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Late Pleistocene and Holocene malacological and theriological faunas from the Tetyukhinskaya Cave (southern Far East, Russia) and their palaeoecological implications

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Abstract

Assemblages of terrestrial molluscs and small vertebrates were recovered from the Tetyukhinskaya Cave, located in the vicinity of the Dalnegorsk city, Primorsky Krai (south of the Far East, Russia), from which we identified characteristic zones of molluscs and small mammals. Based on analysis of the malacofauna and theriofauna, we interpret the molluscs as indicators of the biotopes at the cave entrance, and the mammals as indicators of the cave surroundings, and during late Late Pleistocene and Holocene, forests existed near the area surrounding the cave. The small mammal fauna suggests the development of open spaces of a pasture-like ecosystem during the warm periods of the Late Pleistocene with the development of the forest vegetation. This study demonstrates the importance of complex faunal investigations for the reconstruction of the palaeoenvironment in the Late Pleistocene and Holocene.

Keywords: Late Pleistocene; Holocene; Terrestrial molluscs; Mammals; Southern Far East; Palaeoecology

1. Introduction

Palaeontological remains of invertebrates and vertebrates are often found in unconsolidated deposits of karst cavities, and their study provides important information about the palaeoecological conditions of different time intervals during sedimentation. Molluscs are sedentary animals, and their study allows reconstructing the conditions of their microenvironment in the immediate vicinity of karst cavities. Compared to molluscs, analysis of the distribution of small mammal finds over time makes it possible to obtain information from a larger area around karst cavities. Comparison of data on molluscs and mammals may be used to analyze time ranges and changes in animal habitats.

Karst cavities are often located in mountainous areas, characterized by complicated topography and significant microclimate variations in valleys and on mountain slopes. The study of Quaternary molluscs and mammals from unconsolidated deposits of karst cavities for reconstruction of the natural environment is widely carried out in different areas (e.g. Alexandrowicz, 2000; Ložek, 2000; Stefaniak et al., 2009; Szymanek et al., 2016; Danukalova et al., 2020; Hajna et al., 2021; Osipova et al., 2021).

As noted by various researchers (e.g. Skoczylas-Śniaz and Alexandrowicz, 2022), the shells of terrestrial molluscs are thin-walled; chemical or physical impact easily leads to their destruction. Thus, the well-preserved mollusc shells

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found in cave deposits can be considered as buried in situ; in other words, mollusc assemblages reflect the palaeoecological conditions in which the sediments accumulated (Skoczylas-Śniaz and Alexandrowicz, 2022).

Over the past 17 years, thousands of bone remains of Late Pleistocene and Holocene mammals were extracted from unconsolidated terrigenous-carbonate and clayey deposits of caves in the south of the Russian Far East. At present, the collected fossil material stored in the Laboratory of Theriology of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences has not yet been fully processed, and only some of the research results have been published (Tiunov and Panasenko, 2007, 2010; Panasenko and Tiunov, 2010; Haring et al., 2015; Kosintsev et al., 2016, 2020; Tiunov, 2016; Tiunov et al., 2016, 2022; Voyta et al., 2019, 2021; Omelko et al., 2020; Tiunov and Gimranov, 2020; Tiunov and Gusev, 2021; Vershinina et al., 2021; Vinokurova et al., 2022). Quaternary molluscs from the karst site in the Primorsky Krai area are presented here for the first time.

We present here our comparative analyses of the mollusc and mammal faunas for the reconstruction of the palaeoenvironment of the Late Pleistocene and Holocene in the vicinity of the Tetyukhinskaya Cave, southeast of the Sikhote-Alin' Ridge and north of Dalnegorsk city, Far East, Russia.

2. Regional setting — The Tetyukhinskaya Cave

The Upper Pleistocene deposits of the region include two interglacial and two glacial horizons (Korotkiy et al., 1980; Anonymous, 1984). The Holocene deposits of Primorsky Krai are divided 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). The deposits of Southern Primorsky Krai have been characterized by palynological data, mammals, molluscs; other animals are rare. Materials obtained by the authors significantly supplement the existing knowledge about the development of the regional environment during the Late Pleistocene and Holocene.

The Tetyukhinskaya Cave is located 44°35′N, 135°36′E (Fig. 1), confined to the Upper Triassic carbonate rocks southeast of the Sikhote-Alin' Ridge and north of Dalnegorsk city, close to the Sea of Japan, where karst process is active in carbonate rocks in the temperate monsoonal climate. The entrance to the Tetyukhinskaya Cave is 410 m above sea level and the total length of the described part of the cave is 350 m (Gasilin et al., 2013).

Tatarnikov (2012) reported bones of mammals, birds, and amphibians of the Late Pleistocene and Holocene complexes, and Gasilin et al. (2013), based on the coloration of the bones, suggested that the material was in a mixed form. During the summer of 2012–2015, M.P. Tiunov excavated six pits in the cave, four of them reached the cave bottom.

Deposits in the pits I–VI of the Tetyukhinskaya Cave are described in Tiunov and Gusev (2021), summarized as follows.

Eight lithological layers in the unconsolidated deposits of the cave may be dinstinguished: 1 – greyish-brown uniform medium loam; 2 – brown medium loam with large stones; 3 – brownish heavy loam with small stones; 4 – brown medium loam with small stones; 5 – yellowish-brown light loam with small stones; 6 – light brown loam with small stones; 7 – yellowish clay with small stones; 8 – dark yellow wet clay with small numerous limestone fragments (Fig. 2).

3. Material and methods

Six pits were excavated in the unconsolidated deposits inside the cave; four of them at the entrance (Tiunov and Gusev, 2021). All pits at the entrance were dug to the rocky bottom. Despite some disturbance of the deposits, the sequence of layers can be fairly well traced in the profiles of the pit walls. The excavation was carried out in approximately 10 cm intervals. All faunal samples were wet-sieved (mesh size: 1 mm) and dried in the field; the dried sediment with the fossil remains was sorted and examined in laboratories (Fig. 2).

The mollusc remains include 15246 complete shells and shell fragments. The quantity of extracted shells per sample differs depending on the investigated level (see Table S1 in Supplementary data). The shell abundance is given according to Ložek (1964). The number of complete shells plus the number of apices or apertures which were considered as equivalent to one shell when taken together, were counted. Then, the resulting number of individuals, based on the fragments, was added to the number of unbroken specimens. Average species percentage for the particular layers was calculated for the palaeoecological considerations. Molluscs were identified using the descriptions and published reference keys of Sysoev and Shileyko (2009) and Prozorova et al. (2018).

Malacozones (MZ) 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%), insignificant (single) species (less than 5%) (Bakanov, 1987).

For palaeoecological analysis, the molluscs were classified based on the published results of the modern molluscs of the studied region (Likharev and Rammelmeier, 1952; Ložek, 1964; Riedel, 1967; Puisségur, 1976; Shileyko, 1978, 1984; Likharev and Viktor, 1980; Willis et al., 2000; Alexandrowicz, 2002; Prosorova et al., 2007, 2018; Sysoev and Shileyko, 2009; and taking into account data published by Germain, 1930; Adam, 1960; Kerney et al., 1983; Kerney and Cameron, 1999; Animalbase, www.animalbase.uni-goettingen.de; MolluscaBase, www.molluscabase.org). The shells of molluscs were photographed at the Institute of Geology UFRC RAS (Ufa) on a stereomi-

