyta, 2016 (Tiunov et al., 2016), as has a genus of pikas new to science (Tonomochota Tiunov et Gusev, 2021), which includes three species: T. khasanensis Tiunov et Gusev, 2021, T. sikhotana Tiunov et Gusev, 2021d major Tiunov et Gusev, 2021 (Tiunov & Gusev, 2021). It has become known that in the Late Pleistocene, the territory of modern Primorsky Krai was inhabited by Urocitellus undulatus (Pallas, 1778) (Tiunov et al., 2022), Lemmus amurensis Vinogradov, 1924 (Tiunov & Panasenko, 2010), Rhinolophus nippon Temminck, 1835, Myotis rufoniger Tomes, 1858, and Eptesicus pachyomus Tomes, 1857 (Tiunov, 2022). Myospalax psilurus (Milne-Edwards, 1874) was substantially more widespread (Tiunov & Vinokurova, 2016), as were voles of the genus Alexandromys Ognev, 1914 (Voyta et al., 2019), Myopus schisticolor Miller, 1910 (Omelko et al., 2020), Tscherskia triton (de Winton, 1899), Cricetulus barabensis (Pallas, 1773) (Omelko et al., 2020; Alekseeva, 1986), and Ochotona hyperborea (Pallas, 1811) (Tiunov, 2022).

It has been established that the species profile of shrews during the second half of the Late Pleistocene and Holocene in the Southern Sikhote-Alin did not change much; 12 species have been found, and three of them — Sorex roboratus Hullister, 1913, S. daphaenodon Thomas, 1907, and S. tundrensis Merriam, 1900 — had been more widespread up until the Middle Holocene than they are at present (Nesterenko et al., 2002; Panasenko & Tiunov, 2010; Omelko et al., 2020). During periods of climate cooling, some heat-loving species disappeared from this territory and later repopulated it (Omelko et al., 2020).

Koridornaya Cave is the first Late Quaternary zoogenic site of mammalian remains in Priamurye. As a result of excavation of loose deposits, tens of thousands of bone remains of various animals have been recovered: fishes, amphibians, reptiles, birds, and mammals, which are represented by chiropters, soricomorphs, lagomorphs, rodents, carnivores, artiodactyls, and perissodactyls. The bulk of this material is still being processed, and there are few published data (Tiunov & Vinokurova, 2019; Gusev & Tiunov, 2021; Tiunov & Gusev, 2021; Volyta et al., 2021, 2022).

Any results obtained about Late Quaternary fauna, including data on shrews, will be new for this territory. Shrews from Koridornaya Cave are represented by numerous remains, which allow for correct comparisons.

The purpose of this work was to determine the species profile of shrews by means of remains in the deposits from Koridornaya Cave and to assess these shrews’ abundance levels in the past.

Koridornaya Cave

Regional settings

Koridornaya Cave is located in Jewish Autonomous Oblast (Far East of Russia) in the southern part of the Pompeevskiy Ridge (Fig. 1), on the right side of the Stolbukha River (N 48°00’, E 130°59’). The Pompeevskiy Ridge is a part of the Khabing-Bureninsky Mountain System, located in the northwest of Jewish Autonomous Oblast. The height of the Pompeevskiy Ridge is modest and increases from south to north (from the Sinyukha Mountain [679 m] to the Tsar Peak [1013 m]). The south and southeast part of the Pompeevskiy Ridge rise above the swampy Amur River lowland (Fig. 1C), and numerous tributaries of the Amur River (e.g., Samara, Malaya Samarka, Osinovka, Kulemnaya, Lugovaya, and Mami) flow down from this part of the ridge. Southern slopes of the ridge are covered with broad-leaved monsoon-type forests of oak, linden, maple, and cork tree; coniferous trees stay more numerous on higher and more northern slopes.

Description

Koridornaya Cave is a relic source cave of karst corrosion–erosion origin (Bersenev, 1989). The cave is a natural monument of regional importance. The cave entrance is at 230 m above sea level and is exposed to the south-southeast. It is located at the base of a cliff wall and is a small grotto 1.7 m high and 3 m wide. The main gallery of the cave and a smaller side passage originate in this grotto (Fig. 2A).

