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Holocene palaeoenvironments of southern Sikhote-Alin Mountains (southern Far East), reconstructed from palaeontological data

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Abstract

Due to the rarity of the archaeological cave sites in Primorsky Krai, the site known as "Perspektivnaya Cave" located in the southern part of the hard-to-reach areas of the the Sikhote-Alin mountain system north-north-east of Vladivostok, is of considerable interest. The first results of its study emphasise the importance of further research since human bones and ceramics were found there, as well as numerous mammal and bird bones, shells of terrestrial molluscs, and spores and pollen. These proxies can be utilised to contextualise the migration and presence of humans within an environmental framework. Palynological studies made it possible to reconstruct the landscapes and climatic conditions of the Early–Late Holocene when forest-steppe landscapes were widespread in the adjacent territory. Mesophilous herbs prevailed in open spaces, steppe plants and ferns on rocky slopes, mixed forests on the mountain slopes, and birch forests and swamps on river floodplains. Detailed studies have revealed the various fluctuations in the vegetation development described in the article. The warmest and most humid conditions were observed in the Middle Holocene, the optimal phase of the Holocene. A moderately warm and drier climate was characteristic of the Early and Late Holocene. The composition and structure of faunas from different periods of the Holocene corroborates the results of palynological studies. The Middle Holocene bird and mammal faunas are the most diverse in composition. The fossil molluscs lived under moderate climatic conditions in broadleaved forests growing near the cave, as well as in open spaces (forest edges or meadows) with well-developed herbaceous vegetation and in places of high humidity. Freshwater mollusc remains indicate that a river with a diverse range of near-water vegetation flowed near the cave.

Keywords: Cave deposits; Holocene; fossils; southern Russian Far East; palaeoecology

1. Introduction

During the Holocene, the climate in the southern part of the Sikhote-Alin Mountains was characterised by a moder-

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ate monsoonal pattern. Here, as in the present day, dry and wet seasons linked to monsoon circulation were evident. Summer monsoons were more intense from approximately 11 to 4.3 kyr ago, with the warmest period occurring around 8–5 kyr ago. Following 4.3 kyr ago, the climate shifted to cold and cool-temperate (Korotkiy et al., 2005; Evstigneeva et al., 2025).

Both now and in the past, the diversity of the relief and climate has supported a varied vegetation cover: coniferous and broad-leaved forests, dry and wet meadows, open woodlands, and coastal vegetation. Broad-leaved forests covered the largest areas during the period from 10.4 to 4.6 kyr ago (Korotkiy et al., 2005; Evstigneeva et al., 2025).

The Early Holocene large mammal community in the southern Russian Far East are primarily known from archaeological sites. The species composition of large mammals generally corresponds to the modern one (Gasilin, 2013; Omelko, 2019). The dhole inhabited this area but vanished from the territory by the mid-20th century (Krivosheev, 1984). The Holocene occurence of beavers on the eastern periphery of the Palaeoarctic remains uncertain. Many species of large mammals were more widespread then than they are today, particularly before humans began actively developing the area in the late 19th and early 20th centuries. Thus, even in the Late Holocene, the moose's range extended to the Peschaniy Peninsula (Ermolova, 1963) and the Muravyov-Amursky Peninsula (Vasilieva et al., 2011), while the leopard's range in the Middle Holocene reached further north, up to the middle Sikhote-Alin Mountains (Alekseeva, 1991). Also more common were the grey wolf, goral, musk deer, and so on. However, the distribution of reindeer in the Middle Holocene in the southern part of the Khanka Lake Lowland, as suggested by certain archaeozoological works (Alekseeva and Boldin, 1986; Brodyanskiy, 1987; Alekseeva and Gasilin, 2015), is not confirmed (Omelko and Perfilieva, 2020).

Studies of small mammals from the Holocene in the southern Russian Far East rely primarily on materials from two vertical caves situated in the southern part of the Sikhote-Alin Mountains on the Lozovy Ridge — Bliznets Cave (Alekseeva et al., 1984; Alekseeva and Tiunov, 1987; Nesterenko et al., 2002) and the Medvezhiy Klyk Cave (Tiunov, 2016; Omelko et al., 2020) — as well as from the Tetyukhinskaya Cave in the middle part of the Sikhote-Alin Mountains (Osipova et al., 2024a, 2024b) and Koridornaya Cave in the Khingan-Bureya mountain system (Omelko and Tiunov, 2024). Throughout the Holocene, the fauna of this region included forest species such as *Myodes rutilus* (Pallas, 1779), *Pteromys volans* Linnaeus, 1758, *Sorex mirabilis* (Ognev, 1937), *S. unguiculatus* Dobson, 1890, *S. isodon* Turov, 1924, *S. gracillimus* Thomas, 1907, *Murina hilgendorfi* (Peters, 1880), and *Plecotus ognevi* (Kishida, 1927). The species of open spaces were much more widespread, and the boundaries of the ranges of many of them extended significantly further south and east compared to modern times until the Late Holocene (2 kyr ago). During the Middle Holocene, the heat-loving *Rhinolophus nippon* Temminck, 1835 appeared here (Alekseeva and Tiunov, 1987), currently inhabiting China, Korean Peninsula, and Japan.

The Holocene birds of the southern Primorsky Krai are known from bone finds in archaeological sites and the Bliznets Cave (Alekseeva et al., 1984, 1990; Burchak-Abramovich and Tsalkin, 1985; Panteleev and Alekseeva, 1993). During the Holocene, the species composition of birds resembles that of modern times. Species not currently breeding in the southern part of the Sikhote-Alin Mountains have been noted: *Perdix dauurica* (Pallas, 1811), *Anthus gustavi* Swinhoe, 1863, *Lanius excubitor* Linnaeus, 1758, *Turdus naumanni* (Temminck, 1820), and *Leucosticte arctoa* Pallas, 1811. Most of these birds are northern, typical of the Okhotsk-type taiga or even mountain tundra; one species (*Perdix dauurica*) is an inhabitant of the steppe and forest-steppe. No further "southern" species has been recorded among the modern ones. In the Middle Holocene, the ranges of certain species were broader than they are today: *Pelecanus crispus* Bruch, 1832, *Cygnus olor* (Gmelin, 1789), *Cygnus cygnus* (Linnaeus, 1758), *Anser cygnoides* (Linnaeus, 1758), *Haliaeetus albicilla* (Linnaeus, 1758), and others.

Holocene terrestrial molluscs in the territory of the southern Russian Far East are known from a few described species found in the Medvezhiy Klyk Cave (Prozorova et al., 2006; Prozorova and Kavun, 2007) and from the mollusc complexes from the Bliznets Cave (Prozorova and Alekseeva, 1999) and the Tetyukhinskaya Cave (Osipova et al., 2024a, 2024b). Most of these are modern inhabitants of the region; however, *Eostrobilops coreanus* (Pilsbry, 1927) and *Pyramidula rupestris* (Draparnaud, 1801) are not present in the current fauna.

While Holocene small mammals and mollusc assemblages are generally abundant, they have only been collected from three localities: the Bliznets Cave, the Medvezhiy Klyk Cave, and the Tetyukhinskaya Cave. In contrast, large mammal remains are primarily from archaeological sites. Any additional material enchances our understanding of this period and its reliability, as the factors contributing to accumulation vary in most cases.

In the Perspektivnaya Cave located in the southern part of the Sikhote-Alin Mountains, human bones and ceramics were discovered, as well as numerous remains of mammals and birds, shells of terrestrial molluscs. In addition, samples were taken for spores and pollen analysis.

This paper presents the outcomes of detailed analyses of various proxies and discusses changes in the distribution of individual species, biodiversity, and the palaeoenvironment in the cave area.

2. Regional geological setting — The Perspektivnaya Cave

The Perspektivnaya Cave is situated in the southern part of the Sikhote-Alin Mountains (43°39.820'N, 132°43.645'E), 90 km north-north-east of Vladivostok city

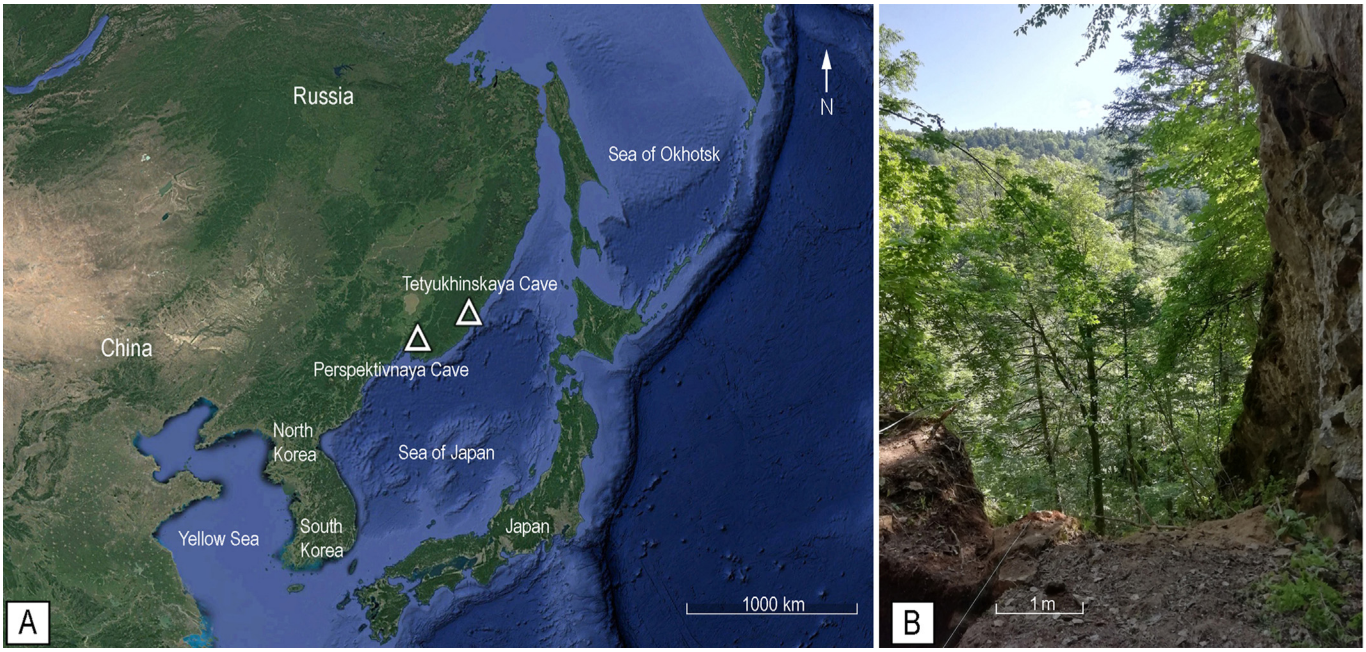


Fig. 1. (A) The Google image demonstrating location of the Perspektivnaya Cave in the southern part of Sikhote-Alin Mountains; white triangles indicate locations of the Perspektivnaya and Tetyukhinskaya caves. (B) View from the Perspektivnaya Cave to the surrounding landscape; photo was taken by M. Tiunov.

(Fig. 1). This area is part of the Mikhailovka region in Primorsky Krai, Russia.

The cave is located 19 km east of the Zmeinaya Mountain, which is the source of Levaya Ilistaya (Left Lefu) River. The Zmeinaya Mountain is part of the low-mountain Shkotovo (Maykhe-Daubikha) Plateau, which has an average height of about 850 m.a.s.l. The Mountains of Przhevalsky (Dadyan-shan) divide the plateau into two segments. The Mountains of Przhevalsky are a mid-mountain, with the highest point being Lysaya Mountain (1241 m.a.s.l.).