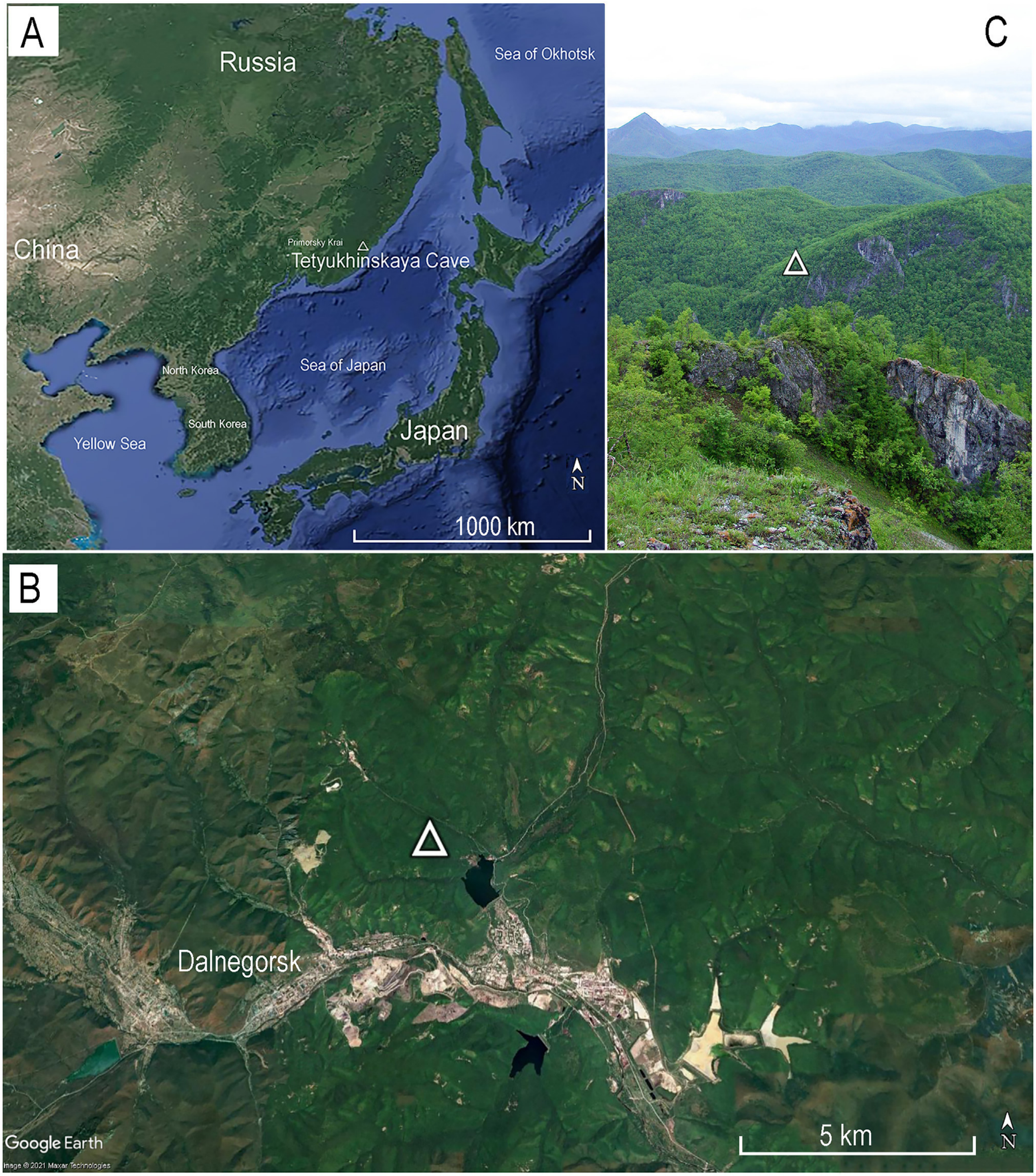


Fig. 1. Location maps of the Tetyukhinskaya Cave, southeast of Sikhote Alin' Ridge (A) and north of Dalnegorsk city (B). (C) Cave surrounding landscape (photo by M.P. Tiunov).

croscope Motic SMZ-171 with a camera Moticam-10+. The collection of mollusc shells (N 389) is stored at the Institute of Geology UFRC RAS (Ufa, Russia).

Sample concentration of mammal material was carried out in laboratory. About 24000 small mammal teeth were extracted. For species diagnostics, a reference collection and Handbooks with identification guides for individual groups of mammals were used (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), lemmings, all molars (m1, m2, m3, M1, M2, M3; mice of the genus *Apodemus* were identified based on the second upper molar (M2); other rodents

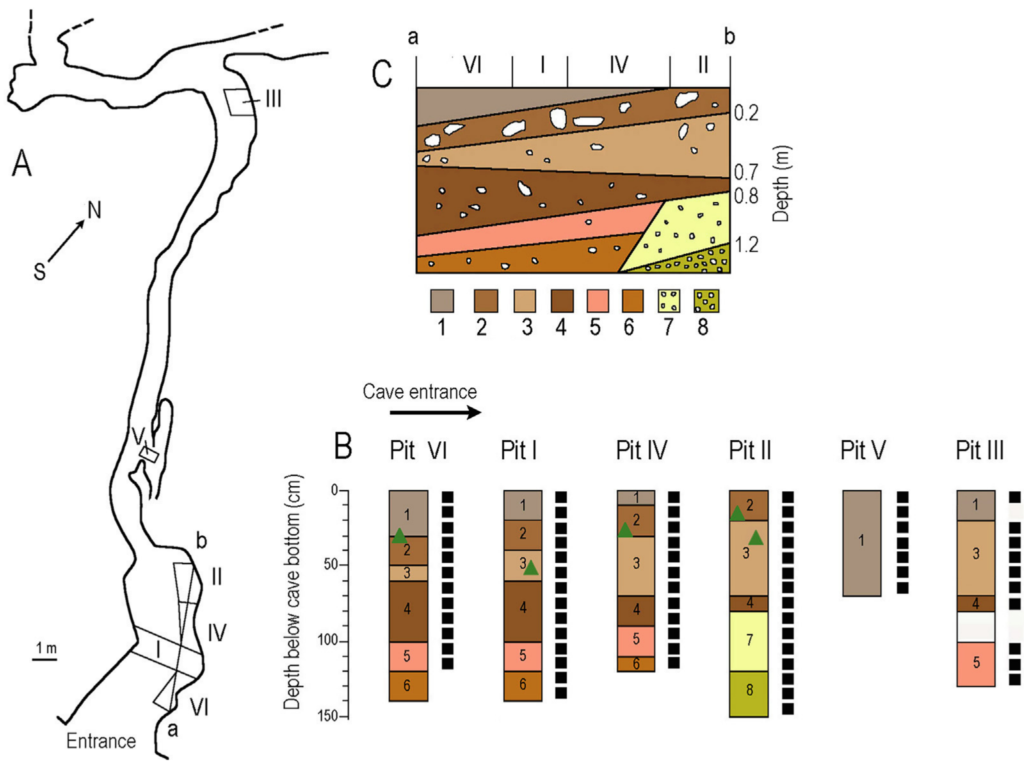


Fig. 2. (A) Scheme of the excavation sites in the entrance part of the Tetyukhinskaya Cave. (B) The pit columns, indicating the layers, and sample positions (black squares for paleontology, triagnles for radiocarbon dating). (C) A summary scheme of the pit section of deposits in the entrance part of the cave (pits VI–I–IV–II). Deposit symbols: 1–8 – numbers of layers which descriptions are given in Section 2.

could be identified based on any isolated teeth. In the Family Ochotonidae, all premolars p3, P3 as well as the isolated lower and upper teeth were sorted and quantified (see Table S2 in Supplementary data). The calculation is based on to the largest number of teeth of the same taxon. Small-mammal zones are indicated as SMZ.

The photographs of the teeth were taken with a SteREO Discovery.V12 stereo microscope and stacked using CombineZM software (Hadley, 2008). All mammal materials are stored at the Federal Scientific Centre of the Eastern Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences (Vladivostok, Russia).

The radiocarbon dating was applied for study material (see Table S3 in Supplementary data). Three radiocarbon dates were obtained from this site: using AMS: 39874 ± 133 BP (Asian black bear tooth; pit II, depth 0.4–0.5 m, layer 3; NSK–850, UGAMS–21786) and 37673 ± 950 BP (pit I, depth 0.5–0.6 m, layer 3, rhinoceros' tooth, NSKA–851; using ^{14}C: 20215 ± 1000 BP (mammal bones, layer 3, SPb–1057). These dates were used to correlate the studied deposits with Marine Isotope Stages (MIS 3–2) (Late Pleistocene to Holocene). Additional dates were obtained from this site (Sun et al., submitted) (see Table S3 in Supplementary data), suggesting early Holocene age for some levels.