The length of the main gallery of the cave is 38 m. It begins with a smooth descent 15 m long, the bottom is covered with stones of various sizes, and then the floor smoothly rises for 23 m (Fig. 2B); at this site, it is covered with a layer of clay. At the end of the gallery, there is a small ledge.

Material and methods
Excavation in Koridornaya Cave

Paleontological excavations were carried out in 2017–2018 under the supervision of Prof. M.P. Tiunov, PhD. The pit is situated in the lowest part of the cave floor at a distance of 16 m from the entrance. The initial pit area was $1.7 \times 1.1$ m; starting from a depth of 0.35 m, the pit area diminished to $1.2 \times 1.1$ m, and from 0.8 m depth down, the pit area was $0.8 \times 1.1$ m (Fig. 2C). Deposits were excavated in layers of 0.1 m thickness. Extracted soil was washed in sieves with a mesh size of 1.0 mm.

The pit depth is 2.1 m (Fig. 2C). Five layers were distinguished based on the color and characteristics of the rock at the excavation site.

Here is a brief description of lithological layers:

1. Layer 1: 0–0.2 m depth, light-brown medium loam;
2. Layer 2: 0.2–0.6 m, brownish-ocherous heavy loam;
3. Layer 3: 0.6–1.2 m, brown heavy loam;
4. Layer 4: 1.2–2.0 m, yellowish-brown clay;
5. Layer 5: from 1.5 m depth down, red crumbly clay, many small well-rounded pebbles, does not contain bones.

Radiocarbon dating

There are two $^{14}$C-dates for deposits of Koridornaya Cave (Table 1). First date ($49,435$ BP; IGANAMS-7598) was determined in Research Resource Centre of the Laboratory of Radiocarbon Dating and Electronic Microscopy of the Institute of Geography, Russian Academy of Sciences (Moscow, Russia), and the Centre for Applied Isotope Studies of the University of Georgia (CAIS; Georgia, USA). Voyta et al. (2021) published it. Kusliy et al. (2020) published second date. However, authors don't enter information about laboratory, where it date was determined, reference number, etc.

<table>
<thead>
<tr>
<th>No.</th>
<th>Depth, m</th>
<th>Layer</th>
<th>Dating bone species</th>
<th>Reference no.</th>
<th>$^{14}$C dates</th>
<th>Calibrated dates ± σ, cal BP</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>1.1–1.2</td>
<td>3</td>
<td><em>Capriolus pygargus</em></td>
<td>IGANAMS-7598</td>
<td>49,435 BP</td>
<td>53.318 ± 941</td>
</tr>
<tr>
<td>2.</td>
<td>1.6–1.7</td>
<td>4</td>
<td><em>Equus ferus</em></td>
<td></td>
<td>50,000 BCE</td>
<td>53.497 ± 747</td>
</tr>
</tbody>
</table>

We calibrate this dates with OxCal 4.4 program software using the IntCal13 calibration curve (Reimer et al., 2013). Both dates is out of range. Meanings of dates are similar and consist from $52430$ cal. BP to $54312$ cal. BP.

Material

In the deposits of Koridornaya Cave, 890 cranial remains of shrews were found represented by mandibles and their fragments with or without teeth, by skull fragments with or without teeth, and by isolated teeth. There were 725 mandibular remains and 165 maxillary remains. The distribution of shrew remains within the excavation site was uneven. The largest number of finds was made at a depth of 90–170 cm (Fig. 3). The number of finds is not proportional to the excavation area, and the largest number of finds comes from a small area.

The material is kept in the collection of the Laboratory of Theriology at the Federal Scientific Center of the East Asia Terrestrial Biodiversity of the Far Eastern Branch of the Russian Academy of Sciences.

Taxon identification of the bone remains

The mandibles was used for the species list of shrews. For this purpose, we employed reference samples of modern and fossil Soricidae from the Far East that are stored in the collection of the Laboratory of Theriology at the FSC of Biodiversity FEB RAS. We analyzed the traits that we have previously chosen and tested for shrews from the Far East (Panasenko, 2011; Panasenko, 2012a, 2012b).