The Shkotovo Plateau is composed of Pliocene 5–3 Ma basalts that cover, like a cloak, more ancient deposits, including carbonate lenses attributed to the upper Permian Chandalaza suite. One of the lenses that cut through the basalts is exposed on both steep sides of the Levaya Ilistaya River valley. On the left side of the valley, limestone forms a rocky outcrop that rises to 12 m in height and extends up to 50 m in width. The entrance to the Perspektivnaya Cave is 421 m.a.s.l. and 20 m above the water table of the river. The total length of the described cave section is 40 m, with an area of 60 m^2 and a volume of 140 m^3 (measurements by Yu.I. Bersenev in 2021). The main entrance to the cave features a triangular outline, measuring 5.4 m in height and up to 4.3 m in width leading to a small grotto with a flat area that is covered by clay deposits. An inclined gallery ascends from the grotto to the west at a 30° angle, ending with a second exit that is 4 m high and 2 m wide. The floor of the gallery is covered with blocks of limestone. In the far part of the grotto, an inclined gallery descends at an angle of 25° into the limestone massif, which is currently covered with limestone fragments (Kluyev et al., 2023). The cave features a second level: a narrow gallery approximately 10 m long, about 1 m wide and 1.2–2 m high. This level connects to the main grotto of the cave through an opening in the side wall and has an independent exit (Fig. 2).

The climate of this area is characterised by moderately hot and rainy summers, dry and sunny autumns, and cold winters with little snow. This is caused by monsoons that blow almost constantly in two directins: in spring and summer from the sea, and in autumn and winter from the land. The warm sea winds in spring and summer carry a significant amount of heat and moisture. Most precipitation occurs in the off-season — during early spring and late summer.

The Perspektivnaya Cave was discovered in the early 1970s during the construction of a logging road. It was examined and named by geologist L.V. Demin in 1975. The cave was rediscovered in 1988, during which excavations were conducted to reveal its continuation (A.V. Gretchenko and others). In 2013, P.S. Panin and colleagues excavated a continuation approximately 10 m long and conducted a visual topographic survey (A.V. Gretchenko). Subsequently, the cave was mapped by Yu.I. Bersenev, A.A. Gladchenkov, and A.E. Gusev.

During the summer of 2021–2023, M. Tiunov, in cooperation with archaeologists from the Institute of History, Archaeology and Ethnology of the Peoples of the Far East, Far Eastern Branch of the Russian Academy of Sciences and speleological group "Vladspeleo" from Vladivostok excavated pits in the grotto of the cave and at the upper level of the cave.

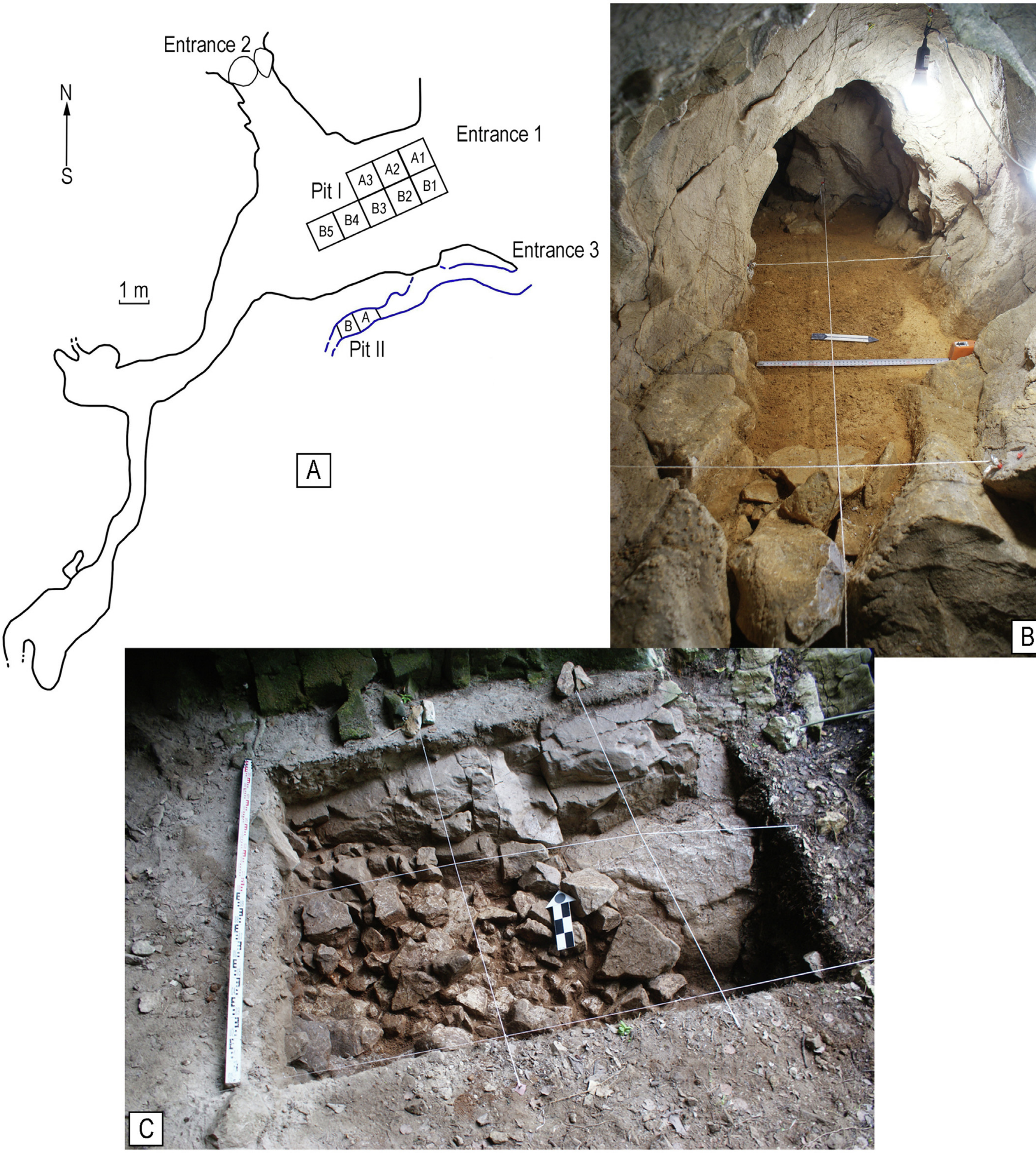


Fig. 2. Plan of the Perspectivnaya Cave and excavations inside it. (A) Plan of the cave mapped by Yu.I. Bersenev, A.A. Gretchenko, and A.E. Gusev. (B) Pit II (upper part of the cave); the length of the ruler is 0.5 m. (C) Pit I; the length of the ruler is 2 m. A1–A3 and B1–B5 are excavation squares of Pit I; and A and B (no numbered) are squares of Pit II; each square is of 1 × 1 m. Photos (B, C) were taken by A.A. Gladchenkov in 2022.

3. Archaeological setting

In June 2021, Dr. M. Tiunov discovered a fragment of ceramics while searching for palaeontological remains in an exploratory pit dug in the Perspektivnaya Cave. He subsequently handed it over to archaeologist E.Yu. Shapovalov. In July 2021, during field work, the archaeological heritage site "Perspektivnaya Cave" was recorded. An archaeological pit covering an area of 1 × 1 m was excavated within the cave. Based on the characteristics of the ceramics found, the site was preliminarily dated to the Middle Neolithic (Rudny archaeological culture) (7–6 kyr ago).

In 2022, stationary research began at the archaeological site "Perspektivnaya Cave", under the supervision of Dr. N.A. Klyuev. Pit I, covering an area of 9 m^2, revealed the northwestern section of the entrance area, while Pit II was excavated at the second level of the cave.

The excavations yielded a collection of artefacts. The ceramic complex is represented by scattered fragments. The main features of the settlement's ceramics include weakly profiled vessels of simple jar shapes, elongated vertically, with a combination of incised and stamped ornamentation and the presence of containers with a smooth body. Similar materials have been noted at certain sites in the central and southeastern parts of Primorsky Krai, associated with the Rudny archaeological culture of the Middle Neolithic (the settlements of Rudnaya Pristan and Moryak-Rybolov). In pits I and II, various bones of ancient humans were discovered — isolated teeth, a lower jaw, a phalanx, and a tarsal bone.

The low concentration of artefacts within a confined space, along with the extremely small number of products from the stone industry (such as chips, flakes, and squeezing flakes), despite the thoroughly washed loose deposits from the excavation fill, supports the assumption that the site was temporary occupied and that ancient humans did not live there continuously. However, due to the rarity and limited study of cave sites in Primorsky Krai, the "Perspektivnaya Cave" site remains of substantial interest. The initial findings from its examinations highlight the significance of further investigations in poorly studied, remote areas of the central regions of Primorsky Krai, which are crucial for reconstructing the migration processes and interactions of primitive societies in this territory.

4. Material and methods

Pit I was excavated in the unconsolidated deposits down to the rocky bottom at the entrance part of the cave in 2022; pit II was excavated in the upper part of the cave in 2023 (Kluyev et al., 2023) (Fig. 2).

To collect faunal remains, 22 sediment samples, each of 0.1 m thick, were collected from B1–B5 squares of pit I; eight samples were collected from A and B (no number) squares of pit II. Each squares measures 1 × 1 m. The samples were wet-sieved (mesh size: 1 mm) and dried in the field; the dried sediment residue containing the fossil remains was sorted and examined in the laboratories.

The total number of extracted shells is 7434 (see Table S1 in Supplementary data). The average percentage of species from various ecological groups was calculated to aid the reconstruction of palaeoecological considerations. Molluscs were identified using the descriptions and published reference keys of Prozorova et al. (2018) and Sysoev and Shileyko (2009); they are presented in a systematic order according to MolluscaBase (https://www.molluscabase.org). Malacozones are defined based on the number of shells identified, and their preferences for specific environments. The zones are described using the following terms: absolute dominant (numerous) (more than 50%), dominant (frequently occurring) (50–30%), subdominant (not numerous) (30–15%), secondary (rare) (15–5%), and insignificant (single) species (less than 5%) (Bakanov, 1987). For the palaeoecological analysis, the molluscs were classified based on their contemporary ecological preferences for air temperature, humidity, and vegetation cover, utilising the available data on the modern molluscs of the studied region (Primorsky Krai, southern Far East, Russia) (see Table S2 in Supplementary data). The shells of molluscs were photographed at the Institute of Geology, Ufa Federal Research Centre of the Russian Academy of Sciences (UFRC RAS) (Ufa, Russia) using a Motic stereomicroscope SMZ-171 with a Moticam-10+ camera. The collections of mollusc shells No. 409 (collected in 2021–2022; sample numbers 7147–7156) and No. 413 (collected in 2023; sample numbers 7202–7219) are stored at the Institute of Geology UFRC RAS (Ufa, Russia).

The sample concentration of vertebrate material was carried out in the laboratory. The collection of bird bones consists of 385 remains. Avifauna taxa were identified based on the bones of the postcranial skeleton (see Table S3 in Supplementary data). About 15000 small and large mammal teeth were extracted (see Tables S4–S6 in Supplementary data). A reference collection and handbooks with identification guides for individual groups of mammals were used to identify the species diagnostics (Krivosheev, 1984; Gromov and Erbajeva, 1995; Kostenko, 2000; Zaitsev et al., 2014). Fragments of the skull and lower jaws were used to identify and quantify the shrews; voles were identified based on the first lower molar (m1), while lemmings were identified using all molars (m1, m2, m3, M1, M2, M3); mice of the genus *Apodemus* were identified based on the second upper molar (M2); other rodents could be identified based on any isolated teeth. In the Family Ochotonidae, all premolars (p3, P3) and the isolated lower and upper teeth were sorted and quantified (see Table S6 in Supplementary data). Large mammal remains are identified through isolated teeth and bones of the postcranial skeleton. The calculation relies on the highest number of teeth or bones from the postcranial skeleton of the same taxon. When identifying zones based on the bone remains of mammals (small-mammal zone, SMZ; large-mammal zone, LMZ) and birds (bird zone, BZ), both the total number of bone remains and their species diversity, including dominant and indicator species that inhabit specific environmental conditions, were considered. Palaeoecological reconstructions are based on the preferrences of modern vertebrate species (birds and mammals) (see Tables S7, S8 in Supplementary data). The photographs of the teeth were taken using a SteREO Discovery.V12 stereo microscope and stacked with

CombineZM software (Hadley, 2008). All the bone specimens are stored at the Federal Scientific Centre of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences (Vladivostok, Russia).