4. Results

4.1. Molluscs

Mollusc shells are unevenly distributed in the deposits (see Fig. S1 in Supplementary data). The shells of *Carychium*, *Cochlicopa*, *Vallonia*, *Columella*, *Vertigo*, *Punctum*, *Discus*, *Hawaiia* are well preserved, there are complete shells of light white colour or with a reddish tint. A carbonate crust ($CaCO_3$) is observed on the surface of many shells. Some Bradybaenidae shells are found as the complete shells, but most of the finds are presented as separate fragments of these shells.

All identified specimens belong to terrestrial molluscs – 14 species, 11 genera (*Carychium* Müller, 1773, *Cochlicopa* Férussac, 1821, *Vallonia* Risso, 1826, *Columella* Westerlund, 1878 (1876), *Vertigo* Müller, 1773, *Punctum* Morse, 1864, *Discus* Fitzinger, 1833, *Euconulus* Reinhardt, 1883, *Hawaiia* Gude, 1911, *Perpolita* Baker, 1928, *Karaftohelix* Pilsbry, 1927) from 11 families (Ellobiidae Pfeiffer, 1854 (1822), Cochlicopidae Pilsbry, 1900 (1879), Valloniidae Morse, 1864, Vertiginidae Fitzinger, 1833, Truncatellinidae Steenberg, 1925, Punctidae Morse, 1864, Discidae Thiele, 1931 (1866), Gastrodontidae Tryon, 1866, Pristilomatidae Cockerell, 1891, Euconulidae

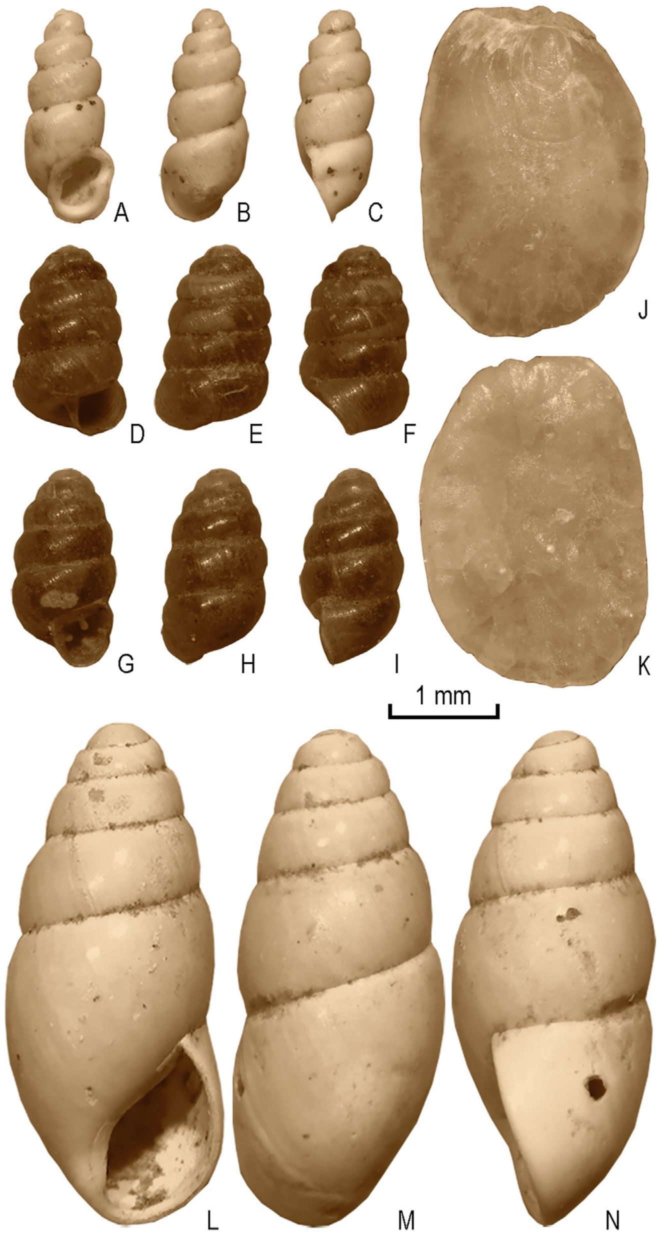


Fig. 3. Key species of mollusc genera *Carychium*, *Columella*, *Vertigo*, *Cochlicopa* and Limacoidea found in unconsolidated deposits of the Upper Pleistocene and Holocene of the Tetyukhinskaya Cave, Primorsky Krai, Russia. (A–C) *Carychium pessimum* Pilsbry, 1902, IG N 389/6685/1, pit VI, depth interval 0.9–1.0 m; (A) apertural view; (B) abapertural view (view from the opposite side of the aperture); (C) lateral view (top right). (D–F) *Columella edentula* (Draparnaud, 1805), IG N 389/6632/5, pit II, depth interval 0.1–0.2 m; (D) apertural view; (E) abapertural view (view from the opposite side of the aperture); (F) lateral view (top right). (G–I) *Vertigo* cf. *japonica* Pilsbry and Hirase, 1904, IG N 389/6633/7, pit II, depth interval 0.2–0.3 m; (G) apertural view; (H) abapertural view (view from the opposite side of the aperture); (I) lateral view (top right). (J, K) Limacoidea, IG N 389/6689/13, pit VI, depth interval 1.3–1.4 m; (J) dorsal view; (K) ventral side (view from the opposite dorsal side). (L–N) *Cochlicopa lubrica* (Müller, 1774), IG N 389/6701/2, pit IV, depth interval 0.4–0.5 m; (L) apertural view; (M) abapertural view (view from the opposite side of the aperture); (N) lateral view (top right).

Baker, 1928, Camaenidae Pilsbry, 1895 (Bradybaenidae) (see Table S1 in Supplementary data; Figs. 3–5). There are also representatives of Limacoidea (Agriolimacidae or Limacidae).

All the identified species belong to mesophilous category of molluscs (taxa tolerating temperate climate) (see Table S4 in Supplementary data). The Mollusc species were also attributed to three groups based on their preference for humidity: subhygrophilous and hydrophilous (requiring constant high humidity), mesophilous (tolerating moderate humidity). Molluscs were also subdivided into two groups based on their preference for the different types of vegetation: intermediate and woodland preferences.

4.2. Small mammals

The remains of insectivore species found in the Tetyukhinskaya Cave are fragmentary (190 fragments of mandibles and maxillaes, isolated teeth) (see Table S2 in Supplementary data; Fig. 6), including four genera (*Erinaceus* Linnaeus, 1758, *Mogera* Pomel, 1848, *Sorex* Linnaeus, 1758, *Crocidura* Wagler, 1832) and twelve species: *Erinaceus amurensis* Schrenk, 1859, *Mogera robusta* Nehring, 1891, *Sorex caecutiens* Laxmann, 1785, *S.* ex gr. *unguiculatus–isodon* (the discovered specimens are mainly represented by fragments of the lower jaws, in which these species do not differ), *Sorex gracillimus* Thomas, 1907, *Sorex mirabilis* Ognev, 1937, *Sorex daphaenodon* Thomas, 1907, *Sorex minutissimus* Zimmermann, 1780, *Sorex roboratus* Hollister, 1913, *Crocidura shantungensis* Miller, 1901, *Crocidura lasiura* Dobson, 1890.

Eighty-nine of the fossil isolated teeth of the ochotonids were found, including the most abundant *Ochotona hyperborea* Pallas, 1811. Teeth of the extinct genus *Tonomochota* Tiunov and Gusev, 2021 were found, which are larger than those of the northern pika.