*Sorex isodon* Turov, 1924, and *S. unguiculatus* Dobson, 1890, currently inhabit the territory of the Pompevskiy Ridge (Nesterenko, 1999). To date, no morphological or morphometric traits have been identified that could distinguish these species by the mandible, as reported earlier (Dokuchaev et al., 2010; Panasenko, 2011a; Voyta & Panasenko, 2011). Despite a claim by Rzebik-Kowalska (2007: 32) that the entoconid crest of lower molars of *S. isodon* "... has the shape of a cusp instead of a typical crest," we see this feature in *S. unguiculatus*. Therefore, all mandibles hypothetically belonging to both species were identified in open nomenclature terms and marks as *S. ex gr. unguiculatus-isodon*.

Two species of white-toothed shrews currently live in the Far East: large-sized *Crocidura lasiura* Dobson, 1890, and small-sized *C. shantungensis* Miller, 1901. Between these species, the mandible differs well in size, and its measurements (such as mandibular length, descending-ramus height, the height of the coronoid process, the height of the ascending ramus, and articulat-process length) do not overlap; unfortunately, morphotypic traits of teeth and of the mandibular bone vary widely within both species and are not suitable for the diagnosis (Panasenko, 2011a, b). Among the shrew mandibles found in the deposits of Koridornaya Cave, there were larger and smaller specimens. All large mandibles were assigned by us to *C. lasiura*. 
Mandibles of the small-sized white-toothed shrew could not be identified to the species level for several reasons. First, the specimens from Koridornaya Cave are damaged. Second, so far, no significant differences in the mandible have been detected among species of the *C. suaveolens* species group, which includes *C. suaveolens* (Pallas, 1811) and *C. shantungensis* (Miller, 1901). At present, small-sized shrews do not inhabit the Pompeevskiy Ridge. The boundary of the geographic range of *C. shantungensis* is the closest to Koridornaya Cave, and the recovered remains are most likely affiliated with this species. Nonetheless, it cannot be ruled out completely that the finds belong to *C. suaveolens*, although the nearest sites of its modern finds are located much farther away. Due to this uncertainty, in this work, we used the open nomenclature, assigning the found specimens of small-sized white-toothed shrews to the species group *C. suaveolens* and designated it as *C. ex gr. suaveolens*.

Upper tooth row features, with the upper antemolar row being the most notable among them, were not used for the species identification owing to the bad condition of the material, e.g., incomplete rows and scarce remains.

Open nomenclature used according to Sigonivi et al. (2016) and Barskov et al. (2004).

**Results**

**Taphonomic factors of accumulation of shrew remains**

There are not many intact unfragmented mandibles (descending and ascending rami being together) in the deposits of Koridornaya Cave: 4–13.8% in various layers. The fragmentation of the bones could be caused by chewing by predatory mammals or crushing by the beak of birds of prey. The highest fragmentation of bones is typical for prey of predatory mammals, and the lowest for nocturnal birds of prey; an intermediate position is occupied by victims of diurnal birds of prey (Andrews, 1990). Thus, judging by the fragmentation of the shrews’ bones, they have mainly been brought here by predators. In this regard, traces of digestion were detected only in half of all mandibles of shrews (43.5–51%). In other words, a second half of the bones was either not subjected to digestion processes or was digested slightly, which cannot be determined by means of external traits of the shrew mandibles (Fernandes-Jalvo et al., 2016). It is known that not all prey bones are digested by birds of prey, especially by nocturnal birds, whose digestion index does not exceed 50–60% (Fernandes-Jalvo et al., 2016). The highest digestion index is characteristic of mammals and reaches 100%; however, it is lower in mustelids (in particular, in the European pine marten *Martes martes*) and viverids and can be ~20% (Andrews, 1990; Fernandes-Jalvo et al., 2016). Thus, taking into account the high degree of fragmentation and the moderate extent of digestion of the bone remains, it can be hypothesized that the bulk of the shrew bones has been brought into Koridornaya Cave by mustelids. Nevertheless, one cannot completely rule out the activity of birds of prey and shrews’ behavior, namely, they could enter the cave on their own and die there.

