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The Use of the Malacofaunistic Method for Reconstructing the Palaeoecological Conditions of the Late Late Pleistocene to Holocene Based on Material from the Tetyukhinskaya Cave Site, Southern Far East, Russia

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Abstract—Results of the study of terrestrial mollusc shells from the unconsolidated deposits of the Tetyukhinskaya Cave, Dalnegorsk, Primorsky Krai, Russia are presented. Brief species descriptions of the molluscs and their images complete the scarce information on the fossil Quaternary mollusc fauna of the region. With the help of malacological analysis, characteristic zones and malacological complexes were identified, which were used as indicators of the habitats near the cave entrance and in the adjacent territory. The data concerning the palaeoecological conditions of individual mollusc species confirm the development of broad-leaved and mixed forests, alongside open meadows with herbage vegetation in the region near the cave, towards the end of the Late Pleistocene and in the Holocene.

Keywords: terrestrial molluscs, malacozones, Quaternary, Primorsky Krai, palaeoreconstructions

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INTRODUCTION

Malacofaunistic studies, along with other methods, are widely used in the study of unconsolidated deposits of various karst cavities (Tatarnikov, 2012; Gasilin et al., 2013; Tiunov and Gusev, 2021). Mollusc shells are quite often found in cave deposits, and their study helps to reconstruct palaeoecological conditions and features of biotopes of different time periods during sedimentation. Molluscs are sedentary animals; at the same time, they are sensitive to various environmental conditions, especially to changes in temperature, humidity, and lighting. Accordingly, the study of Quaternary molluscs makes it possible to reconstruct the microenvironment conditions of their habitat in the immediate vicinity of karst cavities and reconstruct the palaeoconditions in the region as a whole.

Quaternary molluscs from unconsolidated deposits of karst cavities are widely studied for reconstructions of the natural environment (for example, Ložek, 2000; Alexandrowicz, 2000; Stefaniak et al., 2009; Danukalova et al., 2020; Zupan Hajna et al., 2021; Osipova et al., 2021).

As noted by Skoczylas-Śniaz and Alexandrowicz (2022), carbonate rocks (in particular, limestone) are a favourable substrate for terrestrial molluscs, whose shells are thin-walled, so any chemical or physical impact on them easily leads to their destruction. Thus, the satisfactorily preserved mollusc shells found in cave deposits can be considered as buried in situ; i.e., the mollusc complexes will reflect the palaeoecological conditions in which deposits accumulated (Skoczylas-Śniaz and Alexandrowicz, 2022).

This is the first study to present the data on the composition of the malacofauna in the vicinity of Tetyukhinskaya Cave in the Late Pleistocene and Holocene: the systematic position of the identified mollusc species is discussed, their brief morphological descriptions are given, and the natural environment over the discussed time period is reconstructed. Literature sources contain no data on Late Pleistocene terrestrial mollusc assemblages in Primorsky Krai, which indicates the relevance and novelty of the study. Available papers known to us are devoted to the rare terrestrial mollusc *Strobilops coreana* Pilsbry 1927 (Prozorova et al., 2006) from Upper Pleistocene deposits of the Medvezhii Klyk karstic cavity on the Lozovyi

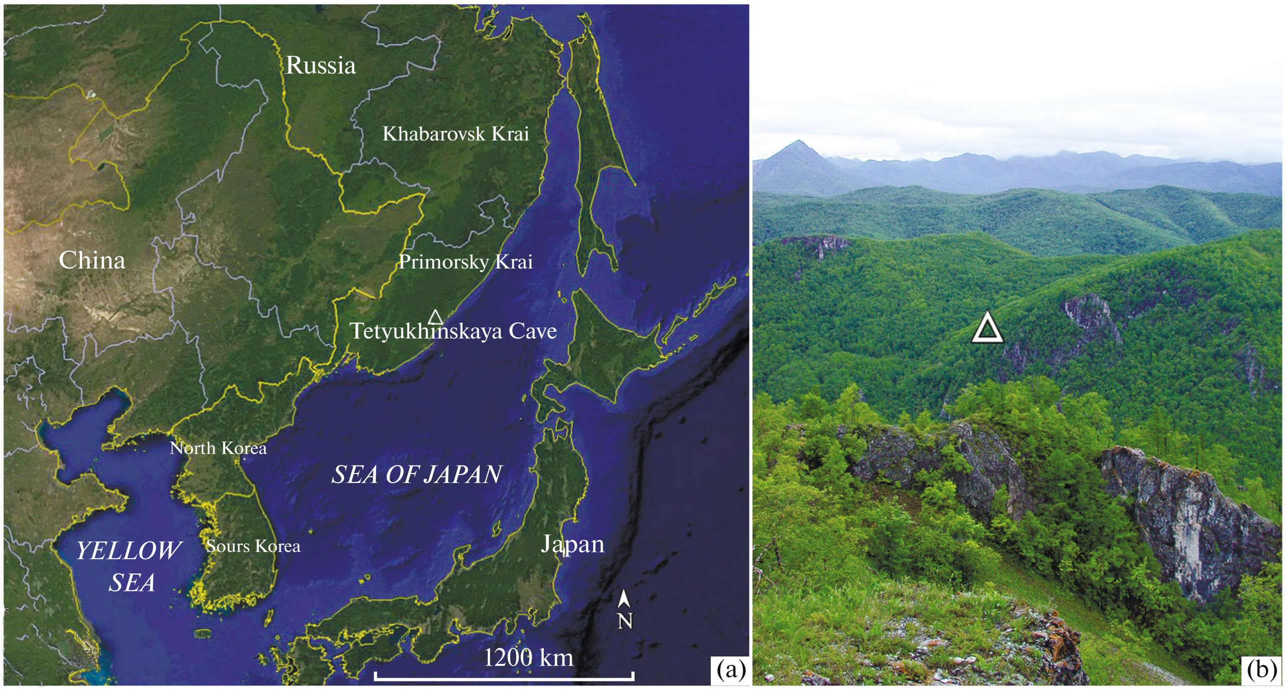

Fig. 1. Location of Tetyukhinskaya Cave south-east of Sikhote-Alin ridge (a) on a Google map. The triangle shows the location of the cave (b). Photo by M.P. Tiunov.

Ridge (Sikhote-Alin) and Late Holocene freshwater, marine, and single terrestrial molluscs from archaeological sites (Rakov, 2002; Vostretsov and Rakov, 2009; Saenko et al., 2015, 2019; Nikitin et al., 2016; Lutaenko and Artem'eva, 2017; Lutaenko et al., 2021, 2022).

MATERIALS AND METHODS

Tetyukhinskaya Cave is located on the right bank of the Inza River (a left tributary of the Tetyukhe River) southeastwards of the Sikhote-Alin Ridge and northwards of Dalnegorsk (44°35′ N, 135°36′ E) (Fig. 1). The cave was formed in carbonate deposits of the Upper Triassic. The entrance to the Tetyukhinskaya Cave is located at an altitude of 410 m above sea level, the length of the described part of the cave is 350 m (Gasilin et al., 2013). The cave was discovered in 1980. Later, it was explored by V.A. Tatarnikov in 2008, 2011 and the Tetyukhe local history club headed by G. Smirnov in 2009–2010. During the excavation of passages in search for extensions of the cave, cavers found animal bone remains. The bones belonged to Late Pleistocene and Holocene mammals, birds, and amphibians (Gasilin et al., 2013). In 2012–2015, M.P. Tiunov laid six pits in the cave, four of which reached the rock bottom. During the excavation, eight lithological layers were described (from top to bottom): (1) greyish-brown loam, (2) brown loam with large fragments of carbonate rocks, (3) brownish heavy loam with small fragments of rocks, (4) brown loam with small fragments of rocks, (5) yellowish-brown light loam with small fragments of carbonate rocks, (6) brownish light loam with stone fragments, (7) clay yellowish with limestone fragments, and (8) dark yellow moist clay with numerous limestone fragments. When excavating pits, unconsolidated deposit was removed at ten-centimetre levels. All selected samples were washed in water on sieves with a mesh diameter of 1 mm and dried in the field, then mammalian and mollusc fossil remains were studied in the laboratory (Fig. 2) (Osipova et al., 2024). This publication describes the results of malacological studies.

As a result of the study, 14369 terrestrial mollusc shells, as well as undetectable detritus, were found. The samples contained different numbers of shells (Table 1). The number of shells was calculated by the method of Ložek (1964), according to which individual shell fragments (the umbo and lower whorl with the aperture) corresponded to one shell. The number of fragments counted in this way was added to the complete shells.

The percentages of taxa in the samples were not calculated, because, according to correct data reflection techniques, one sample from alluvial deposits should contain at least 200 shells (White et al., 2008), and one sample from cave deposits should contain at least 50 specimens (Szymanek et al., 2016). In most cases, the number of shells in samples from cave deposits is less than 50 specimens, which is also evident in our