A total of seven samples (100 g each) from pit I, square B4 (southern wall) were examined using the palynological method (see Table S9 in Supplementary data). The palynological analysis was performed using the standard classical method outlined by Grichuk and Zaklinskaya (1948). The results were calculated by groups: tree and shrub pollen, herbaceous plants, and spore-producing plants. The percentage of identified taxa was derived from the total of all registered pollen grains and spores. The identification is based on the total number of remains, the diversity of spores and pollen taxa, and dominant and indicator taxa. The identifications of pollen and spores were derived according to Kupriyanova and Aleshina (1972, 1978) and Bobrov et al. (1983). Additionally, collections of recent spores and pollen held at the Institute of Geology UFRC RAS were also utilised. Photographs of characteristic taxa were taken using a Zeiss Primo Star microscope.

The authors follow the regional stratigraphic divisions that were correlated many years ago with the Blytt-Sernander scheme which reflects the development of vegetation based on detailed studies conducted in the region. Korotkiy et al. (2005) regard the upper portion of the Partizansky layers (Anonymous, 1987) (upper part of Upper Pleistocene) as having accumulated during the Alleröd and Late Dryas stages (12.7–10.2 kyr ago). The Holocene deposits of the Primorsky Krai region are classified into the Lower Holocene Amur layers (= Preboreal), Khasan layers (= Boreal), the Middle Holocene Barabashev (= Atlantic), Ambinsky (= Subboreal), and the Upper Holocene Ryazan (= Subatlantic) layers (Korotkiy et al., 1980). We have also conducted a formal correlation of our data with the International Holocene subdivisions ratified by the International Comission on Stratigraphy in 2018 (https://stratigraphy.org/news/125) and utilise precisely these subdivisions while comparing our data with the results of other investigations.

A radiocarbon date 6400 ± 25 yr BP (7321 ± 51 cal yr BP) of a human tooth sample (BA231397; pit II, square A, depth interval 0–0.05 m) was obtained using AMS at Peking University Radiocarbon Dating Laboratory. The calibration curve is the IntCal20 atmospheric curve (Reimer et al., 2020). The calibration program used is OxCal v4.4.4 by Bronk Ramsey (2009, 2021). Additionally, there are known artefacts (ceramics and stone products) obtained from the deposits of pit I, attributed to the Middle Neolithic, Rudny archaeological culture (7–6 kyr ago) (Kluyev et al., 2023). Radiocarbon dating aligns with the age of ceramics, suggesting that the deposits in both excavations formed synchronously. These dates allow for correlation of the studied deposits with the Holocene (MIS 1).

5. Results

5.1. Cave deposits

Deposits in the pits I–II of the Perspektivnaya Cave were described during the excavations (Kluyev et al., 2023). The following deposits/layers were identified in pit I, arranged from the bottom to the surface: rocky bottom of carbonate rocks; reddiah-brown clay; blackish-grey sooty loam; brown-grey loam; dark grey loam; yellowish-grey light loam; brown humus loam; humus (soil). All layers contain angular fragments of carbonate rocks of various sizes. The stratigraphical position of the sampled deposits in the pit I (the main archaeological excavation) is illustrated in Fig. 3.

5.2. Molluscs

The shells of molluscs are not distributed uniformly within the sediments. The shells of *Carychium* Müller, 1773, *Cochlicopa* Férussac, 1821, *Vallonia* Risso, 1826, *Columella* Westerlund, 1876, *Vertigo* Müller, 1773, *Punctum* Morse, 1864, *Discus* Fitzinger, 1833, *Euconulus* Reinhardt, 1883, *Hawaiia* Gude, 1911, *Perpolita* Baker, 1928, *Karaftohelix* Pilsbry, 1927 are light white or have a reddish tint, and they are well preserved in the sediments. A carbonate crust forms on the surface of certain shells. Members of the Bradybaenidae family are seldom found in complete preservation (whole shells), and generally, they are located in sediments as numerous fragments that are challenging to identify to the genus or species. Unionidae are present in the samples as individual fragments of the nacreous layer: B2 square (depth interval 0.1–0.2 m, layer 3); B3 square (depth interval 0.1–0.2 m, layers 4–5; depth interval 0.2–0.3 m, layers 5–6; depth interval 0.3–0.4 m, layer 6); B4 square (depth interval 0–0.1 m, layer 3; depth interval 0.1–0.2 m, layer 5; depth interval 0.2–0.3 m, layers 5–6; depth interval 0.3–0.4 m, layer 6); B5 square (depth interval 0.1–0.2 m, layer 5; depth interval 0.3–0.4 m, layers 5–6); B (no number) square of pit II (depth interval 0–0.5 m). In total, 30 unionids shell fragments were found.

The mollusc shells are from 12 species of terrestrial gastropods representing 10 genera and from a freshwater bivalve of the Unionidae family (Fig. 4; see Table S1 in Supplementary data).

The studied species of terrestrial molluscs prefer moderate climate conditions and moderate temperatures (the mesophilous molluscs group) (see Table S2 in Supplementary data). These molluscs were divided into groups depending on their preferences for humidity: subhygrophilous, hygrophilous (living in conditions of high humidity), and mesophilous (tolerating moderate humidity). Furthermore, the molluscs were categorised into groups based on their preferences for various types of veg-

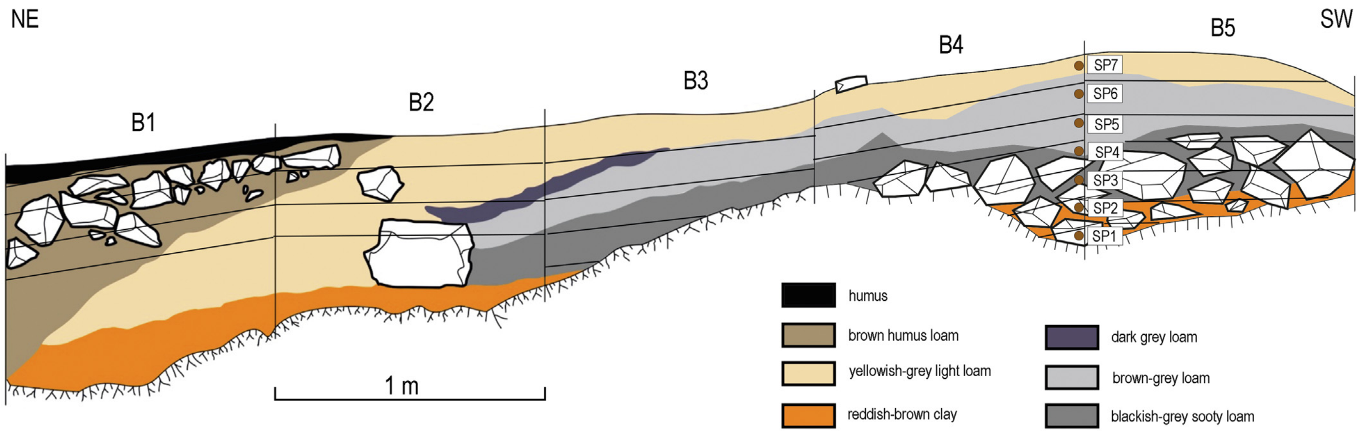


Fig. 3. Lithological cross-section on the line of excavated squares B1–B5 of the pit I in the Perspectivnaya Cave. Orange dots and indices SP1–SP7 indicate places of palynological samples. Line of profile is oriented from the entrance part of the cave (square B1) towards its interior part (square B5).

etation — those forest inhabitants and intermediate habitats.

5.3. *Vertebrates*

Bone remains of birds and mammals were discovered in the loose sediments of the cave (Fig. 5). For vertebrates, zones are designated based on species complexes of small mammals. Zones for large mammals and birds correspond with these zones.

5.3.1. *Birds*

The bird bones are quite fragmentary and evidently of pellet or excrement origin. Representatives of twenty-four species from twenty-two genera were discovered (see Table S3 in Supplementary data).

Medium-sized birds, such as Galliformes, *Rallus aquaticus* Linnaeus, 1758, *Columba rupestris* Pallas, 1811, *Picus canus* Gmelin, 1788, *Garrulus glandarius* (Linnaeus, 1758) could have been caught by the eagle owl. There is a suitable niche for its nesting in the entrance area of the cave. Smaller birds were preyed upon by other owls, including *Surnia ulula* (Linnaeus, 1758), of which remains were discovered at a different section of the cave. In the past, *Surnia ulula*, was common throughout the taiga zone of Eurasia and North America and reached as far south as Lake Khasan. However, over the last century, the southern limit of its nesting range has shifted to the northern half of Primorsky Krai (Gluszhenko et al., 2016).

Furthermore, the birds could have been hunted by foxes, raccoon dogs, sables, and weasels, whose fossil bones were also discovered in the cave, along with other predators, such as wolves, whose bones were not found, yet very likely could have visited the cave.

5.3.2. *Large mammals*

From several thousand small fragmented bone remains of large mammals, 66 fragments of the postcranial skeleton and individual isolated teeth were identified, belonging to 13 species of 12 genera (see Table S4 in Supplementary data). Many small fragments of large mammal bones display predatory gnawed marks, which indicates that accumulation is the result of the activities of large predatory mammals. However, some of the bones may have been brought into the cave by ancient man who hunted animals.

5.3.3. *Small mammals*

The fossil remains of insectivores and bats found in the Perspektivnaya Cave are fragmentary (1703 fragments of mandibles and maxillae, along with isolated teeth).

Soricomorphs include 11 species from three genera (see Table S5 in Supplementary data). Discovered remains of *Sorex* ex gr. *unguiculatus-isodon* are represented by undiagnostic lower jaws fragment. The Cheiroptera include twelve species from seven genera (see Table S5 in Supplementary data).

Among the 30 isolated fossil teeth of ochotonids identified, the largest quantity belong to *Ochotona hyperborea* Pallas, 1811. Teeth from three extinct species were also discovered — *Tonomochota khasanensis* Tiunov and Gusev, 2021, *Tonomochota sikhotana* Tiunov and Gusev, 2021 and *Tonomochota khinganica* Gusev and Tiunov, 2023 (see Table S6 in Supplementary data).