**The shrew species list**

Of 725 mandibles, 687 were identified to the species levels, and 38 to the genus level (*Sorex* spp.). In total, 11 species of shrews from four genera were determined (Table 2): seven from the genus *Sorex* Linnaeus, 1758 (*S. caecutiens* Laxmann, 1788, *S. roboratus* Hollister, 1913, *S. daphaenodon* Thomas, 1907, *S. tundrensis* Merriam, 1900, *S. minutissimus* Zimmermann, 1780, and *S. ex gr. unguiculatus-isodon*), one from the genus *Neomys* Kaup, 1829 [*N. fodiens* (Pennant, 1771)], one from the genus *Beremendia* Koromos, 1934 (*B. minor* Rzebik-Kowalska, 1976), and two from the genus *Crocidura* Wagler, 1832 (*C. lasiura* and *C. ex gr. suaveolens*).
Table 2

<table>
<thead>
<tr>
<th>Depth, m</th>
<th>Layer</th>
<th>Number of mandibles</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>S. caecutiens</td>
</tr>
<tr>
<td>0-0.1</td>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>0.1-0.2</td>
<td></td>
<td>9</td>
</tr>
<tr>
<td>0.2-0.3</td>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td>0.3-0.4</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>0.4-0.5</td>
<td></td>
<td>11</td>
</tr>
<tr>
<td>0.5-0.6</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>0.6-0.7</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>0.7-0.8</td>
<td></td>
<td>18</td>
</tr>
<tr>
<td>0.8-0.9</td>
<td></td>
<td>14</td>
</tr>
<tr>
<td>0.9-1.0</td>
<td></td>
<td>26</td>
</tr>
<tr>
<td>1.0-1.1</td>
<td></td>
<td>48</td>
</tr>
<tr>
<td>1.1-1.2</td>
<td></td>
<td>35</td>
</tr>
<tr>
<td>1.2-1.3</td>
<td>4</td>
<td>22</td>
</tr>
<tr>
<td>1.3-1.4</td>
<td></td>
<td>30</td>
</tr>
<tr>
<td>1.4-1.5</td>
<td></td>
<td>43</td>
</tr>
<tr>
<td>1.5-1.6</td>
<td></td>
<td>36</td>
</tr>
<tr>
<td>1.6-1.7</td>
<td></td>
<td>30</td>
</tr>
<tr>
<td>1.7-1.8</td>
<td></td>
<td>26</td>
</tr>
<tr>
<td>1.8-1.9</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>1.9-2.0</td>
<td></td>
<td>7</td>
</tr>
<tr>
<td>2.0-2.1</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>408</td>
</tr>
</tbody>
</table>

Geometric morphometry analysis of upper mandibles of *C. lasiura* from this locality revealed the presence of two deviating specimens, which were assigned to *Crocidura* cf. *lasiura* (Voyta et al., 2022). There were no deviating specimens among the mandibles.

**Discussion**

**Fauna of Late Quaternary shrews**
The species list of Late Quaternary shrews from the Pompeevskiy Ridge is similar to the modern one (Table 3). Currently, nine species of shrews occur here: seven brown-toothed shrews (S. caecutiens, S. isodon, S. unguiculatus, S. roboratus, S. daphaenodon, S. minutissimus, and S. gracillimus), a brown-toothed water shrew (N. fodiens), and one species of white-toothed shrew (C. lasiura) (Nesterenko, 1999). The deposits contain remains of these species and of three more shrew species that do not currently live here: S. tundrensis, C. ex gr. Suaveolens, and extinct B. minor. No remains of S. gracillimus were found.

### Table 3

<table>
<thead>
<tr>
<th>Taxones</th>
<th>Present time</th>
<th>In the deposits of the Koridornaya Cave</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>S. caecutiens</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>S. ex gr. unguiculatus-isodon</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>S. unguiculatus</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>S. isodon</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>S. daphaenodon</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>S. roboratus</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>S. minutissimus</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>S. tundrensis</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>S. gracillimus</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>N. fodiens</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>B. minor</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>C. lasiura</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>C. ex gr. suaveolens</td>
<td>-</td>
<td>+</td>
</tr>
</tbody>
</table>

At present, the geographic range of S. tundrensis is interrupted here (Nesterenko, 1999). In the cave deposits, the remains of this species occur in eight samples at a depth of 1.8–0.6 m (layers 3 and 4). Above 0.6 m, in layers 2 and 1, the remains of this species are absent. In the southern Sikhote-Alin, it had lived until the Middle Holocene (Omelko et al., 2020).