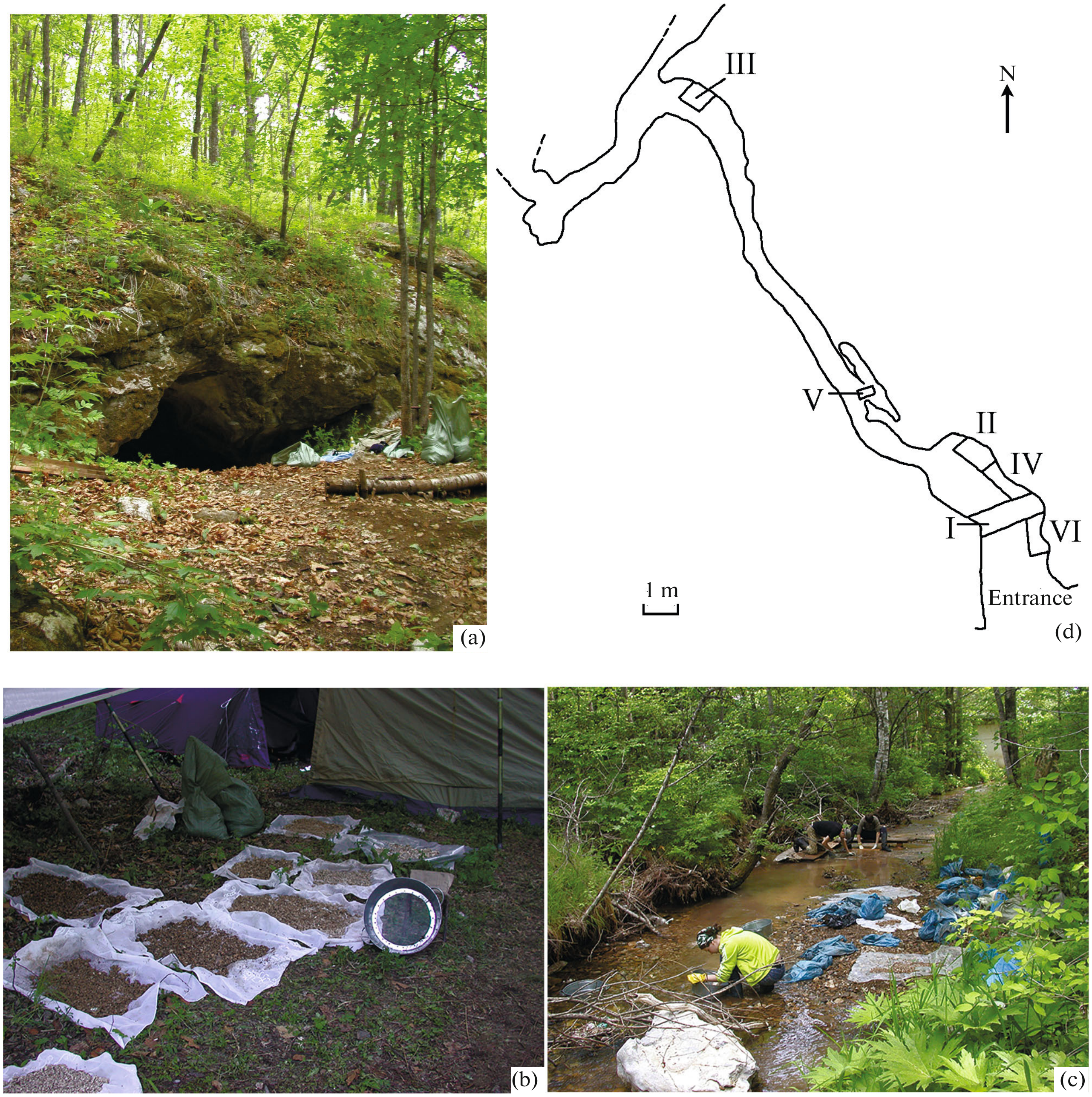

Fig. 2. Entrance to the cave (a); sifting of sediment, washing, and drying of selected samples for faunal remains (b, c); cave plan (d). Photo by M.P. Tiunov. The cave plan was drawn up by D.A. Kosmach, B.E. Panasenko, and G.A. Isaeva (August 30, 2011). Roman numerals indicate the pit numbers.

material. Data on the average parameters of species in certain layers were used for preliminary reconstructions of palaeoecological conditions. Molluscs were identified according to Likharev and Rammelmeyer (1952), Prozorova et al. (2018), and Sysoev and Shileyko (2009) and are given in systematic order according to the World Register of Marine Species (WoRMS).

To describe malacozones (MZs), the following terms are used: absolute dominant (abundant) (more than 50%), dominant (frequent) (50–30%), subdominate (scarce) (30–15%), minor (rare) (15–5%), and insignificant (single) (less than 5%) species (Bakanov, 1987).

For palaeoecological analysis, we used data on air temperature, humidity, and vegetation cover based on the study of extant molluscs, including those from Primorsky Krai (Russia), and analysed the literature on Quaternary malacofauna with references to various

Table 1. Main mollusc species and number of shells in Quaternary deposits of Tetyukhinskaya Cave (Far East, Russia), 2012–2015

Malacozone (MZ)	Sample registration number	Pit	Layer	Depth interval, cm	*Carychium pessimum* Pilsbry 1902	*Cochlicopa lubrica* (Müller 1774)/*Cochlicopa* sp.	*Vallonia patens* Reinhardt 1883	*Vallonia pulchellula* (Heude 1882)	*Vallonia* sp.	*Columella edentula* (Draparnaud 1805)	*Vertigo* cf. *japonica* Pilsbry and Hirase 1904	*Punctum ussuriense* Likharev and Rammelmeyer 1952	*Discus depressus* (Adams 1868)	*Euconulus fulvus* (Müller 1774)	*Hawaiia minuscula* (Binney 1841)	*Perpolita petronella* (Pfeiffer 1853)	*Perpolita* sp.	Agriolimacidae	*Karaftohelix maacki* (Gerstfeldt 1859)	*Karaftohelix* cf. *middendorffi* (Gerstfeldt 1859)	*Karaftohelix dieckmanni* (Mousson 1887)	*Karaftohelix* sp./Bradybaenidae	Fragments of shells	Total number of shells
10	389/6676	VI	1	0–10		1	35						52	4	5	6			5					108
10	389/6677	VI	1	10–20		1	34						70	7	1	16			6			2	+	137
9	389/6678	VI	1	20–30		3	50						174	4	12	36						6		285
8	389/6679	VI	2	30–40		9	27						150	4	3	47						8	+	248
7	389/6680	VI	2	40–50		13	61	1					202	19	7	55			11			6		375
7	389/6681	VI	3	50–60		10	38	1					205	4		21		1	20			13	+	313
6	389/6682	VI	4	60–70		20	24						185	7		32			8			20	+	296
6	389/6683	VI	4	70–80		17	41						172	3	2	32		1			2	18	+	288
6	389/6684	VI	4	80–90		7	50						234	4	5	43				1	2	18	+	364
5	389/6685	VI	4	90–100	1	27	147	1					462	12		86					1	22	+	759
5	389/6686	VI	5	100–110		24	74	30					305	6	3	77						25	+	544
5	389/6687	VI	5	110–120		24		246					437	13	2	136						12	+	870
5	389/6688	VI	6	120–130		15		95					309	6		128						8	+	561
4	389/6689	VI	6	130–140				19					50	2		17		1				1	+	90
		VI		**Sum of shells:**	**1**	**171**	**581**	**393**					**3007**	**95**	**40**	**732**		**3**	**50**	**1**	**5**	**159**		**5238**
10	389/6600, 389/6605, 389/6617	I	1	0–10		3	8						73	3		13	1					16	+	117
9	389/6601, 389/6606, 389/6618	I	1	10–20		7	41		3				153	36		19	1					22		282
8	389/6602, 389/6607, 389/6619	I	2	20–30		2	4						49	1		5						11	+	72
7	389/6603, 389/6608	I	2	30–40		14	24						104	23		35						30		230

Table 1. (Contd.)

Malacozone (MZ)	Sample registration number	Pit	Layer	Depth interval, cm	*Carychium pessimum* Pilsbry 1902	*Cochlicopa lubrica* (Müller 1774)/*Cochlicopa* sp.	*Vallonia patens* Reinhardt 1883	*Vallonia pulchellula* (Heude 1882)	*Vallonia* sp.	*Columella edentula* (Draparnaud 1805)	*Vertigo* cf. *japonica* Pilsbry and Hirase 1904	*Punctum ussuriense* Likharev and Rammelmeyer 1952	*Discus depressus* (Adams 1868)	*Euconulus fulvus* (Müller 1774)	*Hawaiia minuscula* (Binney 1841)	*Perpolita petronella* (Pfeiffer 1853)	*Perpolita* sp.	Agriolimacidae	*Karaftohelix maacki* (Gerstfeldt 1859)	*Karaftohelix* cf. *middendorffi* (Gerstfeldt 1859)	*Karaftohelix dieckmanni* (Mousson 1887)	*Karaftohelix* sp./ Bradybaenidae	Fragments of shells	Total number of shells
7	389/6609, 389/6620	I	3	40–50		6	1						93	4		14						23		141
7	389/6610, 389/6621	I	3	50–60		17	42	2					155	25	2	22			19			4	+	288
6	389/6611, 389/6622	I	4	60–70			3						54	1		7			7	3			+	75
6	389/6612, 389/6623	I	4	70–80		13	1	2					144	6		15			8			5	+	194
5	389/6613, 389/6624	I	4	80–90		8	12	2					221	6	2	22						23	+	296
5	389/6614, 389/6625	I	4	90–100		4	7	6					232	3	3	23			4			13	+	295
5	389/6604, 389/6615, 389/6616, 389/6626	I	5	100–110		13	1	18					231	6		28			5	6		3	+	311
5	389/6627	I	5	110–120		17		72					455	22		64						17	+	647
5	389/6628	I	6	120–130		1		8					59			8						1		77
4	389/6629	I	6	130–140									4			1						1		6
		I		**Sum of shells:**		**105**	**144**	**110**	**3**				**2027**	**136**	**7**	**276**	**2**		**43**	**9**		**169**	**+**	**3031**
9	389/6656	IV	1	0–10		6	54						198	10	3	19						7	+	297
8	389/6657	IV	2	10–20		3	9						77	3		11						6	+	109
7	389/6658	IV	2	20–30		3	27	2					170	4	7	24						15	+	252
7	389/6659	IV	3	30–40		4	22	1					158	1								9	+	195
7	389/6701	IV	3	40–50		1	13						128	2	1	22						4	+	171
6	389/6660	IV	3	50–60		2	6	1					77	4		7			3			11	+	111
6	389/6661	IV	3	60–70		6	11	1					124	2		13			8			10	+	175

Table 1. (Contd.)