The teeth and bones of rodents are the most numerous (n = 4792) in the studied deposits (see Table S2 in Supplementary data), including 5 sciurids (*Petaurista tetyukhensis* Tiunov and Gimranov, 2020, *Pteromys volans* (Linnaeus, 1758), *Sciurus vulgaris* Linnaeus, 1758, *Eutamias sibiricus* Laxmann, 1769 and *Urocitellus undulatus* (Pallas, 1779)), 4 murids (*Rattus norvegicus* (Berkenhout, 1769), *Apodemus agrarius* (Pallas, 1771), *Apodemus peninsulae* Thomas, 1907 and *Micromys minutus* (Pallas, 1771)), and 10 cricetids (*Tscherskia triton* (de Winton in de Winton and Styan, 1899), *Clethrionomys rutilus* (Pallas, 1779), *Craseomys rufocanus* (Sundevall, 1846), *Myopus schisticolor* (Lilljeborg, 1844), *Mimomys* sp., *Alexandromys mongolicus* (Radde, 1861), *Alexandromys fortis* (Büchner, 1889), *Alexandromys maximowiczii* Schrenk, 1859, *Alexandromys oeconomus* Pallas, 1776 and *Myospalax psilurus* Milne-Edwards, 1874).

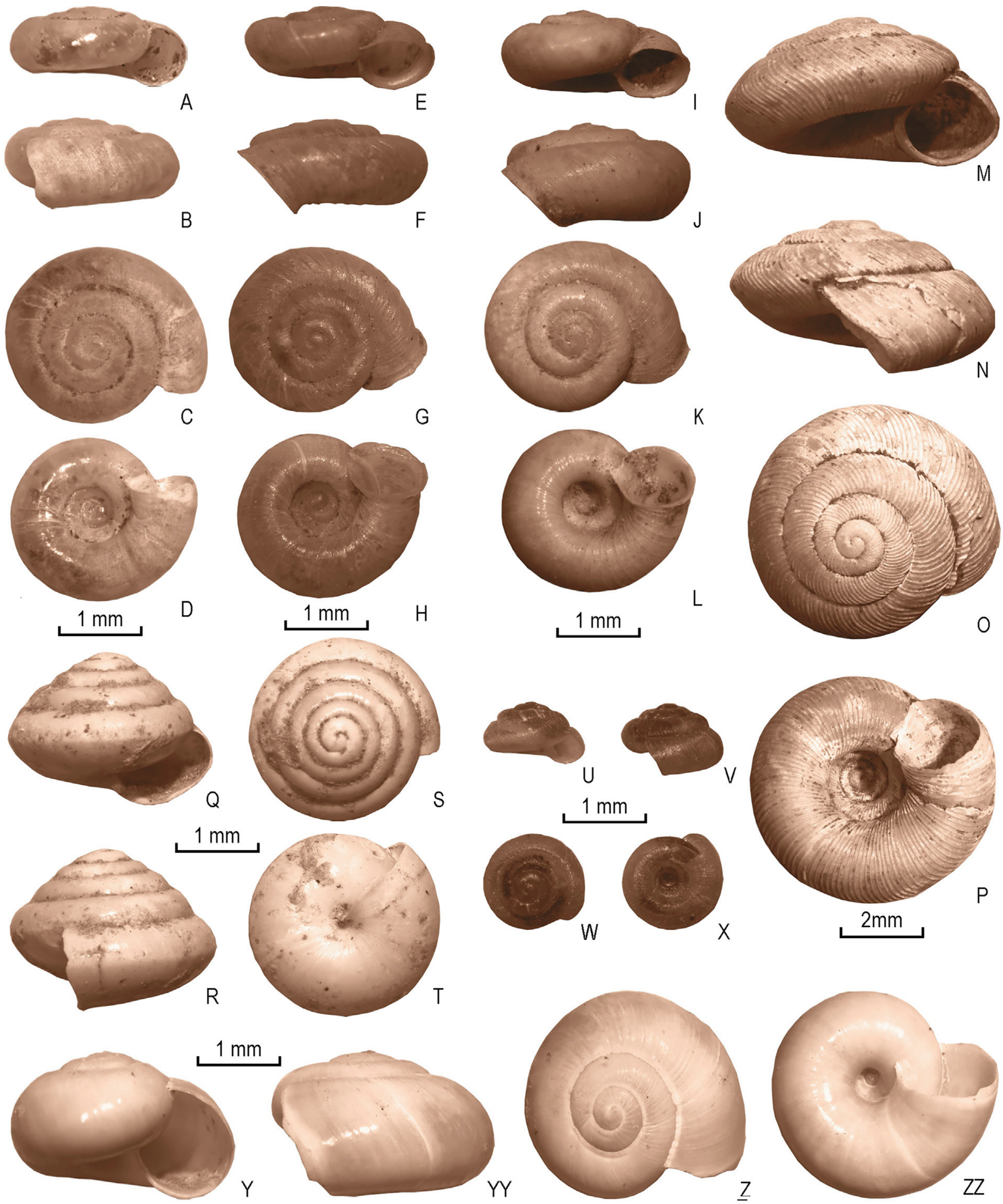


Fig. 4. Key species of molluscs' genera *Hawaiia*, *Vallonia*, *Discus*, *Euconulus*, *Punctum* found in unconsolidated deposits of the Upper Pleistocene and Holocene of the Tetyukhinskaya Cave, Primorsky Krai, Russia. (A–D) *Hawaiia minuscula* (Binney, 1841), IG N 389/6667/10, pit IV, depth interval 0–0.7 m; (A) apertural view; (B) lateral view (top right); (C) apical view; (D) umbilical view. (E–H) *Vallonia patens* Reinhardt, 1883, IG N 389/6669/3, pit V, depth interval 0.1–0.2 m; (E) apertural view; (F) lateral view (top right); (G) apical view; (H) umbilical view. (I–L) *Vallonia pulchellula* (Heude, 1882), IG N 389/6687/4, pit VI, depth interval 1.1–1.2 m; (I) apertural view; (J) lateral view (top right); (K) apical view; (L) umbilical view. (M–P) *Discus depressus* (Adams, 1868), IG N 389/6664/9, pit IV, depth interval 0.9–1.0 m; (M) apertural view; (N) lateral view (top right); (O) apical view; (P) umbilical view. (Q–T) *Euconulus fulvus* (Müller, 1774), IG N 389/6627/11, pit I, depth interval 1.1–1.2 m; (Q) apertural view; (R) lateral view (top right); (S) apical view; (T) umbilical view. (U–X) *Punctum ussuriensis* Likharev and Rammelmeyer, 1952, IG N 389/6633/8, pit II, depth interval 0.2–0.3 m; (U) apertural view; (V) lateral view (top right); (W) apical view; (X) umbilical view. (Y, YY, Z, ZZ) *Perpolita petronella* (Pfeiffer, 1853), IG N 389/6628/12, pit I, depth interval 1.2–1.3 m; (Y) apertural view; (YY) lateral view (top right); (Z) apical view; (ZZ) umbilical view.