Two mandible fragments of Crocidura ex gr. suaveolens were recovered in upper deposit layers at a depth of 0.0–0.2 m (layer 1). Both are light-colored, seeming to be preserved from the Holocene. Currently, small-sized white-toothed shrews do not live near this cave. C. shantungensis occurs in the south of the Russian Far East; it is not seen to the north of Primorsky Krai (Nesterenko, 1999). On the Chinese side, it occurs in the upper and middle reaches of the Amur River and resides on southern spurs of the Lesser Khingan; the boundary of its geographic range lies along the Amur River (Hoffmann et al., 2008). It is likely that during the formation of layer 1, it is this species that lived in the vicinity of this cave, i.e., it occurred along both banks of the Amur. Nonetheless, this expansion of the range did not last long judging by the finds (only from the Holocene). The modern range of C. suaveolens is located to the west of the study area, and the nearest finds from Western Mongolia are known (Bannikova et al., 2009), but its wider dispersal to the east during the Holocene cannot be ruled out.

In layer 3 at 0.6–0.7 m depth, one mandible of Beremendia minor (FSC RJARVKorC-01) was found. Previously, B. minor was registered only in five European localities—four of which were of Pliocene age (RzebikKowalska, 1976; Reumer, 1984; Dahlmann & Storch, 1996) and one of Early Pleistocene age (Botka & Mészáros, 2014) — and at three localities in Asia: two from the Pliocene and one from the Early Pleistocene (Zazhigin & Voyta, 2019). In Koridornaya Cave, B. minor was found in Late Pleistocene deposits. The question of the age of this find was already discussed, as was the possibility of its existence here until the Late Pleistocene inclusively (Voyta et al., 2021). Based on the shape analysis of the mandible by geometric morphometry methods and analysis of its similarity to the shape of other finds from this species, it was concluded that this find is of the same age as the others, that is, it is considerably older than the second half of the Late Pleistocene.

The state of preservation of the B. minor mandible from Koridornaya Cave does not differ from that of other finds from this cave. Its anterior part with incisors is broken off, as is the angular process (Fig. 4). White enamel is degraded on all teeth on the buccal side, probably as a consequence of digestion by a predator. According to the classification of Fernandes-Jalvo et al. (2016), this is a high degree of digestion. It is possible that the mechanical damage (the breaking off of the mandible's anterior part and of the angular process) was also inflicted by a predator. The color of the bone is black, which is not a unique feature of this find; in the deposits of Koridornaya Cave, 22% of the finds were black. In terms of the state of preservation, the lower mandible of B. minor is similar to that of other remains of shrews from these deposits and does not show any unique types of damage. Thus, the damage to (and organoleptic characteristics of) this find do not provide additional information about its age. So far, the question of geological age of this find has not been resolved. Within the framework of this study, B. minor is not considered a part of Late Pleistocene fauna of Far Eastern shrews.

No remains of S. gracillimus, which occurs here today, were detected in the deposits. Apparently, this species did not reside here in the Late Pleistocene and settled on this territory later, or it was rare and did not get into the deposits.

### Stratigraphy of the deposits in Koridornaya Cave
Two consistent radiocarbon dates (52430–54312 cal BC) were determined for the Koridomaya Cave deposits. The time point of 50 ky ago is the boundary between the cold Early Würm and the warm Middle Würm, or the Karginsky interstadial (= the Chemoruchinsky stage for Far Eastern Region according Korotky et al., 2005). The same time point is the beginning of the MIS 3 oxygen isotope stage. The interstadial on this territory is characterized by a climate warmer than the present one. It is thought that south of 60° of North latitude at that time, the climate was influenced by local factors, and for this reason, refugia with certain microclimatic features formed, and forest formations arose with the participation of broad-leaved species (Pushkar et al., 2017). At this time point, the permafrost, which was common here in the early Würm, disappeared (Jin et al., 2020). Karginsky time continued until ~ 26 thousand years ago. Within the interstadial, several phases of relative cooling and warming of the climate can be distinguished (Korotky et al., 2005).

The deposits in question contain at different depths remains of heat-loving species of small mammals (Rattus norvegicus, Cricetulus barabensis, Micromys minutus; and Crocidura lasiura), suggesting that the deposits in Koridomaya Cave formed during the warm period of the Karginsky interstadial from approximately 50 to 26 thousand years ago.