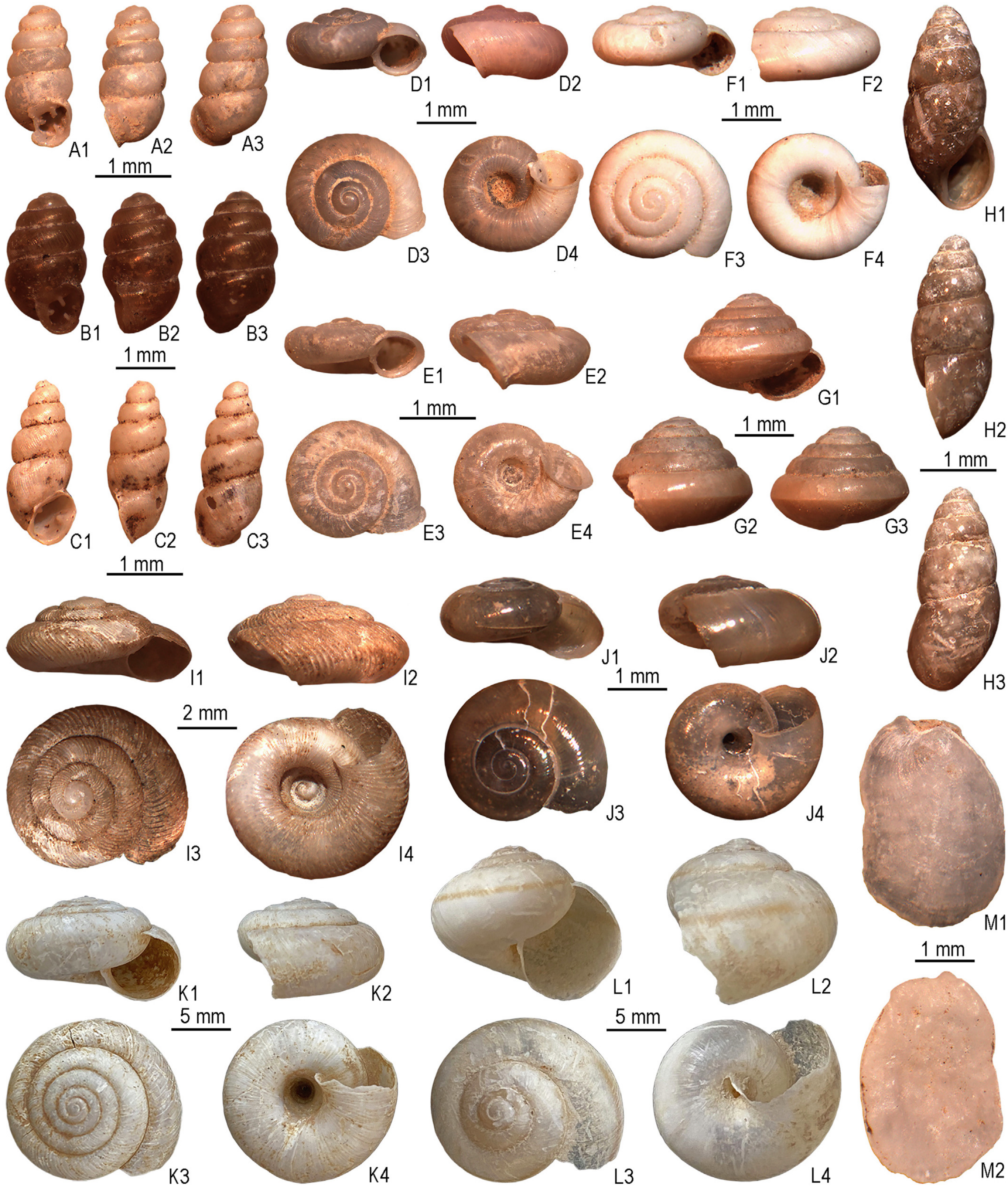
Bone remains of 14 rodent species from 14 genera were found (see Table S6 in Supplementary data).

The preservation of the bone remains of small mammals indicates that they were accumulated by predators; these could have been both predatory mammals and birds.

5.4. *Palynological investigations*

In total, pollen and spores of 44 taxa were diagnosed in the samples.

The group of tree and shrub pollen (arboreal pollen) includes dark conifers (*Picea* Dietrich, 1824), light conifers (*Pinus* Linnaeus, 1753: *Pinus* (Haploxylon) and *Pinus* (Diploxylon)), broadleaved trees (*Quercus* Linnaeus, 1753, *Tilia* Linnaeus, 1753, *Ulmus* Linnaeus, 1753, *Corylus*


A1
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1 mm
B1
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G3
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I1
I2
2 mm
I3
I4
J1
J2
1 mm
J3
J4
K1
K2
5 mm
K3
K4
L1
L2
5 mm
L3
L4
M1
1 mm
M2

Linnaeus, 1753, *Carpinus* Linnaeus, 1753, *Juglans* Linnaeus, 1753, *Aralia* Linnaeus, 1753), and small-leaved trees (*Betula* Linnaeus, 1753: *Betula* sp., *B*. sect. Costatae, *B*. sect. Albae and *B*. sect. Nanae, *Alnus* Miller, 1754, *Alnaster* Spach, 1841, *Salix* Linnaeus, 1753), as well as bushes (*Ephedra* Linnaeus, 1753, *Viburnum* Linnaeus, 1753, Moraceae Gaudichaud-Beaupre, 1835, *Rubus* Linnaeus, 1753).

The group of herbaceous plants (non-arboreal pollen) is represented by Poaceae Barnhart, 1895, Chenopodiaceae Ventenat, 1799, *Artemisia* Linnaeus, 1753, Asteroideae (Cassini) Lindley in Loudon, 1829, Cichorioideae (Jussieu) Chevallier, 1828, Ericaceae Jussieu, 1789, Apiaceae Lindley, 1836, Rosaceae Jussieu, 1789, Cyperaceae Jussieu, 1789, Onagraceae Jussieu, 1789, Fabaceae Lindley, 1836, Scrophulariaceae Jussieu, 1789, Lamiaceae Martynov, 1820, Caryophyllaceae Jussieu, 1789, *Urtica* Linnaeus, 1753, *Polygonum aviculare* Linnaeus, 1753.

The group of spore plants includes Polypodiaceae Presl and Presl, 1822, Ophioglossaceae Martynov, 1820, *Lycopodium annotinum* Linnaeus, 1753, *Huperzia selago* (Linnaeus) Bernhardi ex Schrank and Martius, 1829, *Selaginella* Beauvois, 1805, *Sphagnum* Linnaeus, 1753, Bryales Limpricht, 1876. All the examined samples exhibit a high saturation of spores and pollen. The content of palynomorphs in samples 2–7 was not less than 500, in sample 1 — 431 palynomorphs.

As a result of the analysis, seven representative palynospectra were obtained (Table S9 in Supplementary data). Notably, all the selected spectra exhibited a very high content of spores. Photographs of characteristic taxa are presented in Fig. 6.

6. Palaeoecological implications

6.1. Molluscs

Molluscs in the Perspektivnaya Cave assemblages can be classified into three categories based on the number of individuals found and their percentage content. The dominant species in the studied pits are *Euconulus fulvus* (Müller, 1774) (37.8%) and *Discus depressus* (Adams, 1868) (32.7%) (see Table S1 and Fig. S1 in Supplementary data). Secondary (or rare) species, which account for 6–11%, are Agriolimacidae (11.1%) and *Perpolita petronella* (Pfeiffer, 1853) (6.45%). The third group includes species that occur in small quantities and account for 0.01–1.15% of the total number of shells in a sample. Analysing the taxonomic structure of malacozones and the ecological preferences of their components allows the characterization of the palaeobiotopes (see Table S2 in Supplementary data). A total of 6 malacozones (MZs) were identified (see Fig. S1 in Supplementary data). The characteristics of each established malacozone are generally based on data from the B4 square, including information from the other squares, which is provided below. The climate reconstructions characterise the area surrounding the cave entrance.

MZ1 has been defined based on the mollusc assemblage from square B5 (depth interval 0.5–0.6 m, layers 6–7) and square B4 (depth interval 0.4–0.6 m, layers 6–7, and depth interval 0.5–0.6 m, layer 7). Nine shells of three taxa were identified (*Discus depressus*, *Euconulus fulvus*, Agriolimacidae). The malacofauna comprises species that prefer to live in forests with high humidity. These may have been forest edges adorned with tall grass and dense vegetation. The climate was mild and humid.

MZ2 has been established in square B5 (depth interval 0.3–0.4 m, layers 5–6) and square B4 (depth interval 0.3–0.4 m, layer 6); 198 shells of nine taxa could be identified (*Cochlicopa lubrica* (Müller, 1774), *Vallonia patens* Reinhardt, 1883, *V. pulchellula* (Heude, 1882), *Discus depressus*, *Euconulus fulvus*, *Hawaiia minuscula* (Binney, 1841), *Perpolita petronella*, Agriolimacidae, *Karaftohelix* sp.). Most identified mollusc shells belong to forest species (5 species, 56%) and four mollusc species (44%) prefer intermediate biotopes. This indicates that the forested areas around the cave were still preserved, and the climate was most likely moderate.

Fig. 4. Key species of molluscs found in the Holocene unconsolidated deposits of the Perspektivnaya Cave. (A1–A3) *Gastrocopta theeli* (Westerlund, 1877), IG N 409/7155/12, pit I, square B3, depth interval 0.2–0.3 m, layers 5–6; (A1) apertural view; (A2) lateral view (top right); (A3) abapertural view (view from the opposite side of the aperture). (B1–B3) *Vertigo* cf. *japonica* Pilsbry and Hirase, 1904, IG N 409/7153/16, pit I, square B3, depth interval 0–0.1 m, layer 3; (B1) apertural view; (B2) lateral view (top right); (B3) abapertural view (view from the opposite side of the aperture). (C1–C3) *Carychium pessimum* Pilsbry, 1902, IG N 409/7148/18, pit I, square B1, depth interval 0.1–0.2 m, layer 2; (C1) apertural view; (C2) lateral view (top right); (C3) abapertural view (view from the opposite side of the aperture). (D1–D4) *Vallonia pulchellula* (Heude, 1882), IG N 409/7154/15, pit I, square B3, depth interval 0.1–0.2 m, layers 4–5; (D1) apertural view; (D2) lateral view (top right); (D3) apical view; (D4) umbilical view. (E1–E4) *Vallonia patens* Reinhardt, 1883, IG N 409/7149/24, pit I, square B1, depth interval 0.2–0.3 m, layers 2–3; (E1) apertural view; (E2) lateral view (top right); (E3) apical view; (E4) umbilical view. (F1–F4) *Hawaiia minuscula* (Binney, 1841), IG N 413/7210/25, pit I, square B4, depth interval 0.1–0.2 m, layer 5; (F1) apertural view; (F2) lateral view (top right); (F3) apical view; (F4) umbilical view. (G1–G3) *Euconulus fulvus* (Müller, 1774), IG N 413/7209/28, pit I, square B4, depth interval 0–0.1 m, layer 3; (G1) apertural view; (G2) lateral view (top right); (G3) abapertural view (view from the opposite side of the aperture). (H1–H3) *Cochlicopa lubrica* (Müller, 1774), IG N 413/7216/29, pit I, square B5, depth interval 0.1–0.2 m, layer 5; (H1) apertural view; (H2) lateral view (top right); (H3) abapertural view (view from the opposite side of the aperture). (I1–I4) *Discus depressus* (Adams, 1868), IG N 413/7212/26, pit I, square B4, depth interval 0.3–0.4 m, layer 6; (I1) apertural view; (I2) lateral view (top right); (I3) apical view; (I4) umbilical view. (J1–J4) *Perpolita petronella* (Pfeiffer, 1853), IG N 413/7217/30, pit I, square B5, depth interval 0.2–0.3 m, layers 5–6; (J1) apertural view; (J2) lateral view (top right); (J3) apical view; (J4) umbilical view. (K1–K4) *Karaftohelix* cf. *middendorffi* (Gerstfeldt, 1859), IG N 409/7156/11, pit I, square B3, depth interval 0.3–0.4 m, layer 6; (K1) apertural view; (K2) lateral view (top right); (K3) apical view; (K4) umbilical view. (L1–L4) *Karaftohelix maacki* (Gerstfeldt, 1859), IG N 409/7155/13, pit I, square B3, depth interval 0.2–0.3 m, layers 5–6; (L1) apertural view; (L2) lateral view (top right); (L3) apical view; (L4) umbilical view. (M1, M2) Agriolimacidae, IG N 409/7148/19, pit I, square B1, depth interval 0.1–0.2 m, layer 2; (M1) dorsal view; (M2) ventral side (view from the opposite dorsal side).

