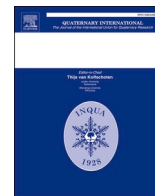




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A Holocene floodplain sequence from the Kirenga Valley, Lake Baikal region (Siberia), and its significance for molluscan and mammalian biogeography

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ABSTRACT

The archaeological record in the Baikal region is characterised by a marked discontinuity separating different groups of hunter-gatherers within the Neolithic period. A range of sedimentary archives has been studied to investigate this issue and whether it had an environmental cause. Our focus has been on floodplain sequences from river valleys, which can augment other higher resolution records such as those from lakes. Here we report on the molluscs and small vertebrates recovered from a Holocene floodplain sequence at a remote locality (Krasniy Yar XI) in the Kirenga Valley, in the Lake Baikal region of eastern Siberia. The sequence lacked the necessary temporal resolution to adequately address this archaeological question, but it did provide a valuable radiocarbon-dated record of local floodplain pedogenesis, molluscs and vertebrates over the last ~7000 cal yr BP. Aquatic molluscs are more frequent during the early part of the record but they become scarce in the upper levels, which are dominated by land snails, especially species of *Vallonia*. Other noteworthy species include *Vertigo microsphaera*, recently discovered living in the area, and the first fossil records of *V. kushiorensis*, *V. chytrii*, and *V. genesioides* from the Baikal region. An exceptional feature of the molluscan record was the relatively high frequency of sinistral specimens of *Cochlicopa*, which occurred in 12/18 samples with a mean frequency of 9.8% (38/385). The vertebrates included specimens of southern birch mouse *Sicista subtilis*, unknown living in this part of Siberia with the closest records some 400 km to the southwest. These data demonstrate marked faunal and distributional shifts within the Holocene, reflecting local and regional environmental changes through time.

1. Introduction

The Holocene environmental and cultural history of the Lake Baikal region in Siberia have been the focus of intense scientific interest over recent decades, arising principally from research by the Baikal Archaeology Project (BAP) and several lake sediment coring programmes. From ~7500 to ~3500 cal yr BP the area to the west of Lake Baikal was inhabited by several hunter-gatherer groups, the Kitoi who occupied the

area during the Early Neolithic, and the Serovo-Glazkovo who appeared later from the Late Neolithic to Early Bronze Age periods (Bronk Ramsey et al., 2021; Weber and Bettinger, 2010; Weber, 2020; Weber et al., 2002, 2010, 2016, 2021 and references therein). A key issue to emerge from this research was understanding the processes involved in the observed discontinuity in mortuary behaviour (i.e., absence of formal cemetery use) during the Middle Neolithic period (~6660-6060 cal yr BP) and whether this and other biocultural differences (e.g., genetic

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affinities, shifting subsistence strategies) may have had an environmental cause (Bezrukova et al., 2013; Tarasov et al., 2017; White and Bush, 2010). In order to address this issue, a range of proxy data were investigated to obtain relevant environmental information, particularly from lake sediment and peat bog records (e.g., Bezrukova et al., 2005a, 2005b, 2010; Demske et al., 2005; Karabanov et al., 2000; Khenzykhe-nova et al., 2021; Kobe et al., 2022; Mackay et al., 2013; Shichi et al., 2009; Tarasov et al., 2009, 2013). Collectively, these research programmes have led to a better understanding of long-term climate and environmental changes during the Holocene and their potential impact on patterns of culture change and continuity in the region.

Floodplain sequences from river valleys around Lake Baikal were also investigated to further document Holocene environmental conditions across the region, and to explore whether they could shed light on broader archaeological questions. Several of these floodplain records contained buried pedogenic horizons and a few yielded abundant shells of land and freshwater molluscs, as well as remains of small mammals and fish. They also contained charcoal that could be used to provide a radiocarbon chronology. We have previously reported data from Burdukovo in the lower Selenga Valley on the southern margin of Lake Baikal (White et al., 2013), and from Basovo in the upper Lena River Valley to the north and west of the lake (White et al., 2008). Here we report on another floodplain sequence at the site of Krasnyi Yar XI in the remote Kirenga Valley, about 125 km to the east of Basovo (Fig. 1). The aim of the investigation was to explore whether the records revealed similar Holocene environmental histories reflected in patterns of soil development and in their malacological sequences, and whether there was any evidence that might help to explain the biocultural discontinuity in the regional archaeological record.

2. Geographical background

The Krasnyi Yar XI site (N 55°42.02, E 107°46.11) is located within the Prilenskoe Plateau region in eastern Siberia along the left bank of the Kirenga River, a large tributary of the Lena River, ~23 km south of the village of Ul'kan (Fig. 1). Elevations in this part of the southern Middle Siberian Plateau range between 300 m along the generally flat valley bottoms and up to 700 m along plateau ridges. Valley slopes are relatively steep and often stepped due to the distinct geological structure of the region. This consists predominantly of monoclinical beds of Cambrian carbonate rocks, which are susceptible to differential denudation. Local bedrock includes members of the Angarskaya and Litvintzevskaya united suites (Cm_{1,2} an + lt) and the overlying Upper Lena suite (Cm_{2,3} vl), the former dominated by grey limestones and dolomites and the latter includes red marl and siltstones interbedded with thin layers of limestone slabs and calcinated sandstone (Buldygerov, 2007). Quaternary sediments include assorted gravelly and loamy alluvium and colluvium together with pedogenic formations overlying Cambrian rocks.

Four terraces can be identified in the local valley bottom. The first is a low floodplain (T-0) ~0.5–1 m in height. On non-meandering reaches of the Kirenga River the low floodplain is narrow and covered by a relatively thin talus tilted in the direction of the river bed. The floodplain widens along stretches of the river where the current slows. Typically, the low floodplain gently grades into a higher ~2–3 m floodplain (T-1), in which the Krasnyi Yar XI section is exposed. The surface of this terrace is generally even and well-drained. Above this level, an upper terrace (T-2) occurs at a height of ~2.5–5 m, the surface of which ranges from several metres up to 2 km in width, often comprising swamp. The higher ~10–15 m terrace (T-3) is fragmentary and its surface, up to 1 km in width, is typically level and often supports modern agricultural fields.