Layers 3 and 4 are characterized by a similar ratio of seven shrew species (S. caecutiens, S. roboratus, S. daphaenodon, S. minutissimus, S. tundrensis, S. ex gr. unguiculatus-isodon, and C. lasiura; Fig. 5). This result implies that they came into being under approximately the same conditions and at the same time. Nonetheless, there are slight differences between them: in layer 4, there are more remains of S. roboratus; whereas in layer 3, there are more remains of C. lasiura. Besides, remains of N. fodiens and B. minor were registered in layer 3.

Layer 2 differs from layers 3 and 4 mainly by an appreciable increase in the number of C. lasiura remains (Fig. 5); here their number reaches a maximum and amounts to 19%.

In some cases, the actuopalaeontological method is used to reconstruct paleolandscapes, which estimates the confinement of species to certain landscapes in modern times. On the other hand, the subdivision of shrews into ecological groups (as is customary for rodents for example) poses difficulties. The reason is that types of open spaces can be distinguished only tentatively. We assign S. roboratus, S. daphaenodon, S. tundrensis, and white-toothed shrews to these types because open landscapes are currently their optimal habitats in the south of the Far East (Nesterenko, 1999). In other geographic regions, they can also live in forests (mainly broad-leaved and small-leaved broken forests).

In total, the number of remains of these species in the deposits of Koridomaya Cave is stable across the layers: 26–28%. In this regard, it can be assumed that there were open spaces on the territories adjacent to the cave throughout the entire period of the deposits’ formation. The presence of remains of open-space rodents (Myospalax psilurus, Cricetulus barabensis, Rattus norvegicus, and Micromys minutus) confirms this notion.

Forest species of shrews, which currently reside only in forests, can be distinguished quite specifically. Among the shrews identified in the Koridomaya Cave deposits, S. isodon and S. unguiculatus are forest species. The amount of their remains in the deposits ranges from 9–17%. These species can inhabit various types of forests, and their presence indicates that throughout the entire period in question, forests were present in the vicinity of the cave along with open spaces. The presence of forest vegetation is consistent with paleogeographic reconstructions (Pushkar et al., 2017) and with the presence of such forest rodent species as Sciurus vulgaris, Pteromys volans, Tamias sibiricus, and Myodes rutilus. Evidently, open spaces of various types in Priamurye were common in river valleys, lowlands, and possibly on low elements of relief, whereas forests were confined to higher relief elements. In Koridomaya Cave, the number of remains and taxonomic diversity of species tentatively classified as open-space taxa are greater than those of forest species, implying the existence of conditions more optimal for the former. More specific conclusions, however, can be drawn when all groups of mammals are taken into account, primarily rodents.

S. caecutiens can be categorized as a eurytopic species, because currently in the south of the Far East, it occupies almost all habitats and is predominant among shrews almost everywhere. S. minutissimus is also a eurytopic species, inhabiting formations of various types, but unlike S. caecutiens, it is rare in modern shrew communities.

A relative increase in the number of remains of C. lasiura in layer 2 compared to the other layers can be explained by expansion of open spaces. Here, there are also two teeth of Myospalax psilurus at depths of 0.3–0.4 and 0.5–0.6 m (Tiunov & Vinokurova, 2019). Another tooth of M. psilurus was discovered lower, in layer 3 at a depth of 0.7–0.8 m. Probably, during the formation of this layer, open spaces were more widespread, which are necessary for M. psilurus and for higher abundance of C. lasiura.

Layer 1 differs from the others by the largest number of light-colored remains (37%) and by the lowest number of black remains (6%). We believe that layer 1 contains the material of the Karginsky interstadial, and there is also an admixture of Holocene material, which, as evidenced by the preservation state, includes remains of C. ex gr. suaveolens.

It seems that in Koridomaya Cave after the Karginsky interstadial in the last glacial maximum (LGM) of the Pleistocene, the sedimentation (deposition of remains) stopped, and therefore finds from the Karginsky period occur almost up to the very surface. By contrast, with the onset of warming in the Holocene, the sedimentation in the cave resumed but was not as intense as the Pleistocene deposition of remains, whereas Holocene and Pleistocene materials got mixed in the upper stack of the deposits.