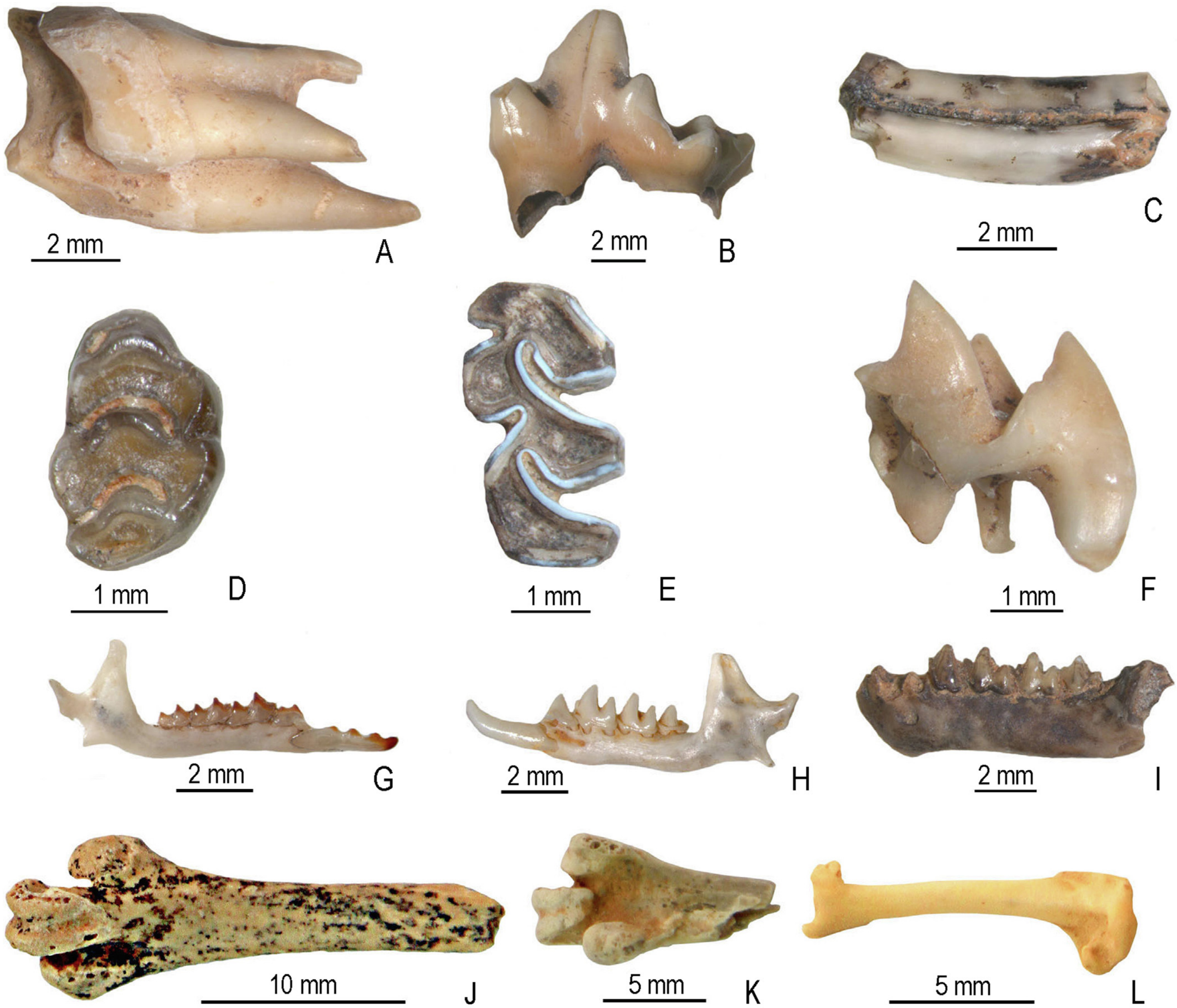

Fig. 5. Key species of small mammals and birds found in the unconsolidated Holocene deposits of the Perspektivnaya Cave, Primorsky Krai, Russia. (A) *Moschus moschiferus* Linnaeus, 1758, p1 sinister, pit I, square B1, depth interval 0.2–0.3 m, layer 2–3. (B) *Nyctereutes procyonoides* (Gray, 1834), m1 dexter, pit I, square B3, depth interval 0.3–0.4 m, layer 6. (C) *Lepus timidus* Linnaeus, 1758, m3 dexter, pit I, square B3, depth interval 0.3–0.4 m, layer 6. (D) *Rattus norvegicus* Berkenhout, 1769, m2 dexter, pit I, square B3, depth interval 0.2–0.3 m, layer 5–6. (E) *Myospalax psilurus* Milne-Edwards, 1874, m2 sinister, pit I, square B5, depth interval 0.3–0.4 m, layer 5–6. (F) *Mogera robusta* Nehring, 1891, M1 dexter, pit I, square B1, depth interval 0.1–0.2 m, layer 2. (G) *Sorex gracillimus* Thomas, 1907, fragment of dexter mandibula, pit II, square B, depth interval 0.05–0.1 m, layer 1. (H) *Crocidura shantungensis* Miller, 1901, fragment of sinister mandibula, pit II, square B, depth interval 0.05–0.1 m, layer 1. (I) *Murina hilgendorfi* (Peters, 1880), fragment of sinister mandibula, pit II, square B, depth interval 0.05–0.1 m, layer 1. (J) *Lagopus lagopus* (Linnaeus, 1758), tarsometatarsus, distal end, pit I, square B2, depth interval 0.2–0.3 m. (K) *Perdix dauurica* (Pallas, 1811), tarsometatarsus, distal end, ventral view, pit I, square B4, depth interval 0.3–0.4 m. (L) *Regulus regulus* (Linnaeus, 1758), humerus, pit I, square B4, depth interval 0.0–0.1 m.

MZ2–3 was established in square B3 (depth interval 0.3–0.4 m, layer 6, and depth interval 0.2–0.3 m, layers 5–6). A total of 1199 shells from 10 taxa were discovered (*Cochlicopa lubrica*, *Vallonia patens*, *Gastrocopta theeli* (Westerlund, 1877), *Discus depressus*, *Euconulus fulvus*, *Hawaiia minuscula*, *Perpolita petronella*, Agriolimacidae, *Karaftohelix maacki* (Gerstfeldt, 1859), *Karaftohelix* cf. *middendorffi* (Gerstfeldt, 1859)). Most mollusc shells belong to forest species (6 species, 60%), while 4 species (40%) prefer intermediate biotopes. These data indicate that forests continued to grow near the cave. The climate was temperate and humid.

MZ3 was established in square B5 (depth interval 0.2–0.3 m, layers 5–6 and depth interval 0.1–0.2 m, layer 5), square B4 (depth interval 0.2–0.3 m, layers 5–6, and depth interval 0.1–0.2 m, layer 5) and square B3 (depth interval 0.1–0.2 m, layers 4–5); 2440 shells from 11 taxa were found (*Cochlicopa lubrica*, *Vallonia patens*, *V. pulchellula*, *Discus*