On valley bottoms pedogenic formations are characteristic of podzol, turf/sod-podzol and marsh-frozen (bog-permafrost) soils (Batuev,

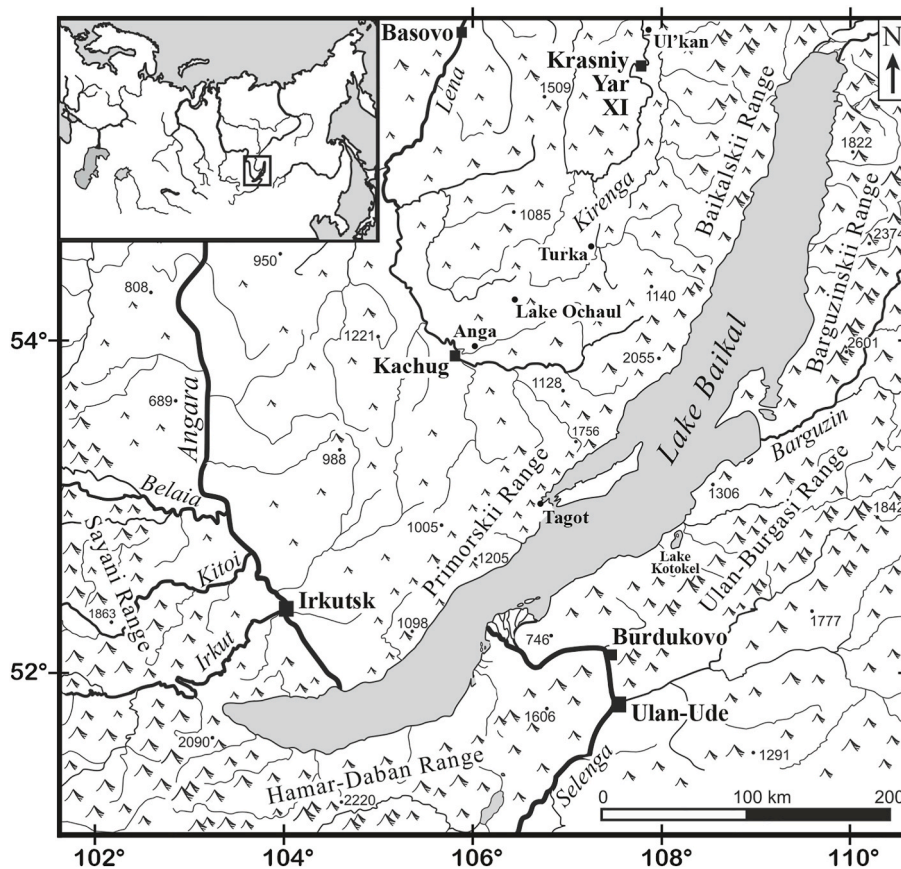


Fig. 1. Map of the study region and location of sites mentioned in text.

2004a; Vorobeva, 2009). Along slopes and watersheds there is a predominance of turf-carbonate leached rendzina (soils on limestone and dolomite eluvium which contain fragments of local bedrocks) and leached reddish-brown pararendzinas (soils on eluvium comprised of carbonated sandstones, mudstones and marls). Modern vegetation is dominated by pine-birch (*Pinus sylvestris*, *Betula*) associations with alder (*Duschekia*) undergrowth. Along valley bottoms spruce-pine (*Picea obovata*, *Pinus sylvestris*, *Pinus sibirica*) woodlands are more widespread with admixtures of larch (*Larix sibirica*), fir (*Abies sibirica*) and willow (*Salix*). Forest density is estimated to be ~97–98% (Batuev, 2004b).

The climate in the Kirenga Valley region is characterised as continental with long cold winters and short warm summers. Average annual air temperature is -4.5 °C. Absolute minimum temperatures can reach -54 °C (January) and absolute maximums 37 °C (July), with annual temperature fluctuations regularly exceeding 80 °C (Irkutsk Meteorological Agency, 2002). Average annual precipitation totals in the valley bottoms range between 300 and 380 mm and reach >800 mm at higher elevations in the watershed (Galazy, 1993). Approximately 70% of annual precipitation occurs during the summer months (June–August). Snowfall first occurs by the end of October/early November and lasts until mid-May, with snow cover averaging ~ 0.5 – 1.5 m in thickness. Spring flood-water accounts for more than $\sim 65\%$ of annual drainage, with $\sim 35\%$ resulting from precipitation. Spring flooding is typical of that throughout eastern Siberia with a distinctive cycle of rapid rise in late May (on average up to ~ 2 – 3 m) during ice break-up, followed by a sharp decline in water levels until the onset of summer rains. Maximum local flood levels reached 4.7 m during an ice-jamming event near the village of Karam, however in some years summer floods can exceed those of the spring (Romanchenko, 1990). Up to 80% of annual runoff occurs during the spring-summer season and $>90\%$ of suspended drift occurs during spring flooding.

3. Materials and methods

3.1. Fieldwork and sedimentology

Fieldwork for this study was undertaken during July 2007 as part of a ~ 150 km boat survey of the remote Kirenga River to the north-west of Lake Baikal, starting near the village of Turka and finishing near Ul'kan (Fig. 1). Our primary objective was to identify and sample Holocene sequences comprised of shell-rich floodplain deposits. Just upstream from the bedrock exposure known as Krasny Yar XI, a sequence of floodplain sediments and generally weakly developed pedogenic horizons was observed containing relatively abundant molluscs throughout much of the section. After thorough cleaning of the profile, field measurements and stratigraphical descriptions were made followed by systematic collection of bulk sediment samples for various sedimentological and macrofossil analyses.

Samples were collected primarily in 10 cm consecutive intervals from a depth of 1.75 m up to the modern surface, respecting natural stratigraphical boundaries. Finer sampling intervals (5 cm) were used for thin horizons. Particle-size distribution was measured using a

Malvern Mastersizer 2000 and for graphical presentation clast sizes grouped into coarse/medium sand (2000–250 μm), fine sand (250–62.5 μm), silt (62.5–4 μm) and clay (<4 μm) fractions. An estimate of sample organic content was measured by loss-on-ignition (LOI). Soil colour was described using the Munsell soil chart and textural classes and other properties are based on the Canadian System of Soil Classification (Soil Classification Working Group, 1998).

3.2. Fossils

For macrofossil analyses (i.e., molluscs, vertebrate remains and charcoal), bulk samples measuring ~ 2.0 L of moist sediment were collected at the Krasny Yar XI section from a depth of 1.75 m up to the modern surface. In total, 18 samples were obtained from depth intervals identical and immediately adjacent to those used for granulometry and LOI. To ensure systematic recovery of macrofossils, each sample was first wet screened through a 500 μm sieve and then air-dried and examined under a binocular microscope (x6–x50) to extract all identifiable fossils using fine forceps and/or a moist fine paintbrush (Ložek, 1986).