Malacozone (MZ)	Sample registration number	Pit	Layer	Depth interval, cm	*Carychium pessimum* Pilsbry 1902	*Cochlicopa lubrica* (Müller 1774)/*Cochlicopa* sp.	*Vallonia patens* Reinhardt 1883	*Vallonia pulchellula* (Heude 1882)	*Vallonia* sp.	*Columella edentula* (Draparnaud 1805)	*Vertigo* cf. *japonica* Pilsbry and Hirase 1904	*Punctum ussuriense* Likharev and Rammelmeyer 1952	*Discus depressus* (Adams 1868)	*Euconulus fulvus* (Müller 1774)	*Hawaiia minuscula* (Binney 1841)	*Perpolita petronella* (Pfeiffer 1853)	*Perpolita* sp.	Agriolimacidae	*Karaftohelix maacki* (Gerstfeldt 1859)	*Karaftohelix* cf. *middendorffi* (Gerstfeldt 1859)	*Karaftohelix dieckmanni* (Mousson 1887)	*Karaftohelix* sp./ Bradybaenidae	Fragments of shells	Total number of shells
6	389/6662	IV	4	70–80		3	15	1					81	3		12			5				+	120
6	389/6663	IV	4	80–90		4	10	1					62	1	3	8			3				+	92
6	389/6664	IV	5	90–100		1	1						36	1		5			4				+	48
5	389/6665	IV	5	100–110		2							58	2		6			3				+	71
5	389/6666	IV	6	110–120			5	20					125	2		22						4	+	178
		IV		**Sum of shells:**		**35**	**173**	**27**					**1294**	**35**	**14**	**149**			**26**			**66**		**1819**
8	389/6631	II	2	0–10		6	44						112	25		15						12	+	214
7	389/6632	II	2	10–20		14	99			2			201	53	2	28		1	14			13	+	427
7	389/6633	II	3	20–30		14	108				1	1	247	53	10	36		1				15		486
7	389/6634	II	3	30–40		14	33	2					211	33	2	21			10					326
7	389/6635	II	3	40–50		10	24						188	25	1	27			6				+	281
6	389/6636	II	3	50–60		8	9						120	12		20						10	+	179
5	389/6637	II	3	60–70		17	24						201	23	1	29			7			10	+	312
5	389/6638	II	4	70–80		29	38						255	23	1	32		1	22			8	+	409
5	389/6639	II	5	80–90		16	26	1					241	17	3	28		1	10				+	343
3–4	389/6640	II	5	90–100		7	6						60	7		6						5	+	91
2	389/6641	II	5	100–110		13	4	1					217	13		27						17		292
2	389/6642	II	5	110–120		6	1	2					170	16		11			11				+	217
1	389/6643	II	6	120–130		2	1	1					55	1		6				3			+	69
1	389/6644	II	6	130–140		6							48	2		7						5		68
1	389/6645	II	7	140–150									12			1						2	+	15
		II		**Sum of shells:**		**162**	**417**	**7**		**2**	**1**	**1**	**2338**	**303**	**20**	**294**		**4**	**80**	**3**		**97**		**3729**
10	389/6668	V	1	0–10		1	6						11	2	1	1							+	22
10	389/6669	V	1	10–20		1	3						16	1								2	+	23
10	389/6670	V	1	20–30		1	12						36	3		4			1				+	57

Table 1. (Contd.)

Malacozone (MZ)	Sample registration number	Pit	Layer	Depth interval, cm	*Carychium pessimum* Pilsbry 1902	*Cochlicopa lubrica* (Müller 1774)/*Cochlicopa* sp.	*Vallonia patens* Reinhardt 1883	*Vallonia pulchellula* (Heude 1882)	*Vallonia* sp.	*Columella edentula* (Draparnaud 1805)	*Vertigo* cf. *japonica* Pilsbry and Hirase 1904	*Punctum ussuriense* Likharev and Rammelmeyer 1952	*Discus depressus* (Adams 1868)	*Euconulus fulvus* (Müller 1774)	*Hawaiia minuscula* (Binney 1841)	*Perpolita petronella* (Pfeiffer 1853)	*Perpolita* sp.	Agriolimacidae	*Karaftohelix maacki* (Gerstfeldt 1859)	*Karaftohelix* cf. *middendorffi* (Gerstfeldt 1859)	*Karaftohelix dieckmanni* (Mousson 1887)	*Karaftohelix* sp./ Bradybaenidae	Fragments of shells	Total number of shells
10	389/6671	V	1	30–40			10						17			4			1				+	32
9	389/6672	V	1	40–50		1	14						37	2	1	4						2	+	61
9	389/6673	V	1	50–60			7						37	1		5			3				+	53
9	389/6674	V	1	60–70		2	26						57	9	1	2			1				+	98
		V		**Sum of shells:**		**6**	**78**						**211**	**18**	**3**	**20**			**6**			**4**		**346**
9–10	389/6646	III	1	0–10		4	3						57	8		4			5				+	81
7–8	389/6647	III	3	20–30									9									4		13
7–8	389/6648	III	3	30–40		1							15						2				+	18
7–8	389/6649	III	3	40–50		1							15	1		1						4	+	22
7–8	389/6650	III	3	50–60		1							10	1									+	12
7–8	389/6651	III	3	60–70									10						2				+	12
7–8	389/6652	III	4	70–80									9	2								7		18
5	389/6653	III	5	100–110			3						4			1						1	+	9
5	389/6654	III	5	110–120		1	2	1					6										+	10
5	389/6655	III	5	120–130				1					6	1		1						2	+	11
		III		**Sum of shells:**		**8**	**8**	**2**					**141**	**13**		**7**			**9**			**18**		**206**
				Total number of shells	**1**	**487**	**1401**	**539**	**3**	**2**	**1**	**1**	**9018**	**600**	**84**	**1478**	**2**	**7**	**214**	**13**	**5**	**513**		**14369**

"+"—uncounted fragments, empty cells—no data, 389/6655—collection number/registration number of the sample.

palaeoecological factors (Likharev and Rammelmeyer, 1952; Ložek, 1964; Riedel, 1967; Puisségur, 1976; Shileyko, 1978, 1984; Willis et al., 2000; Alexandrowicz, 2002; Prozorova et al., 2007, 2018; Sysoev, and Shileyko, 2009) taking into account other published data (Germain, 1930; Adam, 1960; Kerney et al., 1983; Kerney and Cameron, 1999; www.animalbase.uni-goettingen.de).

Photos of mollusc shells were taken using a Motic SMZ-171 stereo microscope with a Moticam-10+ camera. The collection of mollusc shells (no. 389) is stored at the Institute of Geology of the Ufa Federal Research Centre of the Russian Academy of Sciences (Ufa, Russia).

The age of the unconsolidated cave deposits was determined more precisely using radiocarbon AMS dating: 39874 ± 133 years NSK-850, UGAMS-21786 (tooth of *Ursus thibetanus* Cuvier 1823, pit II, depth interval 0.4–0.5 m, layer 3) (Kosintsev et al., 2016, 2020) and 37673 ± 950 years NSKA-851 (tooth of *Stephanorhinus kirchbergensis* (Jäger 1839), pit I, depth interval 0.5–0.6 m, layer 3) (Osipova et al., 2024), as well as radiocarbon ^{14}C dating: 20215 ± 10000 years SPb-1057 (bones of mammals, pit II, depth interval 0.4–0.5 m, layer 3) (Kosintsev et al., 2020); 8590 ± 40 years RUSA14 (tooth of *Panthera tigris* (Linnaeus 1758), pit VI, depth interval 0–0.2 m, layer 1?–2) (Sun et al., 2022, in press); 8585 ± 45 years RUSA06 (tooth of *Panthera tigris* (Linnaeus 1758), pit II, depth interval 0.1–0.2 m, layer 2) (Sun et al., 2022 in press); 8570 ± 60 years RUSA04 (tooth of *Panthera tigris* (Linnaeus 1758), pit IV, depth interval 0.2–0.3 m, layer 2) (Sun et al., 2022, in press); and 8650 ± 70 years RUSA12 (bone of *Panthera tigris* (Linnaeus 1758), pit IV, depth interval 0–0.4 m, stockpile) (Sun et al., 2022, in press). The dates obtained made it possible to compare the unconsolidated deposits with marine isotopic stages MIS 3–1 and with chronostratigraphic divisions from the Late Pleistocene to the Holocene.

Molluscs were conventionally divided into three groups according to their preference for different vegetation types (according to P. Sümegi in Willis et al., 2000): forest habitats, open areas, and intermediate ones (Table 2). The third group includes the mollusc species that can live in different types of vegetation both in forests, in open spaces, as well as in moist areas with sparse vegetation (wet meadows, forests, shrubs, swamps, and stream banks).

RESULTS

Distribution of shells by depth in unconsolidated pit deposits. Mollusc shells are distributed unevenly in the sedimentary deposits (Fig. 3). The largest number of shells is concentrated in pit VI in a depth interval of 0.9–1.3 m (layers 4, bottom—6, middle); in pit I in a depth interval of 0.8–1.2 m (layers 4, middle—5); and in pit II in the depth intervals of 0.2–0.4 m (layer 3, top), 0.6–0.8 m (layers 4, 7, top), and 1–1.2 m (layer 7, bottom). A smaller number of shells were found in pit VI at depths of 0–0.2 m (upper part of layer 1) and 1.3–1.4 m (lower part of layer 6); in pit I at depths of 0–0.1 m (upper part of layer 1), 0.2–0.3 m (upper part of layer 2), 0.6–0.7 m (top of layer 4), and 1.2–1.3 m (layer 6); in pit IV at depths of 0.1–0.2 m (layer 2, top), 0.5–0.6 m (layer 3, middle), and 0.7–1.1 m (layers 4–5); and in pit II at depths of 0.9–1.0 m (layer 7, middle) and 1.2–1.5 (layer 8). In pit V, the number of shells increases downwards with depth, and their maximum number is confined to a depth interval of 0.6–0.7 m (bottom of layer 1), whereas in pit III, conversely, the largest number of mollusc shells was found at a depth of 0–0.1 m (upper part of layer 1), then the number of shells decreases significantly down the section.

Taxonomy. The shells found in the deposits of the cave belong only to terrestrial molluscs. Fourteen species belonging to 11 genera (*Carychium*, *Cochlicopa*, *Vallonia*, *Columella*, *Vertigo*, *Punctum*, *Discus*, *Euconulus*, *Hawaiia*, *Perpolita*, and *Karaftohelix*) and 10 families (Carychiidae, Cochlicopidae, Valloniidae, Pupillidae, Punctidae, Discidae, Zonitidae, Euconulidae, Agriolimacidae, and Bradybaenidae) were identified (Table 1, Figs. 4–8).

Shells of *Carychium*, *Cochlicopa*, *Vallonia*, *Columella*, *Vertigo*, *Punctum*, *Discus*, and *Hawaiia* are well preserved; whole specimens, white or with a reddish tinge, are found. A carbonate crust is observed on the surface of many shells; Bradybaenidae shells are rarely found as a whole, most of the finds are presented as separate fragments.