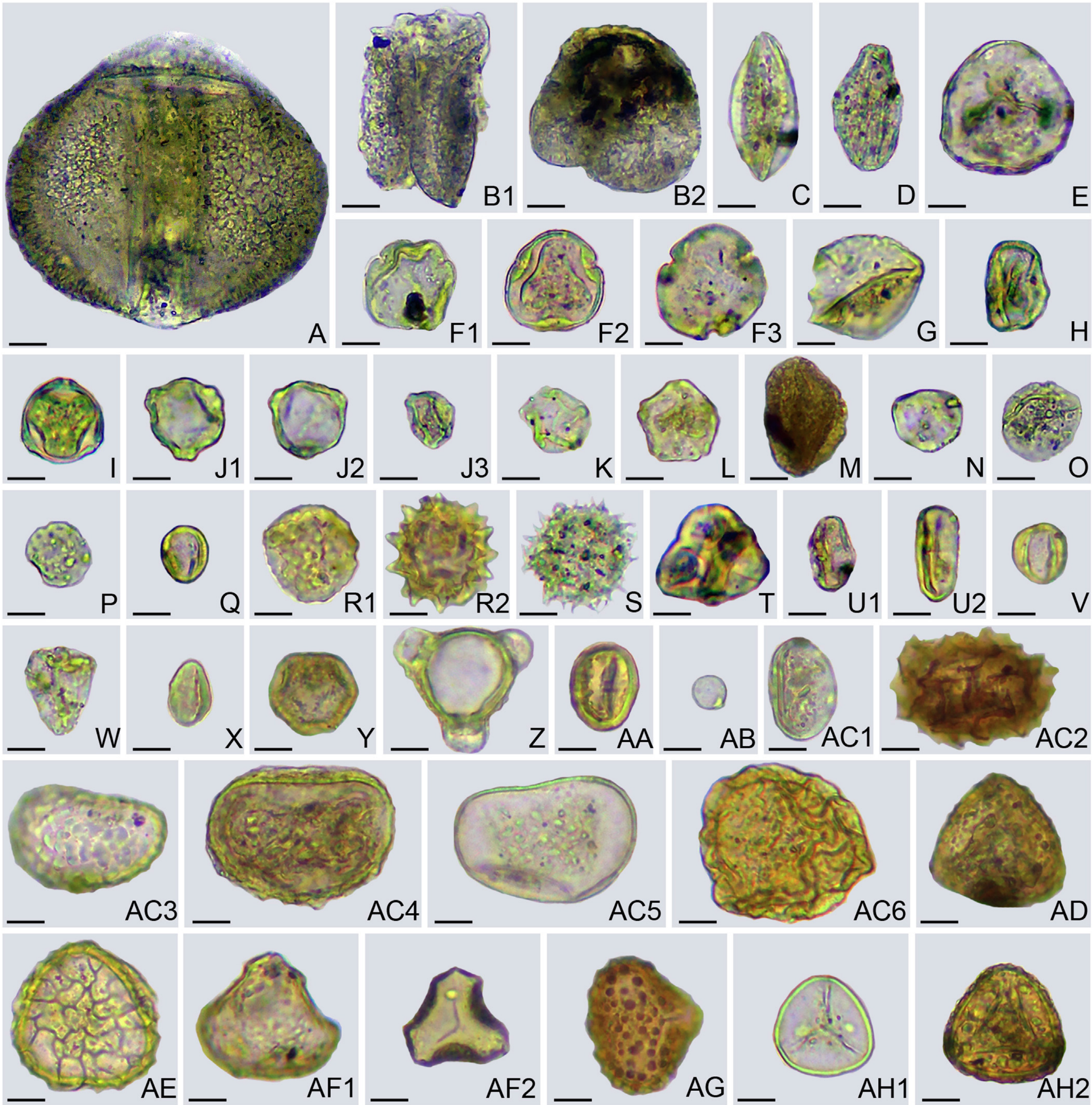

Fig. 6. Spore and pollen images from the deposits of the Perspectivnaya Cave. (A) *Picea* (Dietrich, 1824), sample S2. (B1, B2) *Pinus* (Linnaeus, 1753); (B1) *Pinus* (Haploxylon), sample S4; (B2) *Pinus* (Diploxylon), sample S5. (C) *Ephedra* (Linnaeus, 1753), sample S1. (D) *Quercus* (Linnaeus, 1753), sample S4. (E) *Juglans* (Linnaeus, 1753), sample S3. (F1–F3) *Tilia* (Linnaeus, 1753); (F1) sample S3; (F2) sample S6; (F3) sample S7. (G) *Ulmus* (Linnaeus, 1753), sample S3. (H) *Aralia* (Linnaeus, 1753), sample S3. (I) *Corylus* (Linnaeus, 1753), sample S2. (J1–J3) *Betula* (Linnaeus, 1753); (J1) *B.* sect. Costatae, sample S1; (J2) *B.* sect. Albae, sample S6; (J3) *B.* sect. Nanae, sample S6. (K) *Alnaster* (Spach, 1841), sample S1. (L) *Alnus* (Miller, 1754), sample S6. (M) *Viburnum* (Linnaeus, 1753), sample S4. (N) Moraceae (Gaudichaud-Beaupre, 1835), sample S6. (O) Poaceae (Barnhart, 1895), sample S2. (P) Chenopodiaceae (Ventenat, 1799), sample S2. (Q) *Artemisia* (Linnaeus, 1753), sample S3. (R1, R2) Asteroideae; (R1) sample S2; (R2) sample S3. (S) Cichorioideae, sample S2. (T) Ericaceae (Jussieu, 1789), sample S7. (U1, U2) Apiaceae (Lindley, 1836); (U1) sample S3; (U2) sample S7. (V) Rosaceae (Jussieu, 1789), sample S6. (W) Cyperaceae (Jussieu, 1789), sample S3. (X) Scrophulariaceae (Jussieu, 1789), sample S1. (Y) Caryophyllaceae (Jussieu, 1789), sample S2. (Z) Onagraceae (Jussieu, 1789), sample S7. (AA) *Polygonum aviculare* (Linnaeus, 1753), sample S7. (AB) *Urtica* (Linnaeus, 1753), sample S6. (AC1–AC6) Polypodiaceae (Presl and Presl, 1822); (AC1, AC4–AC6) sample 1; (AC2) sample 5; (AC3) sample 3. (AD) Ophioglossaceae (Martynov, 1820), sample S4. (AE) *Lycopodium annotinum* (Linnaeus, 1753), sample S1. (AF1, AF2) *Huperzia selago* (Linnaeus) Schrank and Martius, 1829; (AF1) sample S1; (AF2) sample S6. (AG) *Selaginella* (Beauvois, 1805), sample S7. (AH1, AH2) *Sphagnum* (Linnaeus, 1753); (AH1) sample S2; (AH2) sample S3. Scale bars = 10 µm.

depressus, *Euconulus fulvus*, *Hawaiia minuscula*, *Perpolita petronella*, Agriolimacidae, *Karaftohelix maacki*, *K.* cf. *middendorffi*, *K. selskii* (Gerstfeldt, 1859)). In this zone, seven species (70%) prefer forest habitats with high humidity, as the number of Agriolimacidae increases, while four species of molluscs (30%) are allocated to intermediate habitats. The climate was moderate and humid.

MZ3–4 was established in square B2 (depth interval 0.2–0.3 m, layers 3–5); 342 shells from eight taxa were recognised (*Cochlicopa lubrica*, *Vallonia patens*, *Discus depressus*, *Euconulus fulvus*, *Hawaiia minuscula*, *Perpolita petronella*, Agriolimacidae, *Karaftohelix* sp.). The zone is characterised by an equal proportion of molluscs from forest habitats (4 species, 95%) and intermediate habitats (4 species, 5%). However, the greater number of forest species (324 shells) suggests that forests grew around the cave in temperate climate conditions.

MZ4 was defined in square B5 (depth interval 0–0.1 m, layer 3), square B4 (depth interval 0–0.1 m, layer 3), square B3 (depth interval 0–0.1 m, layer 3) and square B2 (depth interval 0.1–0.2 m, layer 3). 1573 shells of 12 taxa were identified (*Cochlicopa lubrica*, *Vallonia patens*, *V. pulchellula*, *Vertigo* cf. *japonica* Pilsbry and Hirase, 1904, *Gastrocopta theeli*, *Discus depressus*, *Euconulus fulvus*, *Hawaiia minuscula*, *Perpolita petronella*, Agriolimacidae, *Karaftohelix maacki*, *Karaftohelix* cf. *middendorffi*). The proportion of molluscs inhabiting forest bitopes is 81% (8 species), while molluscs from intermediate habitats account for 19% (4 species). This indicates the existence of a moderate climate and high humidity.

In the zones MZ2, MZ3 and MZ4, fragments of shells of freshwater molluscs of the Unionidae family were found, which indicates the proximity of a body of water (river) near the cave.

MZ5 was established in square B2 (depth interval 0–0.1 m, layers 1–3); 483 shells from 11 taxa were identified (*Vallonia patens*, *V. pulchellula*, *Vertigo* cf. *japonica*, *Gastrocopta theeli*, *Discus depressus*, *Euconulus fulvus*, *Hawaiia minuscula*, *Perpolita petronella*, Agriolimacidae, *Karaftohelix maacki*, *Karaftohelix* cf. *middendorffi*). The majority of taxa indicate forest growth (7 species, 64%) in the study area with intermediate spaces (4 species, 36%). The number of *Gastrocopta theeli* shells, which inhabit the dry southern slopes covered with oak forests in Primorsky Krai (Likharev and Rammelmeyer, 1952), is increasing, indicating that the climate was moderate and humidity has decreased. In contrast to the earlier zones, there are no fragments of Unionidae shells at this section and higher up.

MZ5–6 was established in square B1 (depth interval 0.2–0.3 m, layers 2–3); 366 shells from nine taxa were identified (*Vallonia patens*, *Vertigo* cf. *japonica*, *Gastrocopta theeli*, *Discus depressus*, *Euconulus fulvus*, *Hawaiia minuscula*, *Perpolita petronella*, Agriolimacidae, *Karaftohelix maacki*). Most species prefer forest habitats (5 species, 56%) and some are typical of intermediate spaces (4 species, 44%).

MZ6 was established in square B1 (depth interval 0.1–0.2 m, layer 2, and depth interval 0–0.1 m, layers 1–2); 742 shells of 12 taxa were identified (*Carychium pessimum* Pilsbry, 1902, *Cochlicopa lubrica*, *Vallonia patens*, *Vertigo* cf. *japonica*, *Gastrocopta theeli*, *Discus depressus*, *Euconulus fulvus*, *Hawaiia minuscula*, *Perpolita petronella*, Agriolimacidae, *Karaftohelix maacki*, *Karaftohelix* cf. *middendorffi*). Molluscs that prefer forest habitats account for 50% (6 species), while molluscs typical of intermediate spaces represent 50% (6 species). During the period when molluscs of MZ5–MZ6 lived, the climate was moderate and dryer than before.

6.2. Verterbrates

SMZ1 corresponds to the lowest horizons in pit I of the squares B4 and B5 (see Figs. S2–5 in Supplementary data). Large mammal bone remains are absent. The fossil assemblage includes Chiroptera bone remains from two forest species *Myotis sibiricus* (Kashchenko, 1905) and *Murina hilgendorfi* (Peters, 1880) and two *Sorex* species that prefer to inhabit forests and open spases. Among rodents, single bone remains of the genus *Alexandromys* and *Myospalax psilurus* Milne-Edwards, 1874, the inhabitants of open and semi-open areas were identified in this zone. Single bone remains of *Falcipennis falcipennis* (Hartlaub, 1855) and *Lagopus lagopus* (Linnaeus, 1758) were also found. Currently, in the northern part of Primorsky Krai, *Falcipennis falcipennis* nests in dark-coniferous forests and in *Betula ermanii* forests with thickets of *Pinus pumila* (Pallas) Regel, 1859 (Gluszhenko et al., 2016). The current distribution of *Lagopus lagopus* at the southern boundary of its range extends beyond to the south of Primorsky Krai — south of the upper streams of Zeya River, Selemdzha River, Bureya River, and Argun River; it includes the highlands of the Dusse-Alin Ridge, crosses the lower course of the Amur River, and reaches as far as the Tatar Strait of 51°C (Potapov, 1987, p. 205). As the results of palynological analysis indicate, this zone corresponds to the Early Holocene, when forest-steppe landscapes were prevalent alongside the expansion of polydominant forests.

SMZ2 corresponds to layer 6 of pit I in squares B4 and B5 at a depth of 0.4–0.5 m, it also includes deposits of squares A and B from the upper part of the cave (depth interval 0.1–0.2 m). Bone remains of typical forest species such as *Falcipennis falcipennis*, *Tetrastes bonasia* (Linnaeus, 1758), *Murina hilgendorfi*, *Plecotus ognevi*, *Sciurus vulgaris* Linnaeus, 1758, *Eutamias sibiricus* Laxmann, 1769, and *Lemmus amurensis* Vinogradov, 1924 are present, as well as species of open spaces (*Lagopus mutus* (Montin, 1781), *Cercopis daurica* (Linnaeus, 1758), *Delichon dasypus* (Bonaparte, 1850), *Perdix dauurica*, and *Myospalax psilurus*). It is worth noting that the southern boundary of the *Lagopus mutus* range on the mainland is situated even further north than that of the *Lagopus lagopus*; however, an isolated population of *Lagopus mutus* exists in Japan, specifically on Honshu Island (Potapov, 1987). The habitats of *Lagopus mutus* are confined to the subalpine and alpine belts and alternate with large stone placers, screes and rocks (Potapov, 1987). In Sikhote-Alin Mountains, remains of both *Lagopus lagopus* and *Lagopus mutus* have been found in Chertovy Vorota Cave (Alekseeva et al., 1984, 1990; Panteleev, 1999), in the deposits accumulated 7.1–5.8 kyr ago (Glushankova et al., 1978), and in Tetyukhinskaya Cave and Bezymyannykh Grotto (= Krivoi) (according to A.V. Panteleev, unpublished data). *Ochotona* is represented by *Ochotona hyperborea* and two extinct species *Tonomochota sikhotana* and *T. khinganica*. Among the rodents, *Alexandromys* (43.1%) and *Clethrionomys rutilus* Pallas, 1779 and *Craseomys rufocanus* Sundevall, 1846 (44.8%) are almost equally represented.

SMZ3 corresponds to layers 5–6 in squares B3, B4 and B5 at a depth of 0.2–0.4 m and layer 2 in squares A and B in the upper part of the cave (depth interval 0–0.1 m). It is characterised by the richest species composition and a large number of bone remains. Among the bird bone remains forest species such as *Tetrastes bonasia*, *Falcipennis falcipennis* and *Certhia familiaris* Linnaeus, 1758 were identified. Of the occurrence of open spaces is indicated by the bone remains of *Hirundo rustica* Linnaeus, 1758, *Delichon dasypus*, and three species of partridges (*Lagopus lagopus*, *L. mutus* and *Perdix dauurica*) were found. Large mammals are represented by *Lepus timidus* Linnaeus, 1758, *Sus scrofa* Linnaeus, 1758, *Moschus moschiferus* Linnaeus, 1758, *Cervus nippon* Temminck, 1838, *Capreolus pygargus* (Pallas, 1771), *Alces americanus* (Clinton, 1822), *Meles leucurus* (Hodgson, 1847), *Martes zibellina* Linnaeus, 1758, *Mustela nivalis* (Linnaeus, 1766), *Nyctereutes procyonoides* (Gray, 1834), and *Ursus* sp. Among the Soricomorpha, the largest number of bone remains belong to *Sorex* ex gr. *unguiculatus-isodon* and *Mogera robusta* Nehring, 1891; and among the Chiroptera, the greatest number of bones remains belong to *Murina hilgendorfi*. The Ochotonidae are represented by fossils assigned to *Ochotona hyperborean* and to three extinct species of the recently described genus *Tonomochota* — *T. khasanensis*, *T. sikhotana*, and *T. khinganica*. *Craseomys rufocanus* is with about 61% of the dominant species among the rodents. Species that prefer a forest habitat as well as species that inhabit open spaces are represented by *Rattus norvegicus* Berkenhout, 1769 and *Tscherskia triton* de Winton, 1899. Palynological data indicate a Middle Holocene age. Forest-steppe landscapes are developing, yet simultaneously, there is an increase in the forestation of the area. It is important to note that ceramics (Kluyev et al., 2023) were discovered in the deposits of this zone, which can be linked to the Rudninsky archaeological culture of the Middle Neolithic (7–6 kyr ago).