Land and freshwater molluscs were the most abundant group of fossils recovered. Specimens were sorted by taxa and minimum totals for each species assessed by counting every apex or apical fragment (or hinge fragments in the case of bivalves) for all identifiable adults and juveniles (Ložek, 1986). In samples where diagnostic apertural fragments outnumbered apices for a given species, totals were then based on these non-apical fragments. Juveniles of *Vallonia* were counted separately and for graphical presentation divided in proportion to the number of securely identified adults. Counts for bivalves were rounded up to the nearest even number and then halved to give the minimum number of individuals for each species. Results from the molluscan data are presented as plots of the number of species, number of individuals, terrestrial/aquatic ratios and frequency histograms. Local mollusc zones were distinguished on the basis of marked changes in the frequency of several key species.

Individual skeletal elements were recorded for vertebrate remains (small mammals, fish), which were recovered in 14 of the macrofossil samples. No attempt was made to quantify charcoal abundance since this is prone to fragmentation during sieving. SEM images of vertebrates were obtained using a JEOL JSM-IT500 operated under low pressure mode at the Natural History Museum, London.

3.3. Radiocarbon dating

AMS radiocarbon dates of six individual pieces of wood charcoal from different stratigraphical levels were used in the construction of an age model for the Krasny Yar XI section (Table 1). All materials for radiocarbon dating were pre-treated and analysed at the Poznan Radiocarbon Laboratory, Poland, and calibrated using the Intcal20 radiocarbon calibration curve (Reimer et al., 2020) and OxCal software v4.4.4 (Bronk Ramsey, 2021). All radiocarbon dates are listed in calibrated years BP.

Table 1
Details of the Krasny Yar XI radiocarbon chronology.

| Sample # | Depth (cm) | Radiocarbon date, ^{14}C yr BP | 95.4% age range, cal yr BP | Sample material | Lab # |
|----------|------------|--|----------------------------|-----------------|-----------|
| KrY-03 | 15–25 | 355 ± 30 | 315–420 | Charcoal | Poz-25691 |
| KrY-06 | 50–60 | 1185 ± 30 | 995–1050 | Charcoal | Poz-25692 |
| KrY-08 | 70–80 | 1915 ± 30 | 1735–1905 | Charcoal | Poz-25693 |
| KrY-11 | 100–110 | 1720 ± 30 | 1540–1655 | Charcoal | Poz-25694 |
| KrY-13 | 130–135 | 4580 ± 35 | 5055–5385 | Charcoal | Poz-25695 |
| KrY-16 | 155–165 | 6100 ± 40 | 6805–7105 | Charcoal | Poz-25696 |



Fig. 2. Views (left, upstream; right, downstream) of the upper floodplain (T-1) of the Kirenga River showing the context of the Krasniy Yar XI section.

4. Results and interpretations

4.1. Stratigraphy

The Krasniy Yar XI section is located along an actively eroding bank of the Kirenga River (Fig. 2). The study profile is ~2.5 m in height and is laterally extensive for ~100 m along the exposure, occupying a well-drained high floodplain (T-1) position, comprised primarily of fine-grained alluvium overprinted by multiple generally weak pedogenic horizons. Near the study site the flat valley bottom widens to 2 km with river meanders reaching up to 600 m in radius before gradually shifting to the opposite side of the valley. This stretch of the Kirenga River

meanders intensively, due in large part to the region's stable tectonic position, significantly eroding adjacent valley slopes.

Overlying the basal gravel, finer sediments are distinguishable based on the intensity of preserved soil forming properties, with delineated stratigraphical boundaries conforming to palaeosol surfaces (Ab horizons). Based on these features, the section has been divided into four basic units (Fig. 3), described from the bottom of the sequence upwards:

Unit 1 is a non-fossiliferous (non-shelly), bedded coarse sandy loam with clast-supported pebbles of variable size, colour and mineralogy. Clasts are generally <5 cm in long-axis diameter (although can reach up to ~10 cm) and are predominately well-to sub-rounded. The top of this unit occurs at ~175 cm below the modern surface, is > 35 cm thick and

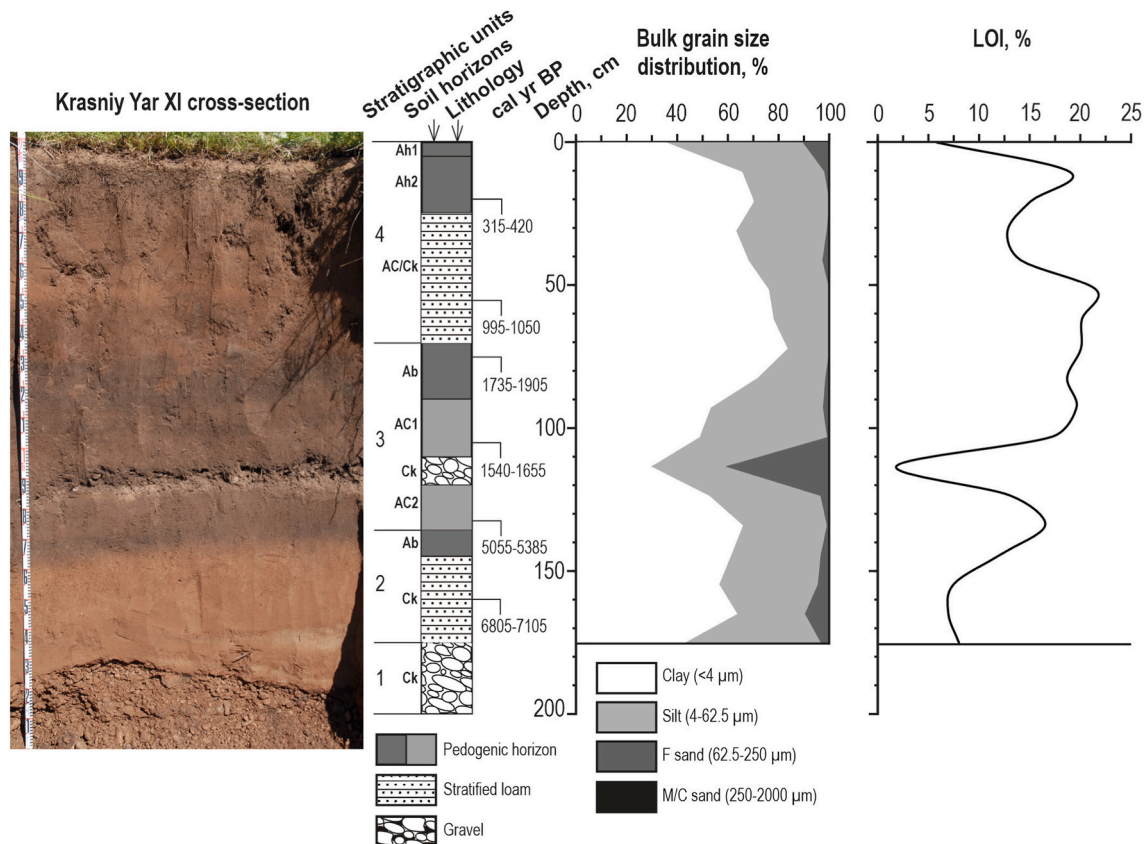


Fig. 3. Krasniy Yar XI section with a stratigraphical log showing the lithology, soil horizons, calibrated radiocarbon dates, particle-size data and loss-on-ignition values.