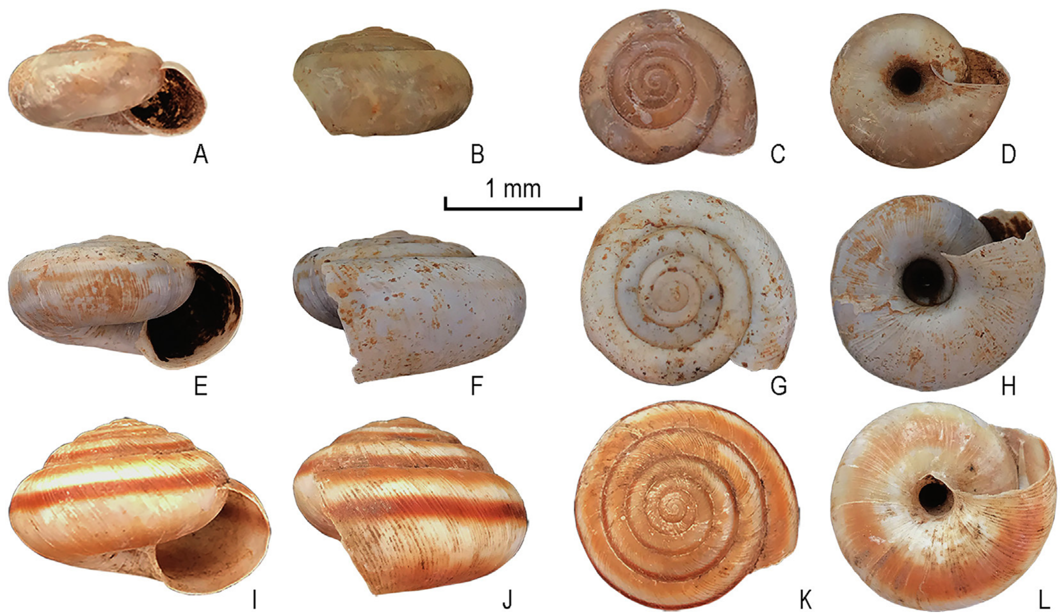


Fig. 5. Key species of mollusc's genus *Karaftohelix* found in unconsolidated deposits of the Upper Pleistocene and Holocene of the Tetyukhinskaya Cave, Primorsky Krai, Russia. (A–D) *Karaftohelix dieckmanni* (Mousson, 1887), IG N 389/6683/16, pit VI, depth interval 0.7–0.8 m; (A) apertural view; (B) lateral view (top right); (C) apical view; (D) umbilical view. (E–H) *Karaftohelix* cf. *middendorffi* (Gerstfeldt, 1859), IG N 389/6626/15, pit I, depth interval 1.0–1.1 m; (E) apertural view; (F) lateral view (top right); (G) apical view; (H) umbilical view. (I–L) *Karaftohelix maacki* (Gerstfeldt, 1859), IG N 389/6676/14, pit VI, depth interval 0–0.1 m; (I) apertural view; (J) lateral view (top right); (K) apical view; (L) umbilical view.

Both the Upper Pleistocene and Holocene layers contained bone remains of forest dwellers and species that prefer open and semi-open habitats (see Table S5 in Supplementary data). In all sediment layers, rodents were dominated by bone remains of the red-backed vole *Craseomys rufocanus*, and the insectivorous common shrew *Sorex caecutiens* (see Table S2 and Fig. S2 in Supplementary data), which indicate a fairly stable ratio of biotopes of these two species during the Late Pleistocene and Holocene. It also indicates that the way the remains have been accumulated hardly changed. The dominance of the bone remains of these species was also recorded in the Late Pleistocene–Holocene deposits of the caves of the Bliznetc (= Twin) and Medvezhiy Klyk (= Bear Fang) in the south of Primorsky Krai. It should be noted that the same species dominate in most modern communities in the south of the Far East.

5. Palaeoecological implications

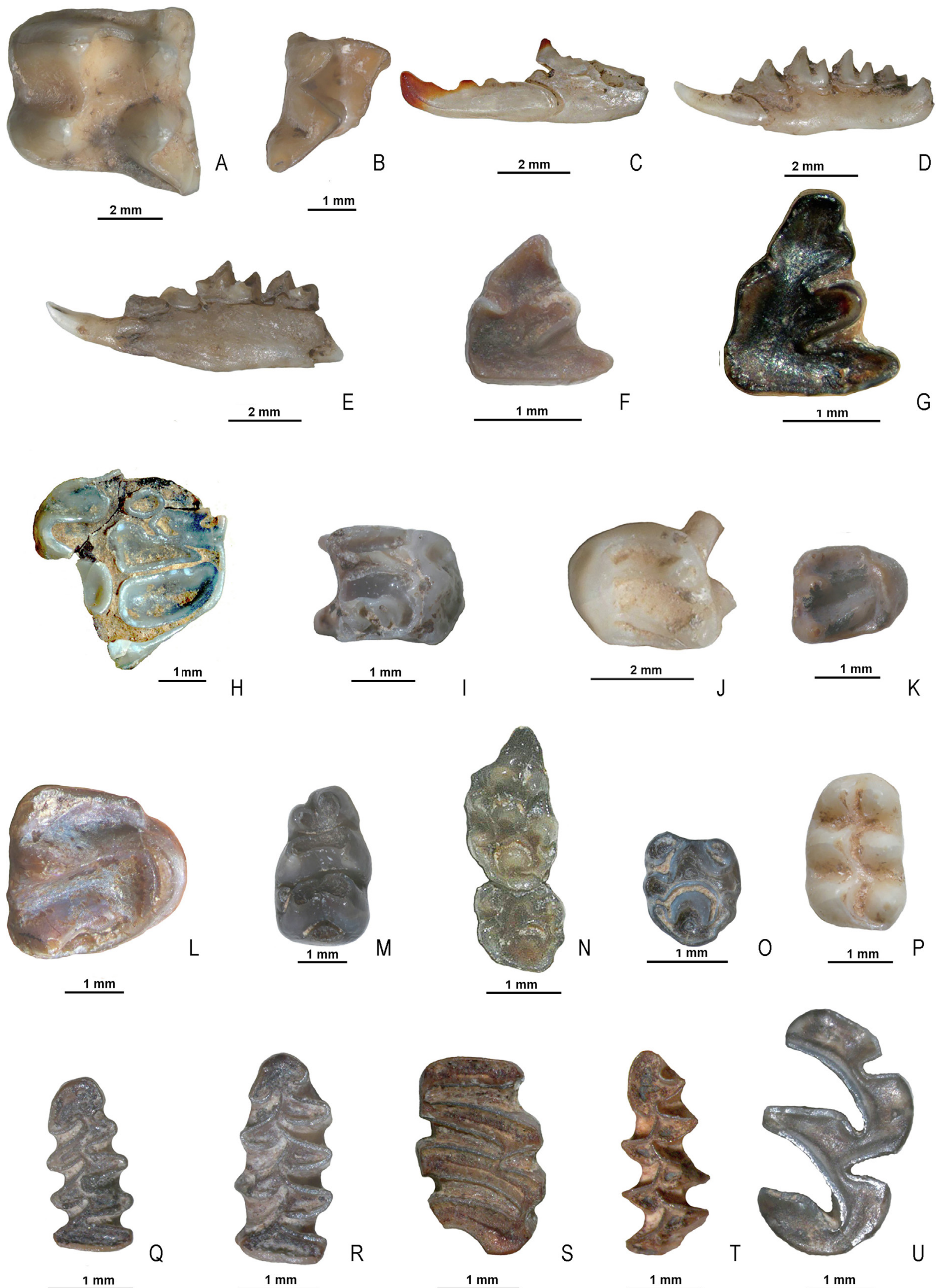
When compiling the characteristics of the ecological zones, the most indicative are the data from pits VI and I, which we took as a basis; materials for other pits are complementary, because further away from the cave entrance, the quantity of fossils and species composition change (see Figs. S1, S2 in Supplementary data).

5.1. Molluscs

The molluscs may be placed in three categories in terms of quantity and percentage. *Discus depressus* is the absolutely dominant species in the sediments of all pits; it makes up 63% of all identified shells (see Tables S1 and S6, Fig. S1 in Supplementary data). Minor (or rare) species are *Vallonia patens* and *Perpolita petronella*, which account for 10% of the total number of identified shells. The third category includes least abundant species, the proportion of which ranges from 0.01 to 4%. Analyzing of the taxonomic structure of malacozones and ecological preferences of their components allows the characterization of the palaeobiotopes (see Table S4 in Supplementary data). A total of 10 malacozones (MZ) were identified (see Fig S1 in Supplementary data).

MZ1 was established in pit II (interval 1.2–1.5 m; layer 8), with 152 shells of seven species identified. Most species prefer mesophilic habitat conditions in terms of temperature and humidity. *Vallonia pulchellula* and *Cochlicopa lubrica* can also live in subhydrophilic conditions; the presence of these species in the upper part of the zone indicates more humid conditions compared to the lower part of the zone. Most species preferred forest habitats (71%, 5 species); some species are typical of intermediate habitats (29%, 2 species). During the accumulation of sediments, the landscape was covered by mixed forests on the slopes and broad-leaved forests in the river valleys with moist leafy litter, as well as open spaces in the forests and wet areas in the river valleys. The climate was probably cool-temperate.

MZ2 was established in pit II (interval 1.0–1.2 m; layer 7), with 509 shells of seven species recorded. Most species, as in MZ1, preferred mesophilic living conditions in temperature and humidity. The ongoing increase in the num-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ber of *Vallonia pulchellula* and *Cochlicopa lubrica* from the bottom up the section indicates an increase in climate humidity. Most of the species preferred forest conditions (71%, 5 species). *Cochlicopa lubrica* and *Perpolita petronella* were typical of intermediate habitats (29%). During the accumulation of the deposits, the landscape remained unchanged. Probably the climate was moderate; we assume an improvement in climatic conditions in the direction of moisturizing, compared with MZ1, as indicated by an almost three times increase in the number of shells.