SMZ4 corresponds to layers 4 and 5 in square B3 and layer 5 in squares B4 and B5 at a depth of 0.1–0.2 m. Here, bone remains of *Eptesicus nilssonii* (Keyserling and Blasius, 1839) appear. This relatively cold-resistant species mainly spreads north of the studied area. This zone likely corresponds to a period about 4.3 kyr ago, when climate cooling was observed following the Holocene Optimum (Evstigneeva and Cherepanova, 2022).

SMZ5 corresponds to the main layer 3 in squares B2 (depth interval 0–0.3 m), B3 (depth interval 0–0.1 m), B4 (depth interval 0–0.1 m) and B5 (depth interval 0–0.1 m). There are still the remains of *Eptesicus nilssonii*, but also the southern appearance of *Pipistrellus abramus* (Temminck, 1838). *Tonomochota khasanensis* and *Myospalax psilurus* reappear. The climate has become warmer, a change that occurred approximately 4–3.22 kyr ago (Razzhigaeva et al., 2016).

SMZ6 corresponds to deposits in the square B1 (depth interval 0–0.3 m). The species composition of the represented birds and mammals corresponds to the modern one. The exception is the single tooth of the *Spermophilus undulatus* Pallas, 1778. Clearly, this species is not typical of this zone and has been redeposited from deeper layers of cave deposits.

6.3. Spores and pollen

The analysis of the taxonomic composition of the spores and pollen samples from pit I square B4 made it possible to distinguish four palynological complexes (PCs). Their description is presented from the bottom to the top of the section.

PC1 is corresponded to reddish-brown clay from the lower part of the pit (layer 4, spore and pollen (SP) SP1 and SP2 samples, depth interval 0.5–0.7 m) with palynospectres that are dominated by spores (86–87%). Among them are the spores of ferns (Polypodiaceae (67–69%) and Ophioglossaceae (single)), lycopodiums (*Lycopodium annotinum* (5–8%) and *Huperzia selago* (single)), and mosses (*Sphagnum* sp. (8%) and Bryales (1–3%)). Among the group of grass plants (7–10%), Poaceae (1–3%) and meadow herbage pollen prevails: Scrophulariaceae (3%), Asteroideae, Rosaceae, Ericaceae, Apiaceae, Fabaceae, Lamiaceae and Caryophyllaceae (single). Single *Artemisia* sp. pollen grains were also identified. Among the synanthropic plants, only ruderal Chenopodiaceae and Cichorioideae taxa are noted. Pollen of tree and shrab plants are rare (3–6%). This group is represented by small-leaved *Betula* sect. Costatae, *B.* sect. Albae, *Alnaster* sp., *Salix* sp., broadleaved *Corylus* sp., *Quercus* sp., *Juglans* sp. and coniferous plants: *Picea* sp. and *Pinus* (Haploxylon), as well as *Ephedra* sp.

In the PC2, detected in a dark loam from the overlying layer (layer 3, SP3 sample, depth interval 0.4–0.5 m), there is an increase in the fraction of the pollen from grasses (18%) and tree-scrub plants (10%). The composition of the grass plants remains unchanged; pollen grains from Poaceae (4%) and various meadow herbage representatives, such as Scrophulariaceae (8%), Rosaceae, Fabaceae, Ericaceae, Asteroideae, Apiaceae, Lamiaceae, Caryophyllaceae and Cyperaceae (single) continue to prevail. Also pollen of *Artemisia* sp. are identified. Cichorioideae and

Chenopodiaceae (single) represent the sinanthropic flora. In the group of tree-shrub plants, the content of pollen grains of small-leaved plants increases: *Betula* sect. Nanae (3%), *B.* sect. Albae, *B.* sect. Costatae, *Betula* sp., *Alnaster* sp. and *Salix* sp. (single); the variety of broadleaved ones increases: *Tilia* spp., *Corylus* sp., *Ulmus* sp., *Juglans* sp. and *Aralia* sp. (single); and the list of conifers is reduced (single *Picea* sp.). In the allocated palynological spectrum, spores (72%) continue to dominate: ferns — Polypodiaceae (56%), and Ophioglossaceae (single), mosses — *Sphagnum* sp. (9%), and Bryales (3%). The percentage of the spore plants is noticeably reduced: *Lycopodium annotinum* (single); *Huperzia selago* has fallen out of the spectrum.

PC3. Above the section, in the sample of brownish-grey loam (layer 2, SP4 sample, depth interval 0.3–0.4 m) and the sample of yellowish-grey loam from the lower part of the layer (layer 1, SP5 sample, depth interval 0.2–0.3 m) spore and pollen spectra with the dominance of spores (74–80%) were determined. The group is dominated by spores of ferns: Polypodiaceae (55–63%) and Ophioglossaceae (12%). The percentage of mosses is reduced: *Sphagnum* sp. (3–5%) and Bryales (single). The quantity of the spores of the lycopodiums remains low: *Lycopodium annotinum* (single); the spores of *Huperzia selago* (single) appear again. In one of the palynospectum (SP4), the highest percentage of pollen from tree-shrub plants is allocated (14%). A significant contribution is made to this group by broadleaved trees: *Tilia* spp. (3%), *Quercus* sp., *Corylus* sp., *Ulmus* sp. (single). A slight increase in the content of pollen grains of coniferous trees was also noted: *Pinus* (*Haploxylon*) and *Pinus* (*Diploxylon*), *Picea* sp. (single). A decrease in the role of small-leaved trees was observed: *Betula* sect. Nanae, *B.* sect. Albae, *B.* sect. Costatae, *Alnus* sp. and *Salix* sp. (single). In addition, single pollen of *Viburnum* sp. and *Rubus* sp. shrubs could be found sporadically in the spectra. Herbs (11–12%) are represented by Poaceae (2–3%), *Artemisia* sp. (single) and herbage: Scrophulariaceae (2–5%), Rosaceae (2–3%), Asteroideae, Fabaceae, Ericaceae and Cyperaceae (single). Among synanthropic plants Cichorioideae, Chenopodiaceae and *Urtica* sp. (single) are observed.

PC4. In the samples of yellowish-grey loam from the upper part of the layer (layer 1, SP6 and SP7 samples, depth interval 0–0.2 m), spore and pollen spectra showed a dominance of spores (86–88%), primarily represented by Polypodiaceae (78–81%). Single spores of ferns (Ophioglossaceae), mosses (*Sphagnum* sp.), and lycopodiums (*Lycopodium annotinum*, *Selaginella* sp. and *Huperzia selago*) were detected. Among the grassy plants (7–8%), the percentage of *Artemisia* sp. (2–3%) pollen increases. The amount of Poaceae (single) and herbage (Rosaceae (2–3%), Scrophulariaceae, Lamiaceae, Ericaceae, Apiaceae, Cyperaceae and Onagraceae (single)) pollen grains decreases. The proportion of the pollen of synanthropic plants remains low: *Polygonum aviculare*, Chenopodiaceae и *Urtica* sp. (single). The content of pollen grains of trees-shrub plants is reduced to 5–6%. This group is represented by various small-leaved trees: *Betula* sect. Albae, *B.* sect. Nanae, *B.* sect. Costatae, *Betula* sp., *Alnus* sp., *Salix* sp.; broadleaved plants: *Tilia* spp., *Quercus* sp., *Corylus* sp.,

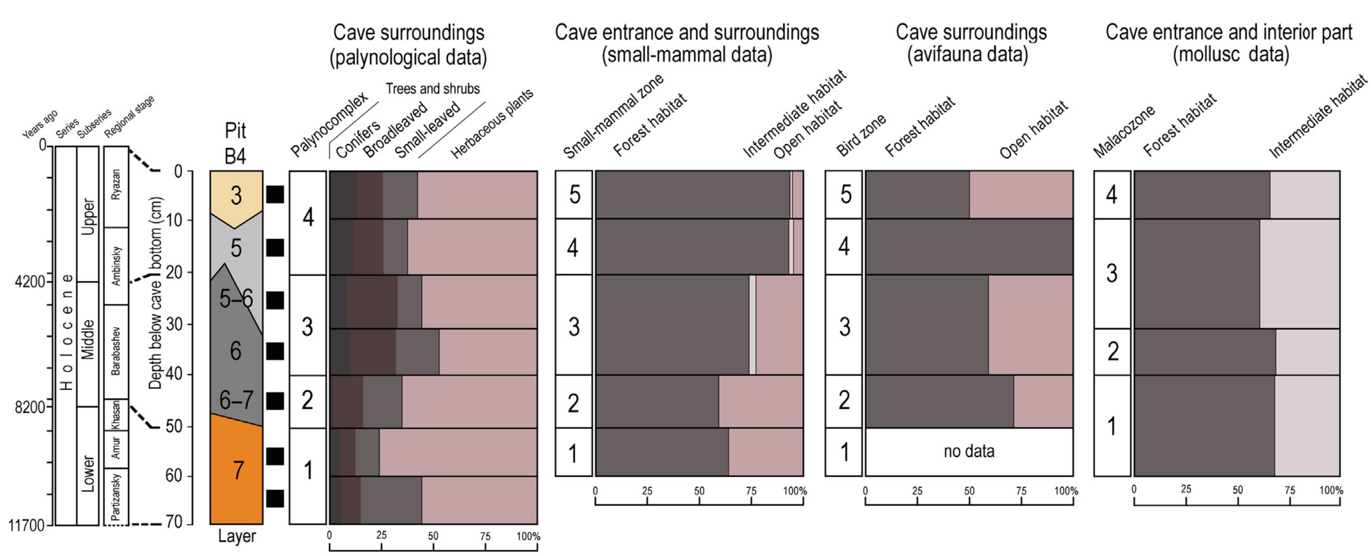

Fig. 7. A summary of the palynological and faunal investigations in the Perspektivnaya Cave site. From left to right: 1) Chronostratigraphical Stages: Formal subdivision of the Holocene Series (https://stratigraphy.org/news/125); Regional Stages for Sikhote-Alin Mountains and south-west Primorsky Krai territory (Korotkiy et al., 1980; Anonymous, 1987) (see text for explanations); 2) Cave surroundings habitat reconstructions are given on the base of the palynological data; 3) Cave entrance and surroundings habitat reconstructions are given on the base of the small-mammalian data; 4) Cave surroundings habitat reconstructions are given on the base of the avifauna data; 5) Cave entrance and interior part habitat reconstructions are given on the base of the malacological data. Malacological, avifaunal and small-mammalian zones descriptions and possible environment reconstructions are given in the text.

Juglans sp., *Ulmus* sp., *Carpinus* sp., and coniferous plants: *Picea* sp., *Pinus* (Haploxylon) and *Pinus* (Diploxylon), as well as bushes Moraceae (single).

6.4. Palaeoenvironment (habitat) reconstruction

The palaeonvironmental reconructions are only based on the Perspectivnaya Cave data from square B4 (Fig. 7), combined with the data from the other squares of pit I and data published by the other authors. Some discrepancies between zones may relate to both the characteristics of the material under study and the nature of its accumulation (such as different possibilities for pollen transfer, various agents for the accumulation of bone remains, etc.) as well as to the living conditions: molluscs do not move the same long distances as vertebrates do and are found primarily in very local habitats.

Early Holocene (from 11.7 to 8.2 kyr ago)

PC1, obtained from the lower part of the section of pit 1 (square B4), made it possible to reconstruct the distribution of forest-steppe landscapes in the surroundings of the cave. Meadow vegetation was represented by mesophilous herbs, dominated open spaces (clearings in the forest and forest edges). Steppe plants (*Artemisia*, *Ephedra*, Poaceae) and ferns occupied the rocky slopes. On the flat areas, floodplain birch forests with *Alnaster* and *Salix* were widespread, on the mountain slopes — mixed forests with *Corylus*, *Quercus*, *Juglans*, *Picea* and *Pinus*. There were marshy areas with *Sphagnum*, *Lycopodium*, Bryales and Ericaceae.