has a very sharp upper boundary with overlying loamy sediments. *Interpretation:* Unit 1 formed in a high-energy fluvial environment characteristic of a gravel bed or bar. The age is unknown although presumed to be late Pleistocene/early Holocene.

Unit 2 is ~40 cm thick and includes in the lower ~30 cm brown (7.5 YR 4/3) silt loam grading upward to a reddish brown (5 YR 4/4) loam. Occasionally thin lenses, some containing more sand, are present in this part of the sequence, which has a clear sharp lower boundary with underlying Unit 1. The upper ~10 cm of Unit 2 is composed of a black (7.5 YR 2.5/1) silt loam with weak sub-angular blocky structure and clear gradual contacts with both underlying and overlying deposits. Organic content increases sharply in this part of the unit. Unit 2 is extremely shelly. Radiocarbon dating of charcoal from the lower part of this unit (155–165 cm below surface), yielded an age of 6805–7105 cal yr BP. Charcoal at the base of overlying Unit 3, which provides an important upper bracketing age for Unit 2, is dated to 5055–5385 cal yr BP. *Interpretation:* Deposition of Unit 2 was initiated sometime during the early-middle Holocene as increasingly fine alluvium (C horizons) began to aggrade onto the floodplain reaching elevations above active water-levels. This resulted in relative surface stability and soil formation (Ab horizon) at the site for the first time.

Unit 3 is ~65 cm in total thickness and in the lower ~45 cm includes a relatively organic-rich dark brown (7.5 YR 3/2) loam with very weak sub-angular blocky structure. Interrupting this sequence is a non-fossiliferous (non-shelly) and inorganic, massive coarse sandy loam between ~5 and 10 cm thick dominated by sub-rounded pebbles of variable size (generally <5 cm in long-axis diameter), colour and mineralogy. These very coarse sediments are discontinuous across the broader floodplain exposure and have clear and sharp boundaries with adjacent loamy deposits, which have a slightly higher silt content below the gravelly sediments and increased sand content above. The upper ~20 cm of Unit 3 is overprinted by a very dark grey (5 YR 3/1 at top) silt loam with sub-angular blocky structure and a clear sharp lower boundary. In general, this unit yielded low mollusc abundance. Radiocarbon dating of charcoal recovered at the base of this unit (130–135 cm below surface) yielded an age of 5055–5385 cal yr BP. In addition, two radiocarbon dates on charcoal from the upper half of Unit 3 (100–110 cm and 70–80 cm below surface), yielded inverted ages of 1540–1655 cal yr BP and 1735–1905 cal yr BP, respectively. *Interpretation:* Unit 3 is a relatively organic-rich sequence of loamy sediments differentially overprinted by pedogenic processes during the middle to late Holocene. In the lower part of the unit increased overbank deposition of fines limited strong soil-forming features (AC horizons) as the floodplain aggraded. A distinct but probably short-term flooding event emplaced a coarse gravel layer (C horizon) during this otherwise sustained period of incipient juvenile pedogenic activity on the floodplain. The two late Holocene inverted radiocarbon ages suggest either minor re-working or intrusion of younger elements in this part of the sequence, but since their calibrated mid-point ages differ by only ~220 years, this chronological issue is rather inconsequential. Greater surface stability by ~1820 cal yr BP led to increased soil formation (Ab horizon) at the top of this unit.

Unit 4 is ~70 cm thick and includes in the lower ~45 cm very dark brown (7.5 YR 2.5/2) to dark brown (7.5 YR 3/3) silt loam with very weak sub-angular blocky to massive structure, and a clear gradual lower boundary and a gradual to transitional upper boundary. Radiocarbon dating of charcoal from 50 to 60 cm below surface yielded an age of 995–1050 cal yr BP. The uppermost ~25 cm of the sequence includes an organic-rich dark brown (7.5 YR 3/2) silt loam ~20 cm thick and a thin (~5 cm thick) brown (7.5 YR 5/3) sandy loam, which forms the modern surface. Roots and rootlets are common throughout this part of the profile, which exhibits weak sub-angular blocky structure. A smooth sharp boundary delineates the contact between the siltier and sandier textures in this part of the profile. In contrast to Unit 3, this unit contains moderate shell abundance. Radiocarbon dating of charcoal recovered from a depth of 15–25 cm yielded an age of 315–420 cal yr BP. *Interpretation:* Unit 4 is a late Holocene sequence of increased overbank

deposition of fines (AC/C horizons), which buried Unit 3. By ~400 cal yr BP the surface began to stabilize to the extent that strong soil formation (Ah horizons) dominates the modern floodplain.

4.2. Molluscs

4.2.1. Analysis of the molluscan succession

The molluscan record at Krasniy Yar XI preserves a middle to late Holocene succession of both land (~80%) and freshwater (~20%) species. The 18 bulk (2.0 L) samples analysed yielded over 8000 specimens representing at least 25 terrestrial and 17 aquatic taxa (Table 2, Figs. 4–5). Seven of the samples contained >500 shells (the richest >1190 specimens), eight samples yielded >140 shells, and three samples produced <70 shells, one of which was unfossiliferous. Importantly, most samples were sufficiently large to recover rarer species that occur at frequencies of <1% or as single specimens. Zonation of the molluscan data was based on the relative abundance, species richness and successional trends of several key species. The genus *Vallonia*, and in particular *V. costata*, dominates the assemblage, represented by 4369 specimens or ~54% of the total shells recovered. Apart from the lowest levels, terrestrial molluscs far outnumber aquatic taxa. The terrestrial assemblages are thought to reflect communities that lived on or near the floodplain rather than including significant elements carried downstream. Aquatic taxa occur primarily at the base of the sequence as initial sedimentation led to the formation of the floodplain, or as occasional specimens deposited during short-term flooding events higher in the sequence.