Below is a brief description of the main species by families.

Ellobiidae. Genus *Carychium*. Species *Carychium pessimum* Pilsbry 1901. The shell is spiral, fusiform (shell height 1.9 mm, diameter 0.5 mm), with 5.5 rounded and stepped whorls with fine striation, separated by a deep suture. The umbo is rounded and high. The aperture is oval, slightly depressed from the palatal margin, the margins of the aperture are thickened and turned away. There are two denticles in the aperture: columellar and palatal. The umbilicus is narrow, covered by the flap of the columellar margin (Figs. 4a–4c).

Cochlicopidae. Genus *Cochlicopa*. Species *Cochlicopa lubrica* (Müller 1774). The shell is spiral, fusiform–conical, smooth (shell height 5–6 mm, diameter 2–2.1 mm), consists of 5.5–6 slightly convex whorls with smoothed striation on the surface. The whorls are separated by a shallow suture. The umbo is rounded, tapering to the top. The aperture is oval, pointed at the top, the margins of the aperture are thickened, not turned. The umbilicus is completely closed by the flap of the columellar margin (Figs. 5a–5c).

Valloniidae is represented by the genus *Vallonia* and two species *Vallonia patens* Reinhardt 1883 and *Vallonia pulchellula* (Heude 1882).

Table 2. Ecological characteristics of mollusc species found in Upper Pleistocene–Holocene deposits of Tetyukhinskaya Cave (Primorsky Krai, Russia)

No.	Species	Current geographical distribution	Temperature	Humidity	Ecology (habitat)	References
1	*Carychium pessimum* Pilsbry 1901	Palaearctic. Southern Primorsky Krai, Japan, Korea	Mesophilous	Hygrophilous	Intermediate habitats. Moist environment (forests, meadows in river valleys, swamps); under fallen leaves, rotten wood, on swamp hummocks. Does not tolerate droughts. Can withstand prolonged floods. Lives on plains and mountains (up to 1800 m)	Pilsbry, 1902; Likharev and Rammelmeyer, 1952; Sysoev and Shileyko, 2009; Prozorova et al., 2018; MolluscaBase
2	*Cochlicopa lubrica* (O.F. Müller 1774)	Palaearctic. From Western Europe to Central Siberia (Irkutsk), in Central Asia, Kuril Islands	Mesophilous	Mesophilous/ subhygrophilous	Intermediate habitats. Broad ecological range. Usually inhabits moderately moist habitats, valley meadows and forests, under rocks and dead wood. Tolerates non-carbonate soils. Lives on plains and mountains (up to 2600 m)	Germain, 1930; Likharev and Rammelmeyer, 1952; Ložek, 1964; Puisségur, 1976; Shileyko, 1984; Alexandrowicz, 2002; Sysoev and Shileyko, 2009; AnimalBase
3	*Vallonia patens* Reinhardt 1883	Palaearctic. Southern Primorsky Krai, China	Mesophilous	Mesophilous	Prefers woodlands (valley broadleaf forests). Inhabits moist leaf litter	Likharev and Rammelmeyer, 1952; Shileyko, 1984; Sysoev and Shileyko, 2009; AnimalBase
4	*Vallonia pulchellula* (Heude 1882)	Palaearctic. Southern Primorsky Krai, Vladivostok, Japan, Korea, China	Mesophilous	Subhygrophilous	Prefers woodlands (valley broadleaf forests). Inhabits moist leaf litter, sod, and moist rock crevices along the coast	Prozorova et al., 2018; Gerber, 1996
5	*Columella edentula* (Draparnaud 1805)	Holarctic. Europe, except southern regions, Caucasus, Transcaucasia, Sakhalin, Kuril Islands, Kamchatka, Korean Peninsula, Japan, partly China, Central Asia, North America	Mesophilous (eurythermic)	Subhygrophilous	Intermediate habitats. Inhabits floodplain meadows with tall grass. Lives near water bodies, in forests, in thickets of shrubs, on edges of deciduous forests. Often climbs along grass stems. Found on well-moistened slopes in scree and in rock cracks. Does not tolerate droughts. Feeds at a daytime temperature of 10°C. Lives on plains and mountains (up to 2300 m)	Likharev and Rammelmeyer, 1952; Ložek, 1964; Shileyko, 1984; Prozorova et al., 2007; Sysoev and Shileyko, 2009; AnimalBase

Table 2. (Contd.)

No.	Species	Current geographical distribution	Temperature	Humidity	Ecology (habitat)	References
6	*Vertigo* cf. *japonica* Pilsbry et Hirase 1904	Palaearctic. Southern Primorsky Krai, Southern Kuril Islands, Japan, Korea	Mesophilous	Subhygrophilous	Intermediate habitats. Inhabits mainly the edges of deciduous forests and woodlands. Lives in deciduous litter	Likharev and Rammelmeyer, 1952; Shileyko, 1984; Sysoev and Shileyko, 2009
7	*Punctum ussuriense* Likharev et Rammelmeyer 1952	Palaearctic. Southern Primorsky Krai, Sakhalin	Mesophilous	Mesophilous	Prefers woodlands or moist open spaces. Lives under fallen leaves, dead wood, and rocks	Likharev and Rammelmeyer, 1952; Sysoev and Shileyko, 2009
8	*Discus depressus* (A. Adams 1868)	Palaearctic. Northern Eurasia from Europe to Eastern Siberia. Including the Far East, Sakhalin, Kamchatka, the Kuril and Commander Islands, north of Khabarovsk Krai, vicinities of Lake Baikal	Mesophilous	Mesophilous	Prefers woodlands. Lives under fallen leaves, under bark of old trees, on mossy trunks, under damp dead wood and stones. Lives on plains and mountains (up to 2800 m)	Likharev and Rammelmeyer, 1952; Sysoev and Shileyko, 2009; AnimalBase
9	*Euconulus fulvus* (O.F. Müller 1774)	Holarctic	Mesophilous	Mesophilous	Prefers woodlands. Is rarely found in dry meadows and grassy mountain habitats. Lives in leaf litter, under bark of dead trees, in moist lichens. Lives on plains and mountains (up to 2900 m)	Germain, 1930; Likharev and Rammelmeyer, 1952; Ložek, 1964; Puisségur, 1976; Alexandrowicz, 2002; Sysoev and Shileyko, 2009; Prozorova et al., 2018; AnimalBase
10	*Hawaiia minuscula* (Binney 1841)	The Palaearctic. Southern Primorsky Krai, North America, Alaska, Japan, Korea, Taiwan	Mesophilous	Mesophilous	Intermediate habitats. Deciduous and mixed forests, shrubs, among rocks on grassy slopes, along roadsides and in open areas	Likharev and Rammelmeyer, 1952; Riedel, 1967; Kaszuba and Stworzewicz, 2008; Sysoev and Shileyko, 2009; AnimalBase

Table 2. (Contd.)

No.	Species	Current geographical distribution	Temperature	Humidity	Ecology (habitat)	References
11	*Perpolita petronella* (L. Pfeiffer 1853)	Palaearctic. Europe, Caucasus, Siberia, Transbaikalia	Mesophilous	Mesophilous	Intermediate habitats. Forests, wet meadows, swamps. Wide ecological range. It lives on plains and mountains (up to 2700 m).	Likharev and Rammelmeyer, 1952; Ložek, 1964; Alexandrowicz, 2002; Sysoev and Shileyko, 2009; AnimalBase
12	Agriolimacidae	Holarctic. Including: Altai, Eastern Siberia, Primorsky Krai, Middle and Southern Amur basin, Southern Sakhalin	Mesophilous	Mesophilous	Prefers woodlands (mixed and deciduous forests). Lives in moist deciduous litter, often found along river banks and in floodplain forests	Likharev and Rammelmeyer, 1952; Sysoev and Shileyko, 2009
13	*Karaftohelix maacki* (Gerstfeldt 1859)	Palaearctic. Primorsky Krai, Lower and Middle Amur basin, Northern China (Yangtze basin), northern part of the Korean Peninsula, Manchuria	Mesophilous	Mesophilous	Prefers woodlands (mixed and deciduous forests). Reaches its highest density in deciduous litter of moist forests. At high humidity, moves to trees. Inhabits plains (floodplains) and rises to hilltops	Likharev and Rammelmeyer, 1952; Shileyko, 1978; Sysoev and Shileyko, 2009; Prozorova et al., 2018
14	*Karaftohelix* cf. *middendorffi* (Gerstfeldt 1859)	Palaearctic. Primorsky Krai, Lower and Middle Amur basin	Mesophilous	Mesophilous	Prefers woodlands (mixed and valley broadleaf forests). Lives in moist places, in floodplains (grass, shrubs), moist leaf litter, near water; often found in wet ravines	Likharev and Rammelmeyer, 1952; Shileyko, 1978; Sysoev and Shileyko, 2009; Prozorova et al., 2018
15	*Karaftohelix dieckmanni* (Mousson 1887)	Palaearctic. Southern Primorsky Krai and nearby islands, Lower and Middle Amur basin	Mesophilous	Subhygrophilous	Prefers woodlands. Most often found in swampy areas, among grass thickets	Likharev and Rammelmeyer, 1952; Shileyko, 1978; Sysoev and Shileyko, 2009