The climate during this period was moderately warm and humid, progressively becoming more humid.

Palynocomplex PC1 is correlated with the Lower Holocene deposits. During the Early Holocene, polydominant forests with a small proportion of coniferous trees became widespread within the Khanka depression in the southwest of Primorsky Krai and *Ulmus*, *Quercus*, *Juglans*, *Carpinus* and *Fraxinus* Linnaeus, 1753 dominated. In the swampy floodplains of rivers and in swamps on the plains, communities with *Betula* sect. Nanae and *Alnaster* still survived. The grass cover was dominated by mesophilous vegetation (Belyanin and Belyanina, 2012, 2020, 2023). Further south, on the Shufan (Borisov) Plateau, mixed forests with *Pinus koraiensis* Siebold and Zuccarini, 1842, *Betula*, *Quercus*, *Juglans*, *Ulmus* and *Corylus* were widespread. The herbs were also highly diverse. In the swamps, there was a reduction in shrub vegetation and an expansion of territories occupied by *Sphagnum* (Razzhigaeva et al., 2021). In the south of Primorsky Krai (western coast of Peter-the-Great Bay), the vegetation cover was dominated by *Picea*, *Pinus koraiensis*, *Betula* sp.; broadleaved trees were also present (Anderson et al., 2017; Belyanin et al., 2019).

The malacofaunal complex (MZ1) corresponds with the transitional interval — the upper part of the Lower Holocene and lower part of the Middle Holocene deposits. It demonstrates the distribution of broadleaved forests (*Discus depressus*), forest-steppe landscapes and the increased humidity of a temperate climate (Agriolimacidae).

The analyses of the small mammal bone remains (SMZ1) (there are no bone remains of birds here), indicate a correlation to the upper part of the Lower Holocene deposits. Species that inhabit dry areas with steppe and forest-steppe vegetation (*Myospalax psilurus*) are present along with species that prefer to live in forests.

Thus, our research indicates that with the onset of the Holocene, the southern region of the Russian Far East began to become forested. By this time, the area of forest-steppes had slightly decreased and become restricted to specific local habitats (Korotkiy et al., 2005; Evstigneeva and Cherepanova, 2022), such as near the Perspektivnaya Cave.

Middle Holocene (from 8.2 to 4.2 kyr ago)

Later, during the period of palynocomplex PC2, there was a minor increase in the open spaces (clearings in the forest and forest edges) occupied by various herbage communities, as well as swampy areas overgrown with *Sphagnum*, *Lycopodium*, Bryales, and Ericaceae in the area. The role of broad-leaved elements in the forests has increased significantly: *Tilia*, *Corylus*, *Ulmus*, *Juglans* and *Aralia*. The climate became warmer and more humid.

PC3 also indicates the occurrence of forest-steppe landscapes. During this period, there was an increase in forestation of the territory. The mountain slopes were covered by polydominant forests with *Tilia*, *Quercus*, *Corylus*, *Ulmus*, *Pinus* and *Picea*. Among the ferns, Ophyoglossaceae makes a significant contribution. As earlier, herbage, Poaceae, and *Artemisia* were widespread in open spaces. The marsh areas containing *Sphagnum*, *Lycopodium*, Bryales, and Ericaceae are starting to diminish. The drained regions are taken over by *Alnus*. The climate remains warm and humid, with an emerging tendency towards cooling and aridification at the end.

PC2 and PC3 are correlated with the Middle Holocene deposits. Climate warming during the Middle Holocene led to the widespread distribution of broad-leaved forests in the Khanka Depression (Belyanin and Belyanina, 2012, 2020, 2023). In the meantime, the area covered by broadleaved trees and *Pinus koraiensis* on the Shufan Plateau increased sharply (Razzhigaeva et al., 2021). In the south of Primorsky Krai, forests with *Quercus*, *Ulmus*, *Betula* and *Pinus koraiensis* dominated. In the structure of the vegetation cover, the plant formations of the Late Pleistocene and Early Holocene — *Alnaster* thickets and sphagnum bogs — have practically disappeared (Anderson et al., 2017; Belyanin et al., 2019). In the southern Sikhote-Alin Mountains, the accumulative plains were covered by small-leaved plant communities, which were replaced by polydominant forests on the accumulative-denudation plains (Belyanin et al., 2021).

The mollusc fauna (MZ2), collected from deposits that are correlated with the Middle Holocene based on palynological data, indicates the further development of forest and forest-steppe areas (*Discus depressus*, *Euconulus fulvus*, *Perpolita petronella*, *Karaftohelix*), and that the climate was moderate and humid (*Cochlicopa lubrica*, Agriolimacidae).

The bird and mammal faunal composition (SMZ2, SMZ3, BZ2, BZ3) indicates a continuation of the dominance of forest vegetation, alongside a slight increase in the distribution area of open spaces in the vicinity of the cave entrance and its surroundings.

The study of both the palynospectra and the species composition of small mammals and molluscs demonstrated that at the beginning of the Middle Holocene, the area around the Perspektivnaya Cave was still covered by forest-steppe, during a later phase forest began to cover larger areas. Our results are consistent with the conclusions drawn by Evstigneeva and Cherepanova (2022), who stated that in the south of the Russian Far East, there was a reduction in open spaces and the forests during the Middle Holocene. It was during this period that ancient humans visited the cave, as indicated by the discoveries of ceramics and the radiocarbon dating of a tooth.

Late Holocene (from 4.2 kyr ago to the present)

The PC4 data indicate the spread of forest-steppe. At that time, various mesophilous herbs, such as *Artemisia* and Poaceae, flourished in open spaces like clearings in the forest and along forest edges. Polydominant forests with *Tilia*, *Quercus*, *Corylus*, *Ulmus*, *Juglans*, *Carpinus*, *Pinus* and *Picea* were widespread as well as floodplain forests with *Betula*, *Alnus* and *Salix*. The areas of swampy territories continued to shrink. In rocky areas, polypod ferns again established a dominant position. The climate turned cooler and more arid.

PC4 is correlated with the Upper Holocene deposits. In southwestern Primorsky Krai, in the Khanka depression, during the Late Holocene, there was a decrease of broadleaved forests and vegetation species diversity in general (Belyanin and Belyanina, 2012, 2020, 2023). On the Shufan Plateau, broadleaved forests with *Pinus koraiensis* were widespread, and an increase in the role of *Abies* Miller, 1754 was noted (Razzhigaeva et al., 2021). In the south of Primorsky Krai, during Middle–Late Holocene transition, dark coniferous and small-leaved vegetation became widespread, and the proportion of polydominant forests noticeably decreases. Later, the cooling is replaced by warming. At that time, there was an expansion of forests with the dominance of Mongolian oak and Korean pine (Anderson et al., 2017; Belyanin et al., 2019). The Late Holocene cooling led, in the southern Sikhote-Alin Mountains, to a reduction of broadleaved forests and an increase in the proportion of small-leaved species (Belyanin et al., 2021). Later, during warming periods, the proportion of broadleaved species increased in forest areas, and during cold periods, Korean pine and dark coniferous species, primarily *Picea*, increased (Razzhigaeva et al., 2016).

The Late Holocene molluscan assemblages (MZ3, MZ4 and MZ6) show the development of broadleaved or mixed forests close to the cave entrance (*Vallonia patens*, *Discus depressus*, *Euconulus fulvus*, *Karaftohelix* sp.) with semi-open areas (*Perpolita petronella*, *Hawaiia minuscula*, *Vertigo* cf. *japonica*) with high humidity (*Cochlicopa lubrica*, Agriolimacidae). The Late and Middle Holocene deposits contain the highest number of shell fragments from freshwater Unionidae, which may suggest the activities of both humans and wild animals, who utilised molluscs for food, decoration, or other purposes.

Based on the bone remains of mammals from all studied materials (SMZ4, SMZ5, and SMZ6), it appears that the area of forest vegetation surrounding the cave increased during the Late Holocene.

Bird remains from BZ4, BZ5, and BZ6 are from both forest species (*Regulus regulus*, *Tetrastes bonasia*, *Troglodytes troglodytes*, and *Parus palustris*), and species inhabiting more open bushes/spaces (*Lanius borealis*, *Delichon dasypus*, *Lagopus lagopus*, and *Perdix dauurica*).

Thus, according to the data from the Perspektivnaya Cave, open spaces covered with rich meadow vegetation, adjacent to polydominant broad-leaved forests, continued to exist in the vicinity of the cave. During this period, the remains of pikas of the genus *Tonomochota* are no longer encountered, this likely indicates their extinction during the Late Holocene.

7. Conclusion

Palynological studies of unconsolidated sediments in the Perspektivnaya Cave have enabled the reconstruction of landscapes and regional climatic conditions of the Early, Middle and Late Holocene. Throughout this period, forest-steppe landscapes were prevalent in the adjacent territory, and ferns consistently thrived in abundance in the entrance area of the cave. In general, meadow vegetation was characterised by mesophilous herbs, which dominated open spaces such as clearings in the forest and forest edges; steppe plants and ferns occupied the rocky slopes. Mixed forests covered the mountain slopes, while floodplain birch forests were widespread in the flat areas, alongside marshy regions. Detailed studies showed fluctuations in the vegetation development. Thus, the most significant changes occurred in the composition of forest formations: during the Middle Holocene, the area covered by small-leaved and coniferous forests decreased, *Alnaster* disappeared, and the territory occupied by broadleaved species expanded. In the Late Holocene, on the backdrop of the dominance of broadleaved forests, the contribution of dark coniferous and light coniferous elements increased. The warmest and most humid conditions were characterised as typical of the Middle Holocene, the optimal phase of the Holocene. A moderately warm and more arid climate was characteristic of the Early and Late Holocene.

The conclusions drawn from the palynological studies are strongly supported by data on the composition and structure of faunas from various periods of the Holocene. Similar to other examined locations in Primorsky Krai, the grey red-backed vole *Craseomys rufocanus* dominated among rodents in all Holocene deposits of this cave. The Early Holocene deposits of the cave feature the presence of isolated bone remains of *Lagopus lagopus*, *Falcipennis falcipennis*, Hirundinidae indet., *Myotis sibiricus*, *Eptesicus nilssonii*, *Alexandromys* spp., *Clethrionomys rutilus* and *Craseomys rufocanus*. The richest composition of bird and mammal faunas was observed in the Middle Holocene (Northgrippian Stage). The most intriguing aspect of the Late Holocene in this region is the presence of *Pipistrellus abramus*, which is currently absent from Primorsky Krai (Tiunov et al., 2021), alongside three extinct species of Ochotonidae: *Tonomochota khasanensis*, *T. sikhotana*, *T. khinganica*, which seemingly became extinct quite recently. This decline is linked to the significant afforestation in the area, with evidence of this process beginning around 2 kyr ago, when the open spaces of steppe and forest-steppe type were reduced to minimum due to the expansion of forest vegetation.

The malacofauna is generally represented by species that are widespread in the study area. Molluscs inhabit broad-leaved forests growing near the cave, as well as open spaces such as forest edges or meadows with well-developed herbaceous vegetation, and areas of high humidity in moderate climatic conditions. Nearby, there was a flowing river with a variety of riparian vegetation, which was also inhabited by molluscs.

Thus, Perspektivnaya Cave served as a temporary habitat for ancient peoples, who visited it occasionally during the Middle Holocene. It would be particularly interesting to explore the connection between the palaeolandscape of the region and human habitation in caves. However, this is the sole cave site where human bone remains have been discovered and pollen data have been acquired (unfortunately, pollen is poorly preserved in cave deposits). The study of a newly identified site near Lake Khanka (Primorskyi Krai), where human bone remains have been found in the cave deposits, will enable a more comprehensive understanding of dynamics of natural changes in the region.

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Supplementary data

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