The following local mollusc assemblage zones can be distinguished:

4.2.1.1. Zone KY1: 130–175 cm (~7000–~5220 cal yr BP). The basal mollusc zone includes the highest abundance and species richness in the entire sequence. The assemblage includes species of 21 terrestrial and 16 aquatic taxa and comprises ~48% of the total shells recovered (~38% of terrestrial and ~89% of aquatic shell totals). Of the land snails, the base of the sequence is dominated by *Vallonia pulchella* (up to 24%) and *V. costata*, which increases from ~20% to ~65% through the zone. *V. kamschatica* and *V. tenuilabris* are also relatively frequent (up to ~14% and ~4%, respectively), although they decline markedly, together with *V. pulchella*, towards the upper part of the zone. *Carychium pessimum* also reaches its maximum (up to ~16%) together with *Punctum pygmaeum* (up to 11%). Subordinate species include *Cochlicopa lubrica* (up to ~5%), *Perpolita hammonis* (up to ~5%), *Euconulus fulvus* agg. (up to ~4%), *Discus ruderatus* (up to ~3%) and *Fruticicola* cf. *schrenkii* (up to ~3%). Rare components (<2% or single specimens) include *Perpolita petronella*, *Carychium minimum*, *Gastrocopta theeli*, *Succinea/Oxyloma*, *Deroceras/Limax*, *Pupilla muscorum* and a relatively diverse *Vertigo* fauna, including *V. chytryi*, *V. microsphaera*, *V. kushiorensis* and *V. genesioides*. Aquatic taxa comprise a significant component of this zone, dominated by *Pisidium nitidum* (up to ~28%), together with *Gyraulus albus* (up to ~13%), *Valvata macrostoma* (up to ~8%) and *V. aliena* (up to ~5%), *Musculium lacustre* (up to ~6%) and *Radix* spp. (up to ~5%). Less common species include *Gyraulus crista* and *Pisidium henslowanum* (up to 3% and 2%, respectively) and *Radix auricularia*, *Galba truncatula*, *Anisus leucostoma*, *Aplexa hypnorum*, *Hippeutis complanatus* and *Pisidium subtruncatum*, *P. obtusale* and *P. milium*, which all occur at values of <1%. Numbers of aquatic taxa sharply decline near the top of this zone.

4.2.1.2. Zone KY2: 70–130 cm (<5220 to ~1025 cal yr BP). This zone, which includes the least abundant shell totals preserved at Krasniy Yar XI, has yielded species of 16 terrestrial and 12 aquatic taxa but represents only ~9% of the total shells recovered (~10% of total land and ~4% of total freshwater shells). The hiatus near the base of this zone coincides with the emplacement unfossiliferous coarse sediment. Terrestrial taxa continue to be dominated by *V. costata* (up to ~76%),

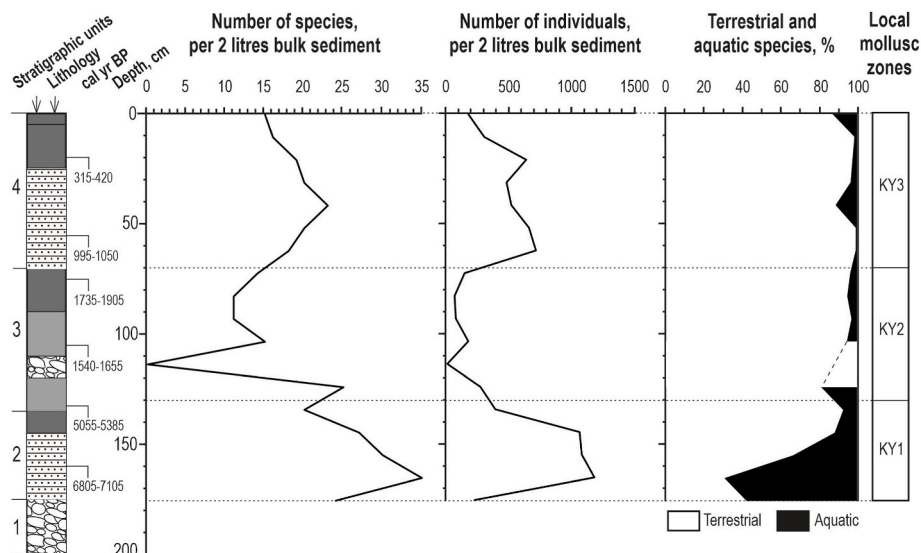


Fig. 4. Ecological profile of the Krasny Yar XI molluscan succession showing number of species and individuals (per 2.0 L of sediment), together with percentage of land and freshwater species.

distribution of *V. chytrii* is poorly known but it has been found at widely scattered sites in the taiga of western and southern Siberia, where it occurred in moderately alkaline habitats, under bark or in *Tilia* leaf-litter (Nekola et al., 2018: 42). Apart from its discovery at Krasny Yar XI, we did not find this species alive in our survey of modern habitats at numerous sites around Lake Baikal undertaken in 2007, nor did we recover it in other Holocene sequences in the region.

Vertigo (Vertigo) microsphaera Schileyko, 1984

The shell of this species (Fig. 7d) is ovate, strongly striated and is reminiscent of *V. substriata* from which it differs by its smaller size, lack of an angular lamella, possession of only a weak apertural crest, and presence of a moderately strong sinulus (Schileyko, 1984; Nekola et al., 2018: 56). We found living populations of *V. microsphaera* at several sites to the west (near Kachug: N 53°59'16", E 105°47'42", Elevation 500 m) and south-east (at Burdukovo: N 52°05'58", E 107°32'02", Elevation 496 m; and sites along the southern coast: N 51°42'50", E 105°53'28", Elevation 488 m; N 51°28'59", E 104°19'38", Elevation 476 m) of Lake Baikal (Fig. 1), where it occurred in a variety of habitats including wetland, damp grassland bordering coniferous forest and leaf-litter in birch-hazel woodland. *V. microsphaera* has a broad geographical range extending from Alaska west to Hokkaido and the northern foothills of the Altai in central Asia (Nekola et al., 2018). Other Holocene records of *V. microsphaera* include Basovo in the upper Lena River Valley (White et al., 2008: 971, Fig. 6e), Burdukovo in the lower Selenga River Valley in Trans-Baikal (White et al., 2013), and in the Krasnoyarsk forest-steppe region (Yamskikh et al., 2022).