Communities of shrews in Priamurye during the Karginsky interstadial

In the course of the Karginsky interstadial, in shrew communities of the Pompeevskiy Ridge, S. caecutiens was dominant; its abundance was 51–63% (Fig. 5). Based on materials from Medvezhiy Klyk Cave, it has been demonstrated that the same species prevailed in shrew communities of the Southern Sikhote-Alin at different stages of the Late Pleistocene and Holocene [the Karginsky Interstadial (MIS 3), the end of MIS 2, and the Early, Middle, and Late Holocene (MIS 1)] despite climatic and landscape alterations (Omelko et al., 2020). This is a fairly stable trend, although in the Holocene, C. shantungensis became a...
The alterations that took place in shrew communities of Priamurye in the course of the Karginsky interstadial affected the abundance of only a few species. The greatest changes in abundance happened to *S. daphaenodon*, and this abundance was in antiphase with that of *C. lasiura*: when the abundance of one species diminished, this parameter of the other species increased. In the Karginsky interstadial, *S. tundrensis* occurred here. The small-sized white-toothed shrew *C. ex gr. suaveolens* emerged for a short period during the Holocene. When *S. gracillimus* populated this territory is unknown.

Because for shrew species, it is difficult to identify strict confinement to a certain landscape type, it is hard to use this group of mammals for paleogeographic reconstructions. Nevertheless, in general, it can be said that both open spaces and forest formations were common in Priamurye during the Karginsky interstadial, in agreement with the species profile of rodents, which is more clearly associated with specific landscapes.

**Conclusion**

Koridomaya Cave deposits formed mainly during the Karginsky interstadial (MIS 3), and only the upper stack formed via an admixture of a small amount of Holocene deposits (MIS 1). The formation of bone-bearing deposits in Koridomaya Cave has been associated with warm climatic conditions; the deposits have not formed during glacial stages. Remains of 11 species of shrews were found here (*S. caecutiens*, *S. roboratus*, *S. daphaenodon*, *S. tundrensis*, *S. minutissimus*, *S. ex gr. unguiculatus-isodon*, *N. fodiens*, *B. minor*, *C. lasiura*, and *C. ex gr. suaveolens*). *B. minor* was not designated by us as a part of Late Pleistocene fauna of Priamurye shrews.

In shrew communities of Priamurye during the Karginsky interstadial, dominance of *S. caecutiens* was revealed. This evidence complements data from the Southern Sikhote-Alin, showing that in shrew communities of the late Pleistocene and Holocene (the last 50 ky) in the Far East, the dominant did not change.

**Declarations**

Competing Interests. The work was supported by a state assignment from the Ministry of Science and Higher Education of the Russian Federation [topic No. 121031000153-7] and was partly supported by the Russian Science Foundation [project No. 22-24-00510] during a taxonomic analysis of shrew remains from Far Eastern caves of 2022 (by Valeriya E. Omelko).

**Author contributions**

All authors contributed to the study conception and design. Data collection, material preparation and data discuss was performed by Mikhail P. Tiunov. Material preparation, taxa identification and analysis was performed by Valeriya E. Omelko. The first draft of the manuscript was written by Valeriya E. Omelko and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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**Data availability statement**

All data generated and analysed during this study are included in this published article.

**References**

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Figures
Figure 1

Location of the Koridornaya Cave (blue circle) in Eurasia (A) and in the Far East (B). (C) – view on the valley of the Stolbukha river from the entrance of the Koridornaya Cave.

Figure 2

The plane (A) and cross-section (B) of the Koridornaya Cave. (C) – scheme of the cross-section by north-east wall in the pit. Legend: 1-5 – lithological layers (description see in the text); 6 – non-excavated deposits.
Figure 3

Distribution of cranial remains of shrews in the deposits of Koridornaya Cave

Figure 4

Mandible of the *Beremendia minor* (FSC RJARVKorC-01) from the Koridornaya Cave. (A) – lateral view; legend is 1 mm; (B) – buccal view of m3; legend is 0.2 mm
Figure 5
Quantitative ratio of shrew remains in the deposits of Koridomaya Cave

Figure 6

Changes in the abundance of a few shrews species of the Pompeevskiy Range in the Late Quaternary