MZ3–4 was established in pit II (interval 0.9–1.0 m; layer 7), 91 shells of six species identified. The analysis of the encountered species prefer mesophilic temperature and humidity living conditions. A sharp decrease in the number of mollusc shells, compared with MZ2, indicates less favorable conditions. As before, forests (3 species, or 60%) occurred in the territory around the cave, but their area decreased and the areas occupied by open habitats (2 species, or 40%) increased. Probably the climate was moderately cool.

MZ4 was allocated in the pits VI and I (interval 1.3–1.4 m; layer 6), 90 (pit VI) to six (pit I) mollusc shells of five species. Most species prefer mesophilic temperature and humidity living conditions. The most species prefer mesophilic living conditions in temperature and humidity. The zone is characterized by a small number of shells of molluscs, as in MZ3–4, which also indicates adverse animal habitats. Forests (65%, 4 species) continued to grow on the territory around the cave, and open spaces occupied by grassy vegetation and shrubs (35%, 1 species) continued to exist. The presence of slugs indicates increased humidity in biotopes. Probably, the climate was still temperate, but more humid compared to MZ3–4.

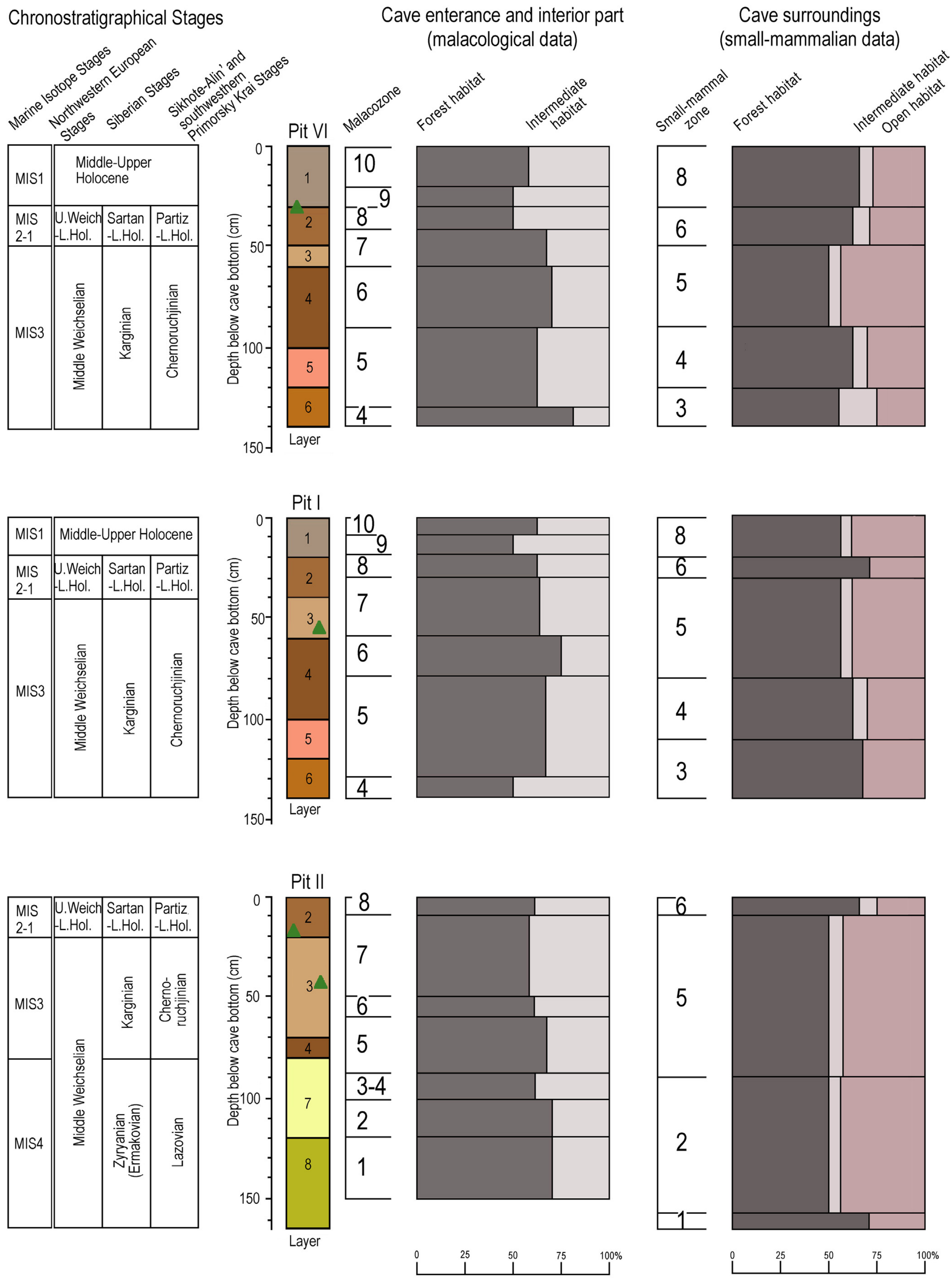
MZ5 was identified in pit VI (interval 0.8–1.4 m; layers 4–6) and pits I–IV, yielding 5703 mollusc shells of 11 species. The modern ecological preferences of the represented species indicate a mesophilic temperature and humidity habitat. The zone is characterized by a large number of mollusc shells and their species diversity compared to other zones, which indicates optimal favorable conditions for their existence. Forests continued to grow in the area around the cave (61%, 8 species of molluscs) and open spaces occupied by herbaceous vegetation and shrubs continued to exist (39%, 4 species of molluscs). The presence of hydrophilic and subhydrophilic species in the zone indicates increased humidity in biotopes. Probably the climate was moderately warm and humid.

MZ6 was established in pit VI (interval 0.6–0.8 m; layer 4) and in the pits I, IV, and II, 1396 mollusc shells of 11 species were identified. The ecological analysis of the assemblage indicates that most species prefer mesophilic habitat conditions in terms of temperature and humidity. The zone is generally characterized by a decrease in the number of mollusc shells compared to MZ5, which indicates some deterioration in their living conditions. Forest areas increased in area (72.5%, 8 mollusc species) compared to open habitats (27.5%, 3 mollusc species). The climate was probably temperate and humid.

MZ7 was identified in pit VI (interval 0.4–0.6 m; layers 2–3) and pits I, IV, II, 3505 mollusc shells of 12 species were identified. The ecological analysis of molluscs according to their modern ecological preferences indicates that most species prefer mesophilic habitat conditions in terms of temperature and humidity. The zone is generally characterized by an increase in the number of mollusc shells compared to MZ6, which indicates some improvement in their living conditions. Forests decreased slightly in area (64.5%, 7 mollusc species) compared to MZ6, open habitats were (35.5%, 5 mollusc species). The climate was probably temperate and humid.

MZ8 was identified in pit VI (interval 0.3–0.4 m; layer 2) and the pits I, IV and II, a total 642 mollusc shells of seven species were identified. An analysis of molluscs according to their modern ecological preferences demonstrates that most species prefer mesophilic habitat conditions in terms of temperature and humidity. The zone is generally characterized by a decrease in the number of mollusc shells compared to MZ7, which indicates some deterioration in their living conditions. Spaces occupied by forests slightly increased in area (55%, 3 species of molluscs); open habitats existed (45%, 2 species of molluscs). The climate was probably temperate (possibly cool).