Vertigo (Vertigo) genesioides Nekola, Chiba, Coles, Drost, von Proschwitz & Horsák, 2018

The shell of this species (Fig. 7e) resembles that of the boreal European species *V. genesii* but differs in its more conical shape, proportionately larger aperture, slightly deeper suture and attainment of maturity in ½-1 fewer whorls. Its separation from *V. genesii* has been demonstrated by molecular phylogenetics, which recovered *V. genesioides* as a highly-supported clade using several reconstruction methods (Nekola et al., 2018: 55). Ecologically it is more catholic than *genesii* and is not restricted to alkaline habitats but often occurs in *Sphagnum*-dominated peatlands (Nekola et al., 2018: 55). *Vertigo genesioides* has an extensive range in boreal regions stretching from North America to Central Asia. We found living populations at a few sites west of Lake Baikal near Anga Village (N 53°58'25", E 106°11'49", Elevation 539 m; generally dry soil conditions, hummocky/grassy floodplain of south-facing river bank, cattle grazed) and at Tagot (N 53°00'42", E

106°45'01", Elevation 462 m; low-lying wet, grassy meadow along north edge of pond-marshland about 1 km south of Mukhur Bay (Lake Baikal), hummocky surface, stagnant pooled water, area of discontinuous permafrost, cattle grazed), and it also occurred in damp grassland bordering birch woodland with larch and pine near the site at Burdukovo (White et al., 2013) (Fig. 1). This species was previously reported from southern Siberia as *Vertigo genesii* (Horsák et al., 2010) or as *V. aff. genesii* (Horsák et al., 2015) and in our previous studies of Holocene sequences in south-east Siberia (White et al., 2008, 2013) we recorded it as *Vertigo extima* (White et al., 2008: 971, Fig. 6g). The small specimen identified as *Vertigo genesii* from Basovo (White et al., 2008: 971, Fig. 6a) may also be *V. genesioides*, although this is uncertain. More recently, *V. genesioides* has also been reported from two Holocene records near Krasnoyarsk (Yamskikh et al., 2022).

Vertigo (Isthmia) kushiorensis Pilsbry & Hirase, 1905

During a malacological survey of sites in the Altai Mountains, Russia, an apparently undescribed species of *Vertigo* was discovered and given the name *Vertigo botanicorum* by Horsák and Pokryszko 2010: 57). In the Altai this taxon was characteristic of low to mid-elevation mesic steppe but it also occurs in adjacent hemiboreal and riparian forest (Nekola et al., 2018: 120). A more extensive study of eastern Palaearctic *Vertigo* later showed that shells of *botanicorum* essentially fall within the range of variation of *V. kushiorensis* Pilsbry & Hirase, 1905 found on Hokkaido, the type locality of that species. Molecular phylogenetic analysis recovered a highly-supported clade containing most *botanicorum* individuals but further work is needed to test the validity of *botanicorum* as a distinct subspecies of *kushiorensis* (Nekola et al., 2018: 120). We did not find *V. kushiorensis* living in the region around Lake Baikal nor in the other Holocene sequences that we have studied in southern Siberia (White et al., 2008, 2013), but only as a single adult specimen at Krasny Yar XI (Fig. 7f). Yamskikh et al. (2022) also identified *V. cf. kushiorensis botanicorum* in the Talaya Holocene succession near Krasnoyarsk.

Gastrocopta theeli (Westerlund, 1877)

This species has a rather patchy distribution in Russia, where it is known from South Primorye, vicinities of Yeniseik and Chelyabinsk, Southern Altai, Kirgiz Ridge, flood debris of the Kura and Rioni river basins, highland of Daghestan (Botlikh) and the North Caucasus (Sysoev and Schileyko, 2009). Outside Russia it is known from Korea, China and Pakistan, where it occurs at numerous sites in FANA, NW Frontier, Baluchistan and Punjab Provinces (Pokryszko et al., 2009). During the Pleistocene it occurred in southern Siberia and had a range that extended into central Europe (Ložek, 1964; Horsák et al., 2010, 2015).