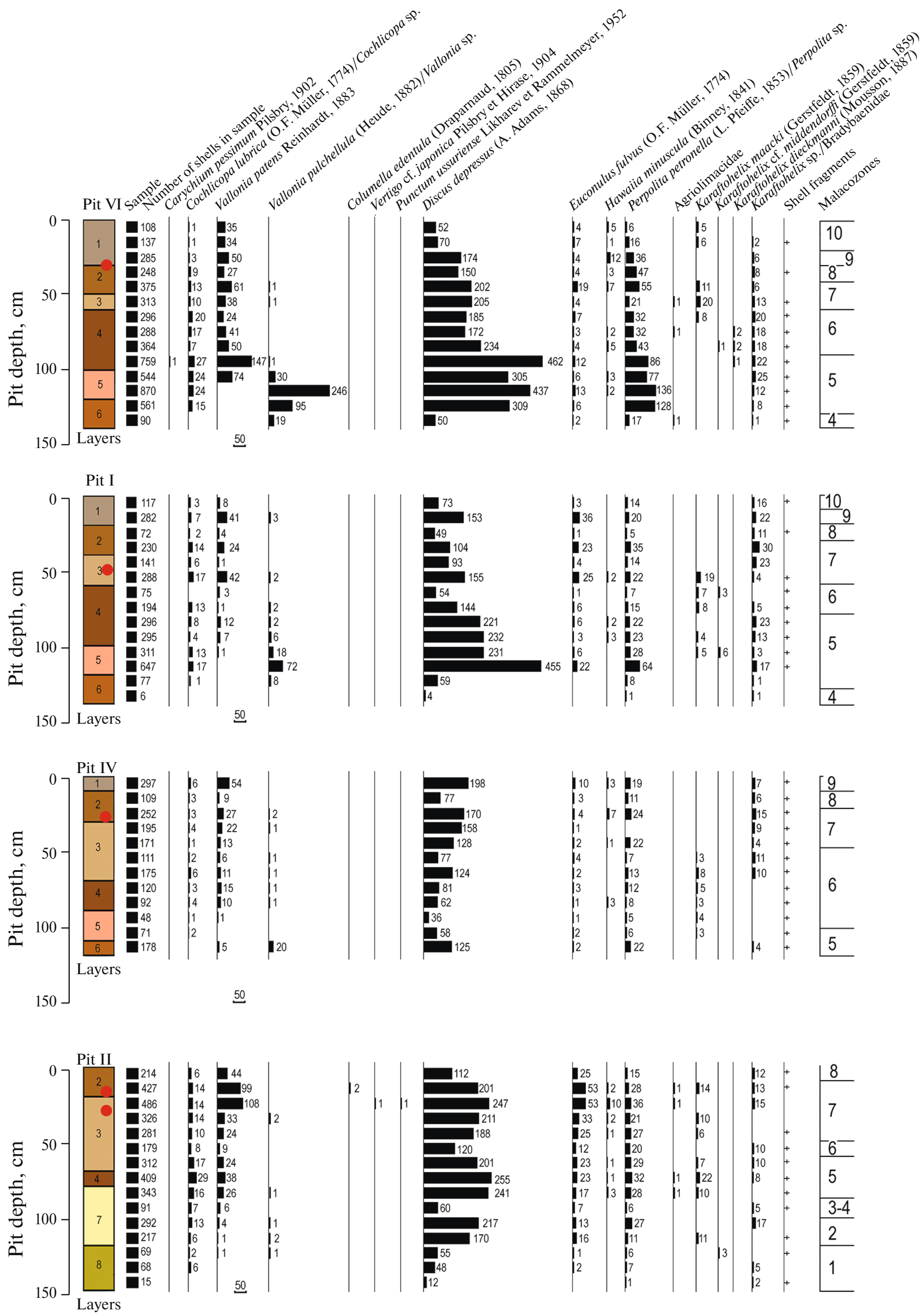

Fig. 3. Summary diagrams of the occurrence of terrestrial molluscs and distinguished malacozones in unconsolidated deposits exposed by pits VI, I, IV, and II (listed from the entrance to the depth) of the Tetyukhinskaya Cave. Red dots indicate the locations of radiocarbon dates. A summary description of the layers in the pits is given in the text.

Vallonia patens Reinhardt 1883. The shell is spiral, in the form of a low cone (shell height 0.8–1 mm, diameter 2–2.1 mm), consists of 3.5 rounded whorls with fine striation. The last whorl towards the aperture is lowered and slightly broadened, flattened from above and angular along the periphery. The umbo is rounded, not protruding. The aperture is oval, its attachment points are close together; the margins of the aperture are turned away, with a very poorly expressed lip. The umbilicus is wide, perspective, all the turns are visible (Figs. 6e–6h).

Vallonia pulchellula (Heude 1882). The shell is spiral, low-conical (shell height 1–1.1 mm, diameter 2–2.1 mm), consists of 3.5 rounded whorls with uneven striation. The last turn towards the aperture widens and slightly lowers. The umbo is rounded and low. The aperture is rounded, its attachment points are close together; the margins of the aperture are thin, not turned away. The umbilicus is very wide (Figs. 6i–6l).

Vertiginidae. Genus *Vertigo*. Species *Vertigo* cf. *japonica* Pilsbry et Hirase 1904. The shell is spiral, oval-conical, thin-walled (shell height 1.9 mm, diameter 0.8 mm), consists of 5.5 convex whorls with fine striation, separated by a deep suture. The last whorl narrows downwards. The umbo is rounded and high. The aperture is rounded, sloping from above, with an indentation on the palatal margin. The margins of the aperture are thin, slightly turned away. There are four denticles in the aperture (parietal, columellar, and two palatal). The umbilicus is narrow, partially covered by the flap of the columellar margin (Figs. 4g–4i).

Truncatellinidae. Genus *Columella*. Species *Columella edentula* (Draparnaud 1805). The shell is spiral, cylindrical, thin-walled, with fine and uneven striation (shell height 2 mm, diameter 1 mm), with 6–6.5 rounded and convex whorls separated by a deep suture. The width of the whorls gradually increases from top to bottom. The umbo is rounded and high. The aperture is rounded, sloping on top, the margins of the aperture are thin. The umbilicus is narrow (Figs. 4d–4f).

Punctidae. Genus *Punctum*. Species *Punctum ussuriense* Likharev et Rammelmeyer 1952. The shell is spiral, low-conical with a dome-shaped whorl outline (shell height 0.7 mm, diameter 1 mm); 3.5 strongly convex whorls with fine and dense striation, separated by a deep suture. The umbo is rounded and high. The aperture is rounded, sloping; the margins are thin, not turned. Inside the aperture, there is a small seal on the columellar side. The umbilicus is very wide (Figs. 4j–4m).

Discidae. Genus *Discus*. Species *Discus depressus* (Adams 1868). The shell is spiral, low-conical (shell height 2–3 mm, diameter 4.5–5.5 mm); 4–4.5 convex and finely ribbed whorls, the last whorl is angular. The umbo is rounded and high. The aperture is rounded, sloping, the margins are thin. The umbilicus is wide and perspective (Figs. 7i–7l).

Gastrodontidae. Genus *Perpolita*. Species *Perpolita petronella* (Pfeiffer 1853). The shell is spiral, low-conical (shell height 1.9–2.1 mm, diameter 2.5–4 mm); 3.5–4 rounded and finely striated whorls are separated by a shallow suture. The last turn is wide. The umbo is low and rounded. The aperture is oval, sloping, elongated, lowered down. The umbilicus is wide and perspective (Figs. 7e–7h).

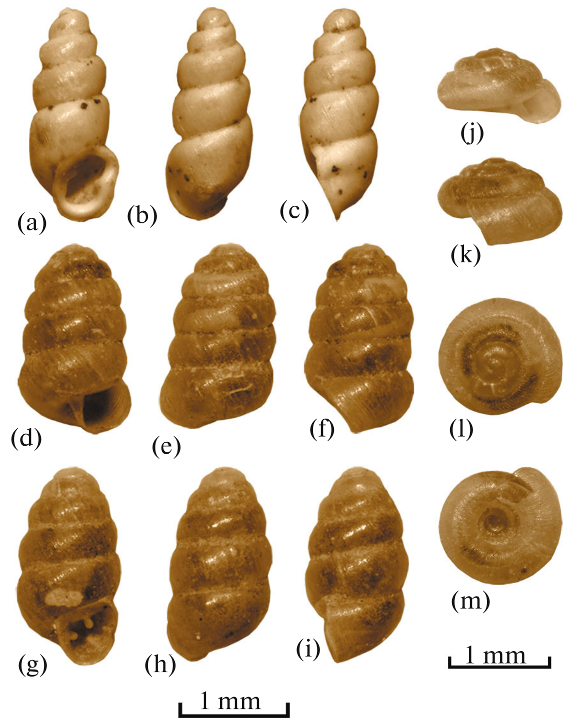

Fig. 4. Species of molluscs of the genera *Carychium*, *Columella*, *Vertigo*, and *Punctum* from unconsolidated deposits of the Late Pleistocene and Holocene of Tetyukhinskaya Cave (Primorsky Krai, Russia). (a–c) *Carychium pessimum*, IG no. 389/6685/1, pit VI, depth interval 0.9–1 m ((a) view from the aperture, (b) view from the side opposite to the aperture, (c) lateral view); (d–f) *Columella edentula*, IG no. 389/6632/5, pit II, depth interval 0.1–0.2 m ((d) view from the aperture, (e) view from the side opposite to the aperture, (f) lateral view); (g–i) *Vertigo* cf. *japonica*, IG no. 389/6633/7, pit II, depth interval 0.2–0.3 m ((g) view from the aperture, (h) view from the side opposite to the aperture, (i) lateral view); (j–m) *Punctum ussuriense*, IG no. 389/6633/8, pit II, depth interval 0.2–0.3 m ((j) view from the aperture, (k) lateral view, (l) view from the umbo, (m) view from the umbilicus). IG no. 389/6685/1—registration number of the sample.

Pristilomatidae. Genus *Hawaiia*. Species *Hawaiia minuscula* (Binney 1841). The shell is spiral, low-conical, thin-walled (shell height 1–1.1 mm, diameter 2–2.1 mm); 4–4.5 rounded, finely and densely striated whorls are separated by a deep suture. The umbo is low and rounded. The aperture is rounded, slightly sloping; the margins of the aperture are thin, not turned. The umbilicus is wide (Figs. 6a–6d).

Euconulidae. Genus *Euconulus*. Species *Euconulus fulvus* (Müller 1774). The shell is spiral, broadly conical (shell height 2–3 mm, diameter 2–2.5 mm); 5–6 convex whorls with fine and dense striation are separated by a deep suture. The last turn on the periphery is slightly angular. The umbo is high and rounded. The aperture is rounded, sloping from above, and narrow.