Fig. 6. Key species of small mammals found in unconsolidated deposits of the Upper Pleistocene and Holocene of the Tetyukhinskaya Cave, Primorsky Krai, Russia. (A) *Erinaceus amurensis* Schrenk, 1859, M1 sinister, pit II, depth interval 0.2–0.3 m, layer 3. (B) *Mogera robusta* Nehring, 1891, M1 dexter, pit I, depth interval 0.2–0.3 m, layer 2. (C) *Sorex mirabilis* Ognev, 1937, fragment of sinister mandibula with i1, p1, pit II, depth interval 0.2–0.3 m, layer 3. (D) *Crocidura shantungensis* Miller, 1901, fragment of sinister mandibula, pit II, depth interval 0.2–0.3 m, layer 3. (E) *Crocidura lasiura* Dobson, 1890, fragment of dexter mandibula, pit IV, depth interval 0.4–0.5 m, layer 3. (F) *Ochotona hyperborea* Pallas, 1811, p3 dexter, pit VI, depth interval 1.0–1.1 m, layer 5. (G) *Tonomochota sikhotana* Tiunov and Gusev, 2021, p3 dexter, pit IV, depth interval 0.6–0.7 m, layer 3. (H) *Petaurista tetyukhensis* Tiunov and Gimranov, 2020, m2 sinister, pit IV, depth interval 0.4–0.5 m, layer 3. (I) *Pteromys volans* (Linnaeus, 1758), M1 or M2 dexter, pit IV, depth interval 0.9–1.0 m, layer 5. (J) *Sciurus vulgaris* Linnaeus, 1758, M2 sinister, pit I, depth interval 0.2–0.3 m, layer 2. (K) *Eutamias sibiricus* Laxmann, 1769, M1 or M2 dexter, pit IV, depth interval 0.9–1.0 m, layer 5. (L) *Urocitellus undulatus* (Pallas, 1779), P4 dexter, pit II, depth interval 1.9–1.7 m, layer 8. (M) *Rattus norvegicus* (Berkenhout, 1769), m1 sinister, pit IV, depth interval 0.9–1.0 m, layer 5. (N) *Apodemus agrarius* (Pallas, 1771), M1, M2 sinister, pit I, depth interval 0.6–0.7 m, layer 4. (O) *Apodemus peninsulae* Thomas, 1906, M2 sinister, pit I, depth interval 0.6–0.7 m, layer 4. (P) *Tscherskia triton* (de Winton in de Winton and Styan, 1899), M1 sinister, pit II, depth interval 0.7–0.8 m, layer 4. (Q) *Clethrionomys rutilus* (Pallas, 1779), m1 sinister, pit VI, depth interval 1.0–1.1 m, layer 5. (R) *Craseomys rufocanus* (Sundevall, 1846), m1 sinister, pit VI, depth interval 1.0–1.1 m, layer 5. (S) *Myopus schisticolor* (Lilljeborg, 1844), M3 dexter, pit VI, depth interval 0.7–0.8 m, layer 4. (T) *Alexandromys fortis* (Büchner, 1889), m1 sinister, pit I, depth interval 0.6–0.7 m, layer 4. (U) *Myospalax psilurus* (Milne-Edwards, 1874), M1 dexter, pit VI, depth interval 0.7–0.8 m, layer 4.


Chronostratigraphical Stages
Cave enterance and interior part
(malacological data)
Cave surroundings
(small-mammalian data)
Marine Isotope Stages
Northwestern European Stages
Siberian Stages
Sikhote-Alin' and southwestern Primorsky Krai Stages
Malacozone
Forest habitat
Intermediate habitat
Small-mammal zone
Forest habitat
Intermediate habitat
Open habitat
Pit VI
Pit I
Pit II
MIS1
Middle-Upper Holocene
MIS 2-1
U.Weich -L.Hol.
Sartan -L.Hol.
Partiz -L.Hol.
MIS3
MIS4
Middle Weichselian
Karginian
Chernoruchjinian
Zyryanian (Ermakovian)
Lazovian
Depth below cave bottom (cm)
Layer
0
25
50
75
100%

MZ9 was identified in pit VI (interval 0.2–0.3 m; layer 1), and the pits I, IV, and V, a total 1059 shells of molluscs of seven species were identified. The ecological analysis of molluscs according to their current ecological preferences indicates mesophilic habitat conditions in terms of temperature and humidity. The zone is generally characterized by a slight increase in the number of mollusc shells compared to MZ8, which indicates some improvement in their living conditions. Forests (50%, 3 species of molluscs) and open habitats (50%, 3 species of molluscs) occupied approximately the same areas. Probably the climate was temperate.

MZ10 was identified in pit VI (depth interval 0–0.2 m; layer 1) and the pits I and V, a totally 362 shells of seven species were identified. The ecological analysis demonstrates that most species prefer mesophilic habitat conditions in terms of temperature and humidity. The zone is generally characterized by a decrease in the number of mollusc shells compared to MZ9, which indicates some deterioration in their living conditions. Forests (58.5%, 4 species of molluscs) and open habitats (41.5%, 3 species of molluscs) occupied approximately the same areas. The climate was most probably temperate.

5.2. Small mammals

We analyzed the taxonomic composition of the small-mammal zones (SMZ) and the ecological preferences of the component species for the characterization of the palaeobiotopes (see Tables S2 and S5, Fig. S2 in Supplementary data). Eight SMZs have been established. We compared our data with the results of the environmental reconstructions and their references of Korotkiy et al. (1996, 1997).

SMZ1 corresponds to the lowest horizon of layer 8 in pit II. The dominant species is *Craseomys rufocanus*. Of the seven species of this zone, five belong to the inhabitants of open habitats. A single tooth of *Spermophilus undulatus*, which does not currently inhabit the area, was found here. Its preferred habitats are the forest-steppes and steppes of the mountainous and foothill regions of Yakutia and Altai, savannahs and grassy steppes bordering the Gobi Desert. There are no bone remains of such typical forest species as *Pteromys volans*, *Sciurus vulgaris*, *Eutamias sibiricus* and *Myopus schisticolor*. It is most probable that this period corresponds to the middle phase of the Early Würmian, 75–50 ka. The main changes in landscapes developed under the influence of the strongest cooling of the climate. The Sikhote-Alin at this time is characterized by the development of oligodominant birch-larch forests with areas of forest-tundra and tundra (to the north of 48°N) on the dried shelf.

SMZ2 corresponds to most of the layers 8 and 7 of pit II. The dominant species is *Craseomys rufocanus*. Compared to the underlying layer, the number of forest species significantly increases: out of 16 species, eight (50%) are forest species. Climate warming may correspond to the last phase of the Early Würmian. The phase is characterized by the development of birch-larch forests with elements of southern taiga vegetation.

SMZ3 corresponds to layer 6 in pit I, layer 6 and part of layer 5 in the pits I and IV. The dominant species is *Craseomys rufocanus*. Of the 12 species, six inhabit in forests (50%). In terms of species composition and the number of forest species and species that prefer open habitats, SMZ3 is close to SMZ2. There are bone remains of a relatively warm-loving species *Crocidura shantungensis*. Climate warming continues, which may correspond to the first phase of the Middle Würmian (50–45 ka).

SMZ4 corresponds to the layer 5 in the pit VI, the upper part of the layer 5 and the lower part of the layer 4 in the pit I, the layer 4 and the upper part of the layer 5 in the pit IV. The dominant species is *Craseomys rufocanus*. Of the 17 species, nine prefered forest habitats (54%). There is a further increase in the number of forest species, but the difference from the underlying layer is insignificant. In this zone, there are no bone remains of warm-loving insectivorous species, but bone remains of *Mimomys* sp. Possibly, this zone corresponds to the second phase of the Middle Würmian (45–43 ka), when a rather strong cooling was observed with the development of dark coniferous taiga on the mountains' slopes and birch–larch forests with elements of broad-leaved trees in the river valleys.