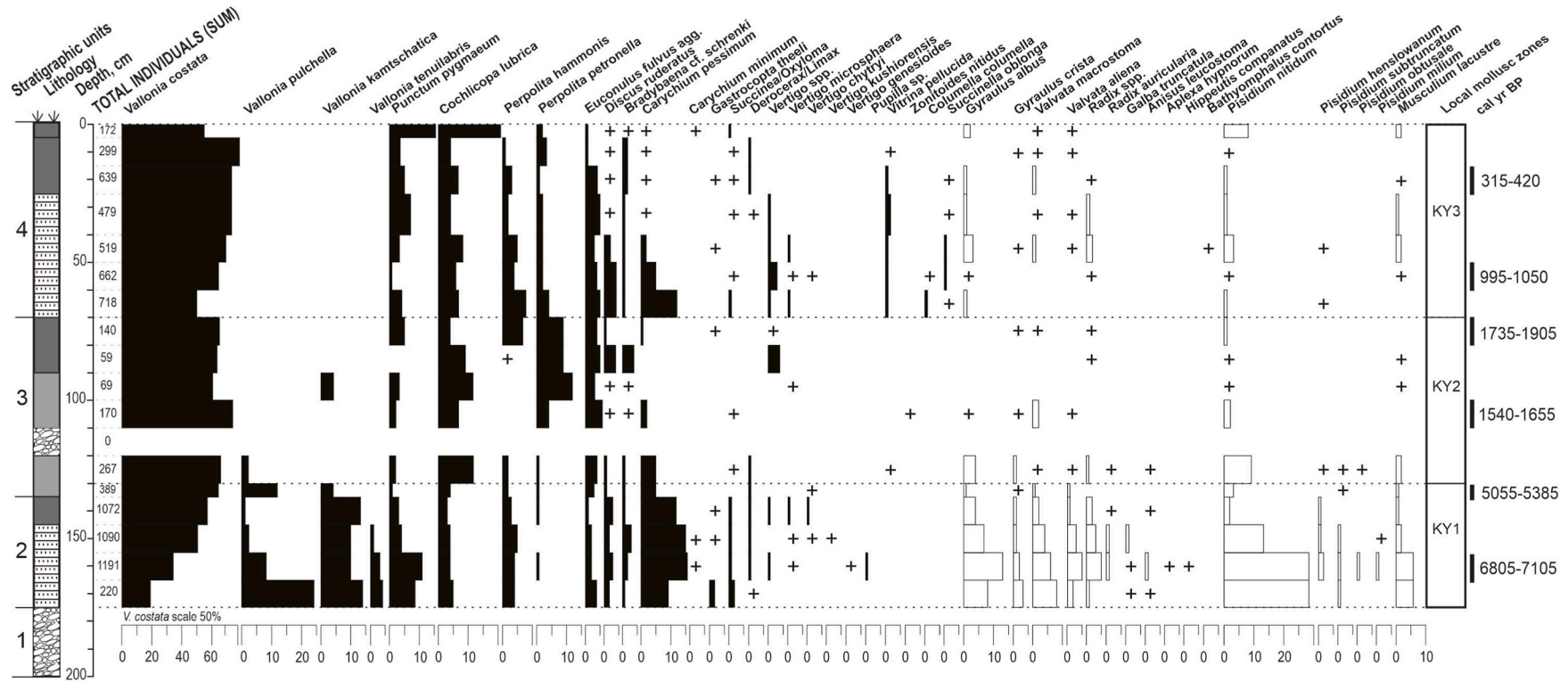


Fig. 5. Mollusc diagram plotting the frequency of terrestrial (closed bars) and aquatic (open bars) taxa through the sequence at Krasniy Yar XI. Values of land snails are expressed as percentages of total terrestrial shells, and values of aquatic snails are expressed as percentages of total individuals. The fauna is dominated by *Vallonia costata*, which has been scaled independently. Aquatic taxa and hygrophilous land snails are more frequent beneath the gravel unit, whereas drier conditions are suggested by the assemblages in the upper levels. The symbol (+) indicates single shells.

Table 3
Incidence of sinistrality in shells of *Cochlicopa lubrica* at Krasniy Yar XI.

| Depth (cm) | Number of dextral shells | Number of sinistral shells | % sinistral |
|--------------|--------------------------|----------------------------|-------------|
| 0–5 | 33 | 0 | 0 |
| 5–15 | 13 | 0 | 0 |
| 15–25 | 43 | 2 | 4.4 |
| 25–40 | 17 | 3 | 15 |
| 40–50 | 35 | 4 | 10.2 |
| 50–60 | 35 | 5 | 12.5 |
| 60–70 | 39 | 13 | 25 |
| 70–80 | 5 | 1 | 16.7 |
| 80–90 | 4 | 1 | 20 |
| 90–100 | 8 | 0 | 0 |
| 100–110 | 11 | 0 | 0 |
| 110–120 | 0 | 0 | 0 |
| 120–130 | 23 | 2 | 8 |
| 130–135 | 11 | 2 | 15.4 |
| 135–145 | 29 | 2 | 6.4 |
| 145–155 | 25 | 1 | 3.8 |
| 155–165 | 11 | 2 | 15.3 |
| 165–175 | 5 | 0 | 0 |
| Total | 347 | 38 | 9.8 |

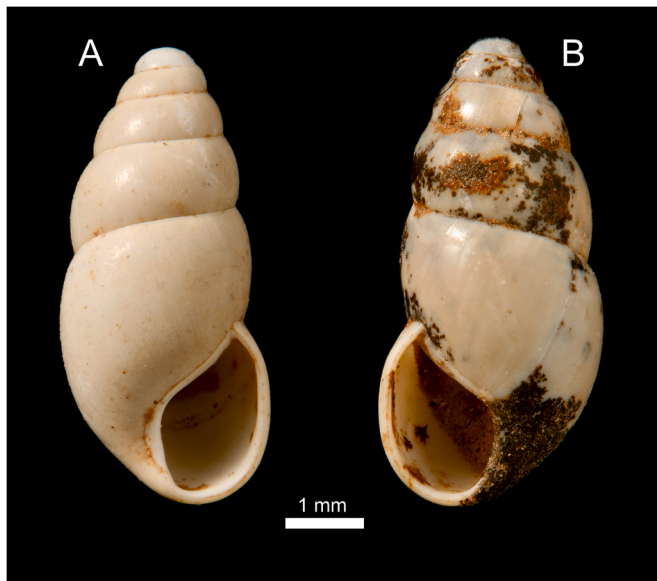


Fig. 6. (A) Dextral (145–155 cm) and (B) sinistral (135–145 cm) *Cochlicopa lubrica* from Krasniy Yar XI. The dark encrustation is manganese dioxide.

As a Holocene fossil it has been found in a number of sequences in a wide area from Muya-Kuanda and Tunka depressions in the Baikal Rift Zone, through the Cis-Baikal Trough near Irkutsk, to the Lena River Valley within the Upper Lena Plateau (Filippov et al., 2000). We found it, also at low frequency as in the Krasniy Yar XI sequence, at Basovo in the upper Lena River Valley (White et al., 2008: 971, Fig. 6i), and at Burdokovo in the lower Selenga River Valley in Trans-Baikal (White et al., 2013). We did not find *G. theli* living in our survey of the Lake Baikal region in 2007.

Discus ruderatus (Férussac, 1821)

This boreo-montane species lives in coniferous woods, marshes and moist grassland. It has an enormous range extending from central Europe and Scandinavia right across the Palaearctic region as far as the Pacific coast. Forms in North America, such as *D. cronkhitei*, may be conspecific, so its range may prove to be Holarctic. Throughout much of the western part of its range there is little variation in the morphology of the shell but in the eastern part it becomes rather variable, particularly with respect to the height of the spire and the angulation of the periphery. Such forms have been separated as subspecies but there is

considerable variation even at a single site (Umiński, 1962). At Basovo, 125 km to the west of the Krasniy Yar XI site (Fig. 1), the shells of *ruderatus* had a rounded periphery (White et al., 2008, 2013, Figs. 6 and 1a), resembling those of western Eurasia. At Burdokovo, to the south-east of Lake Baikal (Fig. 1), many of the shells had a strong angulation and possessed a distinct apical microsculpture of transverse riblets crossed by an irregular series of spirally oblique striation (White et al., 2013, Figs. 6 and 1b). These were assigned to the subspecies *pauper*. The *ruderatus* shells from the Krasniy Yar XI site were also keeled (Fig. 8a), a feature that was especially noticeable in juvenile specimens (Fig. 8b), but they lacked this distinct apical microsculpture. An extensive phylogenetic study of these forms is needed to resolve their taxonomic status.

4.3. Vertebrates

Small mammals are often indicators of climate and vegetation, and changes in species composition and individual species' ranges can also be used to infer changing environmental conditions (Andrews, 1990). Small mammal remains from Krasniy Yar XI are relatively scarce but include taxa with specific habitat requirements that are useful for reconstructing aspects of the surrounding landscape during the Holocene.