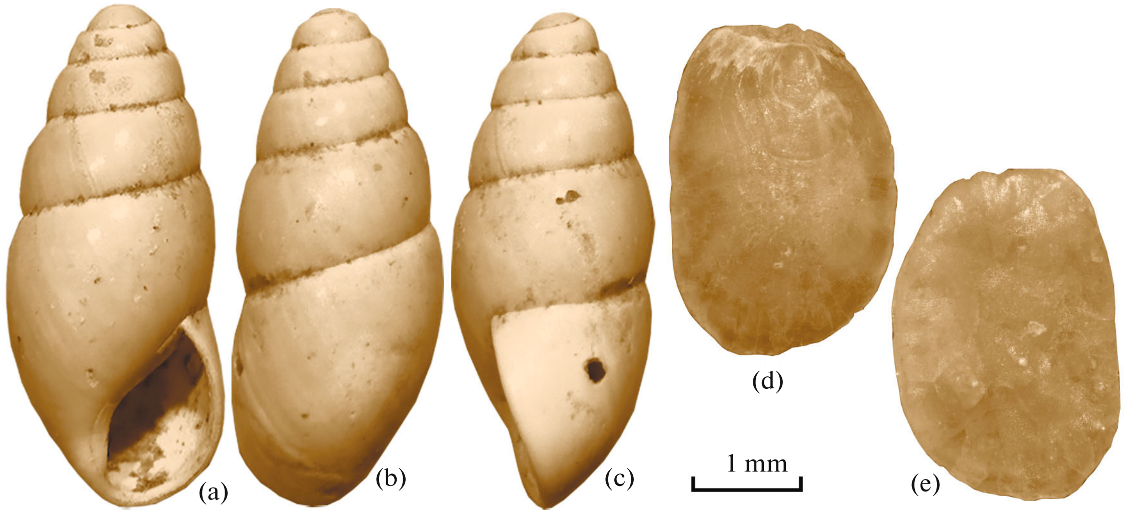

Fig. 5. Species of molluscs of the genus *Cochlicopa* and the family Agriolimacidae from unconsolidated deposits of the Late Pleistocene and Holocene of Tetyukhinskaya Cave (Primorsky Krai, Russia). (a–c) *Cochlicopa lubrica*, IG no. 389/6701/2, pit IV, depth interval 0.4–0.5 m ((a) view from the aperture, (b) view from the side opposite to the aperture, (c) lateral view); (d–e) Agriolimacidae, IG no. 389/6689/13, pit VI, depth interval 1.3–1.4 m ((d) shell from the side of the nucleus, (e) shell from the side opposite to the nucleus). IG no. 389/6701/2—registration number of the sample.

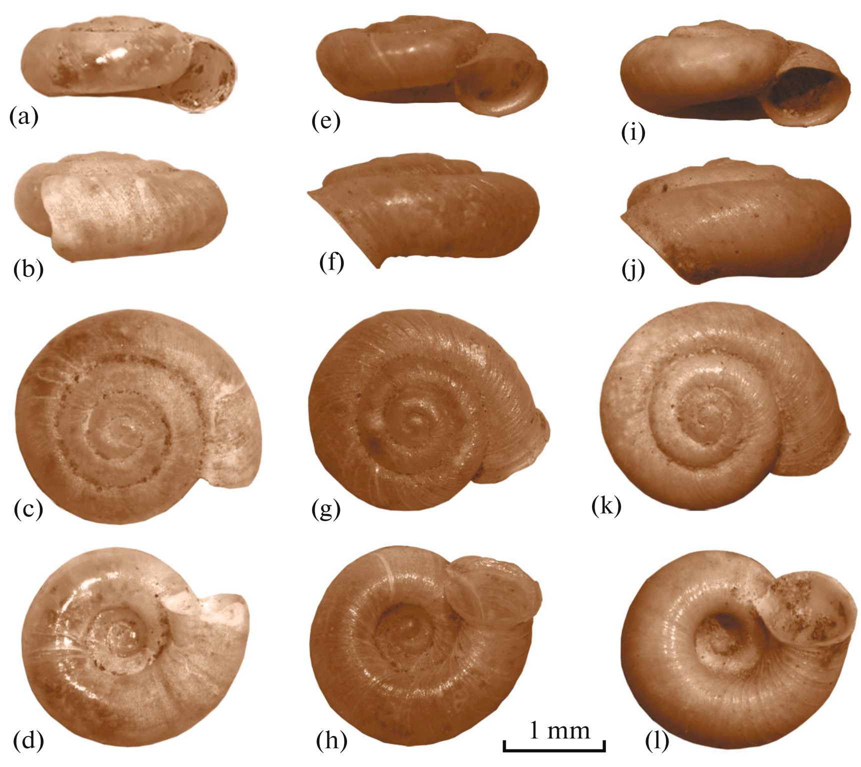

Fig. 6. Species of molluscs of the genera *Hawaiia* and *Vallonia* from unconsolidated deposits of the Late Pleistocene and Holocene of Tetyukhinskaya Cave (Primorsky Krai, Russia). (a–d) *Hawaiia minuscula*, IG no. 389/6667/10, pit IV, depth interval 0–0. 7 m ((a) view from the aperture, (b) lateral view, (c) view from the umbo, (d) view from the umbilicus); (e–h) *Vallonia patens*, IG no. 389/6669/3, pit V, depth interval 0.1–0.2 m ((e) view from the aperture, (f) lateral view, (g) view from the umbo, (h) view from the umbilicus); (i–l) *Vallonia pulchellula*, IG no. 389/6687/4, pit VI, depth interval 1.1–1.2 m ((i) view from the aperture, (j) lateral view, (k) view from the umbo, (l) view from the umbilicus). IG no. 389/6667/10—registration number of the sample.

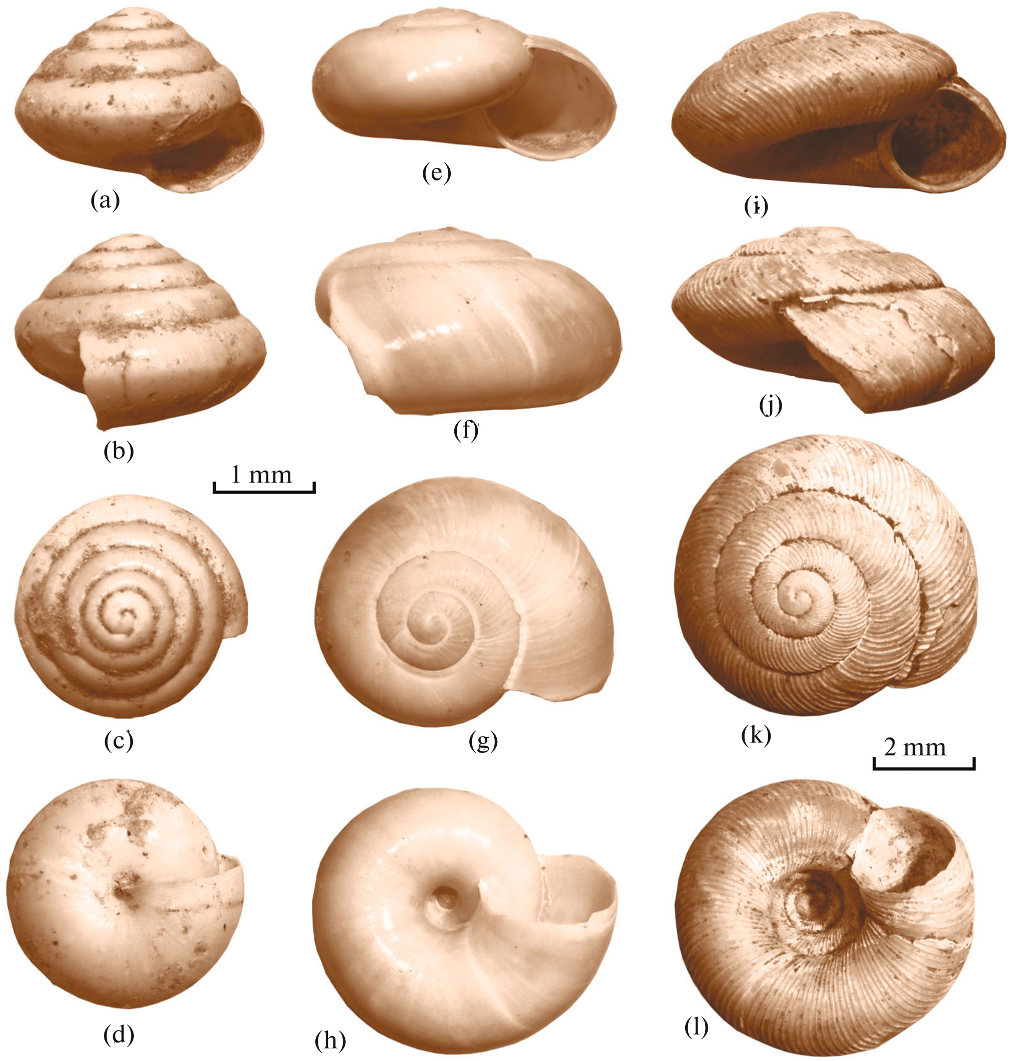

Fig. 7. Species of molluscs of the genera *Discus*, *Euconulus*, and *Perpolita* from unconsolidated deposits of the Late Pleistocene and Holocene of Tetyukhinskaya Cave (Primorsky Krai, Russia). (a–d) *Euconulus fulvus*, IG no. 389/6627/11, pit I, depth interval 1.1–1.2 m ((a) view from the aperture, (b) lateral view, (c) view from the umbo, (d) view from the umbilicus); (e–h) *Perpolita petronella*, IG no. 389/6628/12, pit I, depth interval 1.2–1.3 m (e) view from the aperture, (f) lateral view, (g) view from the umbo, (h) view from the umbilicus); (i–l) *Discus depressus*, IG no. 389/6664/9, pit IV, depth interval 0.9–1 m ((i) view from the aperture, (j) lateral view, (k) view from the umbo, (l) view from the umbilicus). IG no. 389/6627/11—registration number of the sample.

The umbilicus is closed by the columellar margin of the aperture (Figs. 7a–7d).

Agriolimacidae. This family is represented by reduced mollusc shells; calcareous, thickened oval white plates. The nucleus (the embryonic part of the shell) is small, shifted to the margin of the plate; the spatula (the main part of the plate) with indistinct lines of growth (the length of the spatula is 3–4.1 mm, the width is 2 mm) (Figs. 5d–5e).