SMZ5 corresponds to layers 3 and 4 in pit VI, the lower horizon of layer 2, layer 3 and part of layer 4 in pit I, the lower horizon of layer 2 and layer 3 in pit IV, the lower horizons of layer 2, layers 3 and 4 and the upper horizon of layer 2 in pit II. The dominant species is *Craseomys rufocanus*. Of the 29 species, 14 species prefered forest habitats (48%). In this zone, bone remains of the largest number of species were found, however, this is also the thickest zone (from 50 to 100 cm thick in pit VI). Only in this zone we found the remains of a new species, an inhabitant of tall forests, *Petaurista tetyukhensis*. There were bone remains of relatively warm-loving forest species *Erinaceus amuren-*

Fig. 7. Summary of the mollusc and small-mammal faunas in the Tetyukhinskaya Cave. Chronostratigraphical Stages: Marine Isotope and northwestern European Stages (after Cohen and Gibbard, 2019); Siberian Stages (Anonymous, 1983); Sikhote-Alin' and southwestern Primorsky Krai Stages (Anonymous, 1987). Cave entrance and interior habitat reconstructions are based on the malacological data; cave surroundings habitat reconstructions based on the small-mammalian data. Malacological and small-mammalian zones and possible environment reconstructions are explained in the text. Green triangles: sample positions for ^{14}C dating (see Table S3 in Supplementary data). U.Weich–L.Hol. – Upper Weichselian–Lower Holocene; Sartan–L. Hol. – Sartanian–Lower Holocene; Partiz–L.Hol. – Partizanian–Lower Holocene (see text for explanations).

sis, *Mogera robusta*, *Sorex mirabilis* and species of open habitats — *Crocidura shantungensis*, *Crocidura lasiura*. This zone corresponds to the climatic optimum of the Middle Würmian (43–33 ka) in terms of the intensity of temperature increase and the humidification regime similar to the climate of the Middle Holocene. The period is characterized by the development of polydominant broad-leaved and *Pinus sibirica*-broad-leaved forests.

SMZ6 corresponds to the upper horizons of layer 2 in pits VI, I, IV and II. The dominant species is *Craseomys rufocanus*. Of the 18 species, nine prefered forest habitats (50%). Judging by the remains of small mammals, this zone corresponds to a time characterized by a significant cooling and drying of the climate.

SMZ7 corresponds to the lower horizons of layer 1 in pit V, of layer 3 and layer 4 in pit III. The dominant species is *Craseomys rufocanus*. Of the 19 species, nine prefered forest habitats (48%), but in terms of the number of individuals, without the dominant species *Craseomys rufocanus*, the inhabitants of the forest (58%) exceed the inhabitants of intermediate (2%) and open habitats (40%). This is probably still a cold period, but compared to SMZ6 some warming of the climate is possible.

SMZ8 corresponds to layer 1 in pits VI, I, IV, part of layer 1 in pit V, and layer 1 and part of layer 3 in pit III. The dominant species is *Craseomys rufocanus*. Of the 26 species, 13 species preferred forest habitats (50%), but in terms of the number of individuals, without the dominant species *Craseomys rufocanus*, the inhabitants of the forest (66%) exceed the inhabitants of intermediate (3%) and open habitats (31%). Climate warming continued; the time of deposits accumulation probably corresponds to the Middle–Late Holocene.

5.3. Palaeoenvironmental (habitat) reconstruction

On the basis of the identified malacozones in comparison with the mammalian data, we summarize the chronological development of the biotopes (from the base to the top) from the reference pit VI, located at the cave entrance, supplemented by data from pit II for the bottom of the section, schematically shown in Fig. 7.

The Lazovian time (Korotkiy et al., 1980; Anonymous, 1984), about 75–50 ka. Forests dominate, open biotopes existed in the vicinity of the cave (pit II, layer 8 (lower part); SMZ1). The climate was cold. This period probably corresponds to the second half of the Ermakovo (Zyryansk) glaciation (Rasskazov and Levi, 2014)/the first phase of the Early Wurmian (Korotkiy et al., 1996, 1997). Middle Weichselian (MIS 4) (Cohen and Gibbard, 2019).

The Chernoruchjinian time (Korotkiy et al., 1980; Anonymous, 1984), about 50–45 ka. Forest biotopes dominate both at the cave entrance and at a distance; open and intermediate biotopes were widespread in the vicinity of the cave (layer 6; MZ4, SMZ3). The climate was warm. This period probably corresponds to the Siberian Karginian time, which was characterized by early warming (Rasskazov and Levi, 2014) or the first phase of the Middle Wurmian (Korotkiy et al., 1996, 1997). Middle Weichselian (MIS 3) (Cohen and Gibbard, 2019).

The Chernoruchjinian time (Korotkiy et al., 1980; Anonymous, 1984), about 45–43 ka. Forest biotopes dominate; open and intermediate biotopes existed in the vicinity of the cave (layer 5, layer 4 (lower part); MZ5, SMZ4). The climate was cold (cool). This period probably corresponds to the Karginian time of Siberia, which was characterized by an early cooling (Rasskazov and Levi, 2014) or the second phase of the Middle Wurmian (Korotkiy et al., 1996, 1997). On the regional scale, this period can be compared with the Chernoruchinsky time (Korotkiy et al., 1980; Anonymous, 1984). Middle Weichselian (MIS 3) (Cohen and Gibbard, 2019).

The Chernoruchjinian time (Korotkiy et al., 1980; Anonymous, 1984), about 43–33 ka. Forest biotopes dominated, open and intermediate biotopes are widespread in the vicinity of the cave (layers 4, 3, 2 (lower part); MZ6, MZ7, SMZ5). The climate was warm. The dating of bones from layer 3 (see Table S3 in Supplementary data) indicates that this period probably corresponds to the second half of the Karginian time of Siberia, including the Malaya Kheta optimum in southern Siberia (Laukhin, 1995; Rasskazov and Levi, 2014) or climatic optimum of the mid Wurmian (Korotkiy et al., 1996, 1997). Middle Weichselian (MIS 3) (Cohen and Gibbard, 2019).

The transitional interval — the Partizanian time — Early Holocene (Korotkiy et al., 1980; Anonymous, 1984), about 30–11 ka and continued up to 8.5 ka. There were open and intermediate habitats and forests in equal proportions (layers 2, 1 (lower part); MZ8, MZ9, SMZ6). The climate was cold and dry. According to molluscs' data, it can be said that the time of accumulation of the upper part of the sediments of layer 2 (MZ8) was the coldest, while the sediments of the lower part of layer 1 (MZ9) were also formed under cold conditions. Late Weichselian–Early Holocene (MIS 2–1) (Cohen and Gibbard, 2019).

Middle–Late Holocene (MIS 1). Dominance of forest biotopes at the cave entrance; in the vicinity of the cave there were open and intermediate biotopes (layer 1 (top); MZ10, SMZ8). The climate was warm.

As the cave was most probably used as a temporary shelter by various predators, both small (siberian weasel, sable) and large (badger, yellow-throated marten, raccoon dog, fox, wolf, bear, and tiger) (Tiunov and Panasenko, 2007; Tatarnikov, 2012; Kosintsev et al., 2016) and the hunting ranges of predatory animals are quite significant (e.g., a fox can move away from the hole up to 8 km, our data), it may be assumed that, on average, the feeding territories of predators cover a space within a radius of approximately 10 km from the den (Smirnov and Sadykova, 2003). Thus, based on the species composition of the bone remains of small mammals, taking into account their relative abundance, a general picture of the landscape-climatic and biotopes in the vicinity of the study location and their evolving history may be visualized, while the species composition of molluscs characterizes the situation in the immediate vicinity of the cave. The presence of a significant number of remains of open space species in the sediments of the warm periods of the Late Pleistocene during the development of forest vegetation can be explained by the wide distribution of pasture ecosystems inhabited by large ungulates and proboscideans of the mammoth fauna (Kalyakin, 2014).

6. Conclusion

The composition of the small mammal and mollusc faunas indicates the wide distribution of mosaic landscapes of forests together with open and semi-open biotopes in the Primorsky Krai area during Late Pleistocene and Holocene. The faunas are characterzied by species that lived in broadleaf and coniferous forests as well as in intermediate and open habitats under a continental climate.

Mammal bone remains accumulated inside the cave were most likely brought in by predatory animals that used the caves as a dwelling or temporary shelter. Molluscs inhabited the entrance part of the cave feeding on abundant organic matter there. Therefore, we interpret the molluscs as indicators of biotopes near the entrance of the cave, and mammals as indicators of the wider cave surroundings.

Although terrestrial mollusc and small mammal assemblages differ in the the structure of faunal complexes, especially when moving from the entrance into deep cave, and in the ecological preferences of animals, they generally reveal the global changes in the structure of biotopes and, accordingly, the climate of the study area during Late Pleistocene–Holocene.

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Supplementary data

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