Due to the lack of comparative collections and scarce published data both on fossil and recent materials related to descriptions of mollusc shells, we did not assign the found specimens to any genus or species and indicated only the family whose name was agreed with P.V. Kiyashko.

Camaenidae. Genus *Karaftohelix*. Species *Karaftohelix maackii* (Gerstfeldt 1859), *Karaftohelix* cf. *middendorffi* (Gerstfeldt 1859), and *Karaftohelix dieckmanni* (Mousson 1887).

The shell of *Karaftohelix maackii* (Gerstfeldt 1859) is spiral, domes (shell height 8.5–13 mm, diameter 14–19 mm); 6.5–7 rounded whorls with fine striation are separated by a deep suture. The last whorl is slightly larger than the penultimate one. Spiral brown stripes are preserved on the whorls, which are located under the suture, on the periphery of the last whorl, and on the underside of the shell. The umbo is broad and

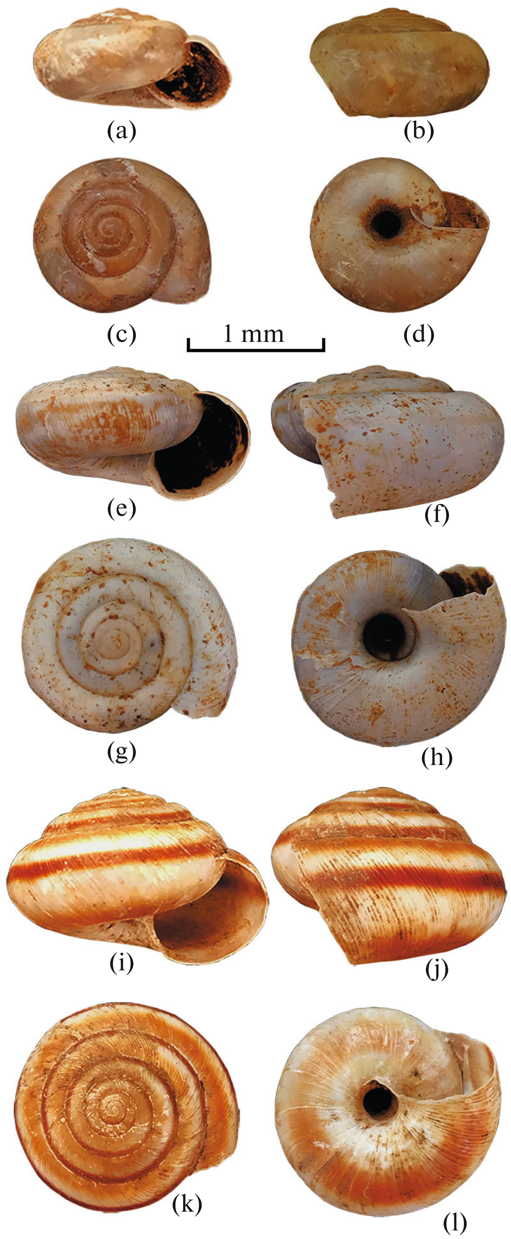

Fig. 8. Species of molluscs of the genus *Karaftohelix* from unconsolidated deposits of the Late Pleistocene and Holocene of Tetyukhinskaya Cave (Primorsky Krai, Russia). (a–d) *Karaftohelix dieckmanni*, IG no. 389/6683/16, pit VI, depth interval 0.7–0.8 m ((a) view from the aperture, (b) lateral view, (c) view from the umbo, (d) view from the umbilicus); (e–h) *Karaftohelix* cf. *middendorffi*, IG no. 389/6626/15, pit I, depth interval 1–1.1 m ((e) view from the aperture, (f) lateral view, (g) view from the umbo, (h) view from the umbilicus); (i–l) *Karaftohelix maacki*, IG no. 389/6676/14, pit VI, depth interval 0–0. 1 m ((i) view from the aperture, (j) lateral view, (k) view from the umbo, (l) view from the umbilicus). IG no. 389/6683/16—registration number of the sample.

rounded. The aperture is rounded, sloping, drawn down and laterally. The margins of the aperture are thin and turned away. The umbilicus is open, slightly covered by the flap of the columellar margin (Figs. 8i–8l).

The shell of *Karaftohelix* cf. *middendorffi* (Gerstfeldt 1859) is spiral, low-conical, thin-walled (shell height 10–17 mm, diameter 14–19 mm); 6–6.5 rounded whorls are ribbed with thick and thin spiral lines. The last turn to the aperture is not lowered down; along the periphery of the last whorl there is a dark band (may be absent), smoothly passing to the previous whorls, where it tightly adjoins the base of the suture. The umbo is rounded, broad, and low. The aperture is rounded, slopes, the margins of the aperture are turned away, with a white lip inside. The umbilicus is wide (Figs. 8e–8h).

The shell *of Karaftohelix dieckmanni* (Mousson 1887) is spiral, low-conical, low (shell height 5–7 mm, diameter 12–13 mm); 5 rounded whorls are ribbed with fine spiral lines. The umbo is rounded and low. The aperture is rounded, drawn laterally and slightly lowered down; the margins of the aperture are wide and turned away (Figs. 8a–8d).

Palaeoecological data. The sensitivity of molluscs to environmental conditions, especially to factors such as temperature, humidity, and vegetation, is clear. Therefore, all the studied species were characterized according to the above criteria. An analysis of the data showed that the found molluscs are mesophilous in terms of temperature preference (i.e., they prefer temperate climates). In relation to humidity, three groups of molluscs were distinguished: subhygrophilous, hygrophilous (living at high humidity), and mesophilous (tolerating moderate humidity). According to preferences for different types of vegetation, molluscs were divided into species inhabiting forest areas and species occupying intermediate habitats (Table 2).

DISCUSSION

To characterize ecological zones, we used the most illustrative data for pits VI and I as a basis, whereas the materials for other pits were used as supplementary, because changes in the quantitative and species composition of malacocomplexes are clearly observed from the entrance to the interior part of the cave (Fig. 3).

An analysis of the faunal composition demonstrated that, in terms of abundance and percentage, all found mollusc shells belong to three categories. The absolutely dominant species in the deposits of all pits is *Discus depressus*, which accounts for 63% of all identified shells (Table 1, Fig. 3). Minor (or rare) species are *Vallonia patens* and *Perpolita petronella*, which account for 10% of the total number of identified shells. The insignificant (or single) species, the proportion of which varies from 0.01 to 4% for different species, belong to the third category. As a result of the analysis of the species composition of molluscs and their ecological preferences, ten malacozones (MZs) were distinguished; malacozones were compared with layers in pits; palaeohabitats were characterized on the basis of malacozones. The characteristics of malacozones are given below.

Malacozone 1 (MZ1) was distinguished in pit II (depth interval 1.2–1.5 m., layer 8). A total of 152 shells were identified, which belong to molluscs of seven species. The majority of molluscs were forest species (71%, five species) and preferred mesophilic conditions in terms of temperature and humidity. Some species are characteristic of intermediate habitats (29%, two species). During the accumulation of deposits, the landscape was represented by mixed forests on slopes and broad-leaved forests in river valleys with moist deciduous litter, as well as open spaces among forests (margins and clearings) and in river valleys (wet meadows and shrubs). The climate was probably moderately cool.

Malacozone 2 (MZ2) was distinguished in pit II (depth interval 1–1.2 m, layer 7). A total of 509 shells of seven species were identified. Similarly to MZ1, this zone was dominated by forest species (71%, five species) and typical species of intermediate habitats (29%, two species), which live in mesophilic conditions in terms of temperature and humidity. An increase in the number of specimens *of Vallonia pulchellula* and *Cochlicopa lubrica* from the bottom up along the section indicates an increase in climate humidity. During the accumulation of deposits, the landscape remained unchanged (as during the formation of MZ1). The climate was probably temperate, but more humid as compared to MZ1, as indicated by a threefold increase in the number of shells.

Malacozone 3–4 (MZ3–4) was distinguished in pit II (depth interval 0.9–1 m, layer 7). A total of 91 shells of six species of molluscs were identified. This zone was dominated by forest species (four species, or 60%), which prefer mesophilic habitat conditions in terms of temperature and humidity. A sharp decrease in the number of mollusc shells compared to MZ2 indicates less favourable habitat conditions for animals. Forests still grew in the area around the cave, but their area decreased, and the areas occupied by the intermediate habitats increased (two species, or 40%). The climate was probably moderately cool.

Malacozone 4 (MZ4) was distinguished in pits VI and I (depth interval 1.3–1.4 m, layer 6). A total of 96 shells were identified, which belong to molluscs of five species. The majority of species preferred mesophilic habitat conditions in terms of temperature and humidity, and forest species also predominated. This zone is characterized by a small number of mollusc shells, as in MZ3–4, which also indicates unfavourable living conditions for animals. Forests continued to grow in the area around the cave (65%, four species), and there were intermediate spaces occupied by herbage vegetation and shrubs (35%, one species). The findings of mollusc shells indicate increased humidity in biotopes. Probably, the climate was still moderately cool, but more humid compared to MZ3–4.

Malacozone 5 (MZ5) was distinguished in pit VI (depth interval 0.9–1 m, layers 4–6) and in pits I–IV. The zone is characterized by 5703 shells of 11 species of molluscs. Most of the shells belong to molluscs of forest species, which preferred mesophilic living conditions in terms of temperature and humidity. This zone is characterized by a large number of shells and species of molluscs compared to other zones, which indicates optimal conditions for their existence. The cave was surrounded by forests (61%, eight species) with intermediate spaces occupied by herbage vegetation and shrubs (39%, three species). The presence of hygrophilic and subhygrophilic species (*Carychium pessimum*, *Cochlicopa lubrica*, and *Karaftohelix dieckmanni*) indicates increased humidity in habitats. The climate was probably moderately warm and humid.

Malacozone 6 (MZ6) was distinguished in pit VI (depth interval 0.6–0.9 m, layer 4) and in pits I, IV, and II. A total of 1396 shells of 11 species of molluscs were identified. Forest species that lived in mesophilic conditions in terms of temperature and humidity predominated. The zone is generally characterized by a decrease in the number of mollusc shells compared to MZ5, which indicates a slight deterioration in their habitat conditions. The areas occupied by forests (72.5%, eight species) increased in comparison with intermediate habitats (27.5%, three species). The climate was probably temperate and humid.

Malacozone 7 (MZ7) was distinguished in pit VI (depth interval 0.4–0.6 m, layers 2–3) and in pits I, IV, and II. This zone was characterized by 3505 shells of 12 species of molluscs. The species are mostly forest, living in mesophilic conditions in terms of temperature and humidity. The zone is generally characterized by an increase in the number of mollusc shells, which indicates some improvement in their habitat conditions. The spaces occupied by forests slightly decreased in area (64.5%, seven species) compared to zone MZ6; there were also intermediate habitats (35.5%, five species). The climate was probably temperate and humid.

Malacozone 8 (MZ8) was distinguished in pit VI (depth interval 0.3–0.4 m, layer 2) and in pits I, IV, and II. A total of 642 shells of 7 species of molluscs were identified. Most species preferred mesophilic habitats in terms of temperature and humidity. The zone is generally characterized by a decrease in the number of mollusc shells compared to zone MZ7, which indicates a slight deterioration in their habitat conditions. The area occupied by forests slightly increased (75%, 5 species) compared to MZ7; intermediate habitats were also present (25%, two species). The climate was probably temperate (possibly cool).

Malacozone 9 (MZ9) was distinguished in pit VI (depth interval 0.2–0.3 m, layer 1) and in pits I, IV, and V. A total of 1059 shells of 6 species of molluscs were identified. An analysis of molluscs, according to their current ecological preferences, shows that most

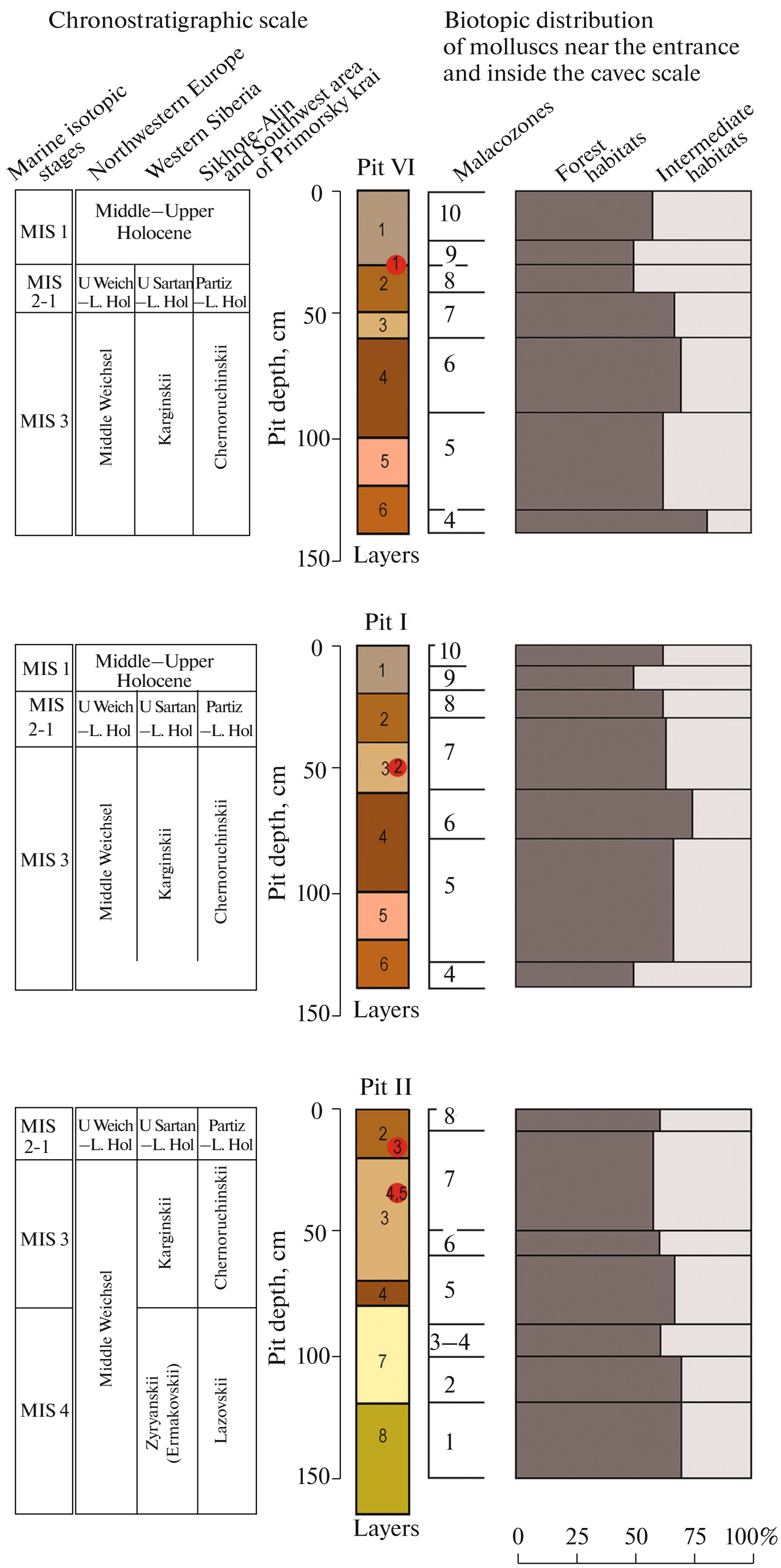

Fig. 9. Reconstruction of palaeoecological conditions of the Late Pleistocene and Holocene in the Tetyukhinskaya Cave area based on data obtained from studying the species and quantitative diversity of terrestrial molluscs. Red dots with numbers indicate the locations of radiocarbon dates: 1—8590 ± 40 years RUSA14; 2—37 673 ± 950 years NSKA-851; 3—39874 ± 133 years NSK-850, UGAMS-21786; 4—20215 ± 10000 years SPb-1057; 5—8585 ± 45 years RUSA06. Chronostratigraphic data are given according to Cohen and Gibbard, 2019; *Resheniya*..., 1983, 1987.

species lived in mesophilic conditions in terms of temperature and humidity. The zone as a whole is characterized by a slight increase in the number of mollusc shells compared to MZ8, which indicates a slight improvement in their habitat conditions. Forest areas (50%, three species) and intermediate habitats (50%, three species) occupied approximately equal areas. The climate was probably temperate.

Malacozone 10 (MZ10) was identified for pit VI (depth interval 0–0.2 m, layer 1) and in pits I and V. A total of 362 shells of 7 species of molluscs were identified. Most species preferred 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 a slight deterioration in the conditions of their existence. The areas occupied by forests (58.5%, four species) and intermediate habitats (41.5%, three species) were approximately equal. The climate was probably temperate.

At this stage, it is difficult to compare the obtained data on the fossil malacofauna with the extant species occurring in the vicinity of Tetyukhinskaya Cave, since the extant molluscs in the cave area were not collected. Publications on the study of the malacofauna in the region as a whole and adjacent areas (Prozorova et al., 2007, 2018, 2020; Prozorova, 2012, 2020, 2020a; Prozorova and Fomenko, 2015), as well as the literature sources given in Table 2, indicate that almost all species of molluscs from Late Pleistocene and Early Holocene, according to data from the Tetyukhinskaya Cave, still occur in Primorsky Krai. For the species *Cochlicopa lubrica* (Müller 1774) and *Perpolita petronella* (L. Pfeiffer 1853), according to the publications, there is no indication of their distribution on the territory of Primorsky Krai: *Cochlicopa lubrica* occurs from Western Europe to Central Siberia (Irkutsk), in Central Asia, and on the Kuril Islands (Pearce et al., 2002; Sysoev and Shileyko, 2009); *Perpolita petronella* inhabits the forests of the Eastern European Plain and Siberia (Sysoev and Shileyko, 2009), as well as Transbaikalia (Likharev and Rammelmeyer, 1952). The study of extant molluscs on the territory of Primorsky Krai will help to clarify the ranges of these species.

CONCLUSIONS

As a result of studying the unconsolidated deposits of Tetyukhinskaya Cave, the shells of terrestrial molluscs of 14 species from 11 genera (*Carychium*, *Cochlicopa*, *Vallonia*, *Columella*, *Vertigo*, *Punctum*, *Discus*, *Euconulus*, *Hawaiia*, *Perpolita*, *Karaftohelix*) and 10 families (Carychiidae, Cochlicopidae, Valloniidae, Pupillidae, Punctidae, Discidae, Zonitidae, Euconulidae, Agriolimacidae, and Bradybaenidae). To clarify and supplement the materials on Pleistocene molluscs of Primorsky Krai, species descriptions and photographs of the studied shells were made.

The data obtained as a result of studying the species and quantitative diversity of terrestrial molluscs made it possible to trace the changes in the structure of habitats in general and reconstruct the palaeoecological conditions in the Tetyukhinskaya Cave area from the Late Pleistocene to the Holocene (Fig. 9).

In the Late Pleistocene (MIS 4–3), approximately 75–43 thousand years ago (Korotkii et al., 1980; *Stratigrafiya SSSR*..., 1984), forest vegetation (broad-leaved and mixed forests) prevailed in the study area. It was developed both near the entrance to the cave and around it. In the vicinity of the cave, open and intermediate habitats (clearings and margins with meadow vegetation) were widespread; along the river valleys, moist meadows and shrubs were widespread (pit II, layers 8–7, MZ1–3; pit VI, layer 6, MZ 4; layer 5–4 (lower part), MZ5; layer 4, 3, 2 (lower part), MZ6–7).

During the Late Pleistocene–Early Holocene (MIS 2–1), approximately 30–8.5 thousand years ago (Korotkii et al., 1980; *Stratigrafiya SSSR*..., 1984), intermediate (open) habitats and forest habitats were equally present around the cave (pit VI, layers 2, 1 (lower part), MZ8–9). A malacological study showed that the time of accumulation of deposits in the upper part of layer 2 (MZ8) was the coldest, and deposits in the lower part of layer 1 (MZ9) also accumulated in cold conditions. In general, the climate was cold and dry.

The results of the study of the Middle–Late Holocene malacocomplex (MIS 1) indicate a moderately warm climate and a predominance of forest habitats, mainly at the entrance to the cave, and intermediate habitats in the vicinity of the cave (pit VI, layer 1, MZ10).

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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