The small mammals were analysed from the same samples as those processed for molluscs. These yielded 19 rodent/insectivore teeth and mandibles together with less diagnostic postcranial fragments and occasional fish remains. The scarcity of small mammal remains is not surprising considering the small size of the samples (~36 L in total). What is surprising is the fact that they represent such a large number of individuals and taxa relative to the number of skeletal elements recovered (Table 4).

The depositional context gives clues to the taphonomic history of the small vertebrate assemblage. The sediments are mostly fine-grained and were probably deposited in a river backwater or floodplain. The proximity of the aquatic environment is indicated by the presence of fish remains, which may have been washed in during flood events. Fish remains are present in low numbers in the sequence between 130 and 165 cm; their rarity in the overlying units is noteworthy in view of the close proximity of the river (Fig. 9).

The preservation of the terrestrial component is variable, ranging from small bone fragments to complete mandibles (Fig. 10). The more complete bones often exhibit reasonably well-preserved surfaces, with no signs of subaerial weathering or abrasion and so must have been buried relatively quickly. The less well-preserved component appears to be weathered; it is clear that these elements, in particular those recovered between 130 and 165 cm, were exposed on the surface as part of the ground-litter for some time prior to burial. Many of the more fragmentary bones and teeth are also marked by root-etching, which is consistent with their burial in a biologically-active soil. Given the range of cranial and postcranial elements represented, there is no indication of fluvial transport or winnowing of lighter elements (e.g., vertebrae and phalanges). The characteristic corrosion of a few of the small mammal teeth does, however, indicate that at least some of the material was brought to the site in the pellets of predatory birds, and perhaps in the droppings of mammalian carnivores (e.g., Fig. 10h).

The habitats indicated by the small mammals are consistent with the molluscan evidence and suggest a mix of open herbaceous vegetation or scrub on the floodplain and woodland nearby. Each of the small mammal species recovered still occurs in the region today, with the notable exception of *Sicista subtilis*, which may have become locally extinct within the last two millennia.

4.3.1. Notes on vertebrate identification and ecology

4.3.1.1. *Sorex minutus*, pygmy shrew. A complete mandible of a small

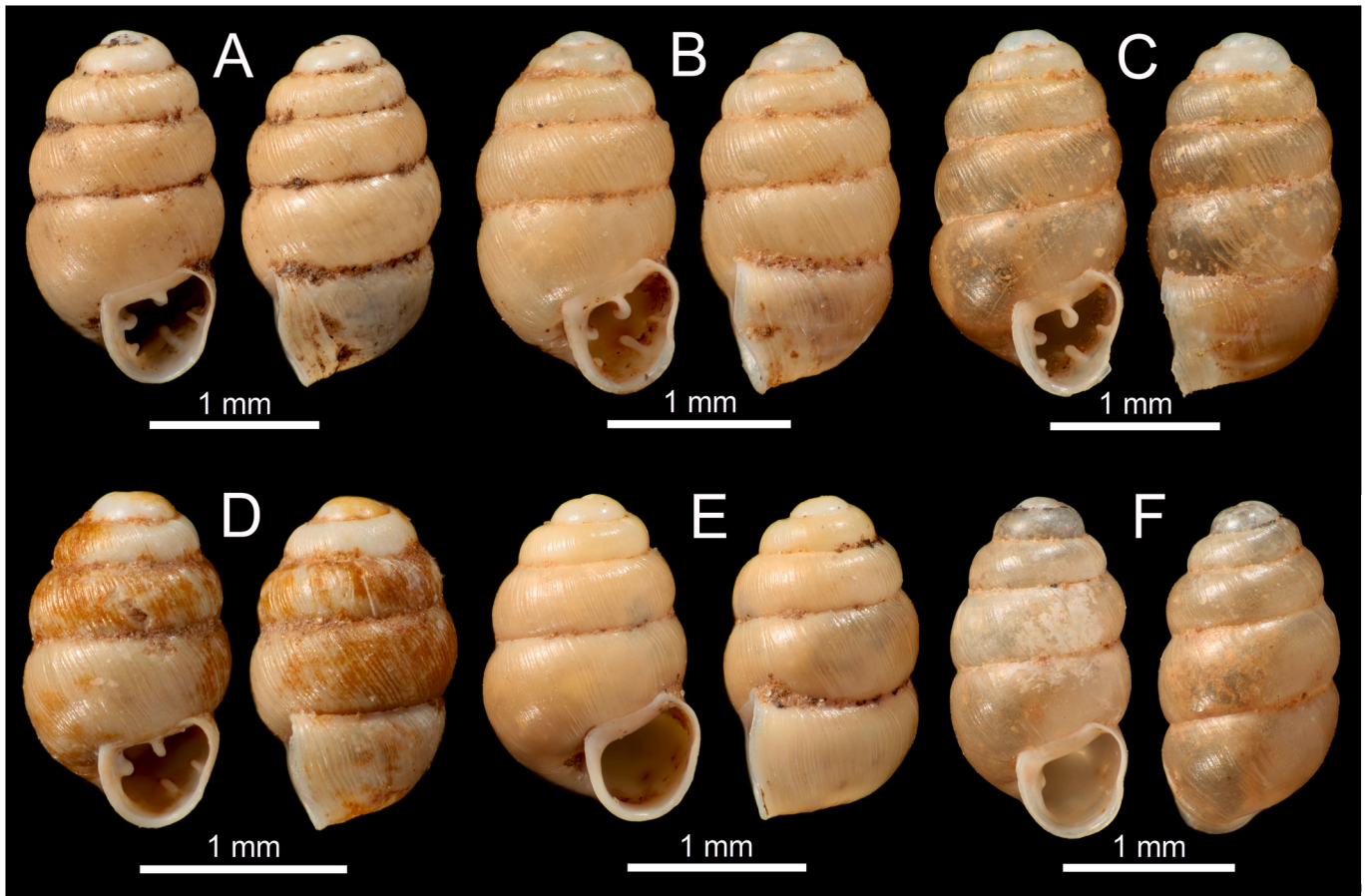


Fig. 7. Species of *Vertigo* from various depths in the Krasniy Yar XI section: (A) *V. chytryi* (50–60 cm); (B) *V. chytryi* (135–145 cm); (C) *V. chytryi* (145–155 cm); (D) *V. microsphaera* (135–145 cm); (E) *V. genesioides* (155–165 cm); (F) *V. kushiorensis* (145–155 cm).

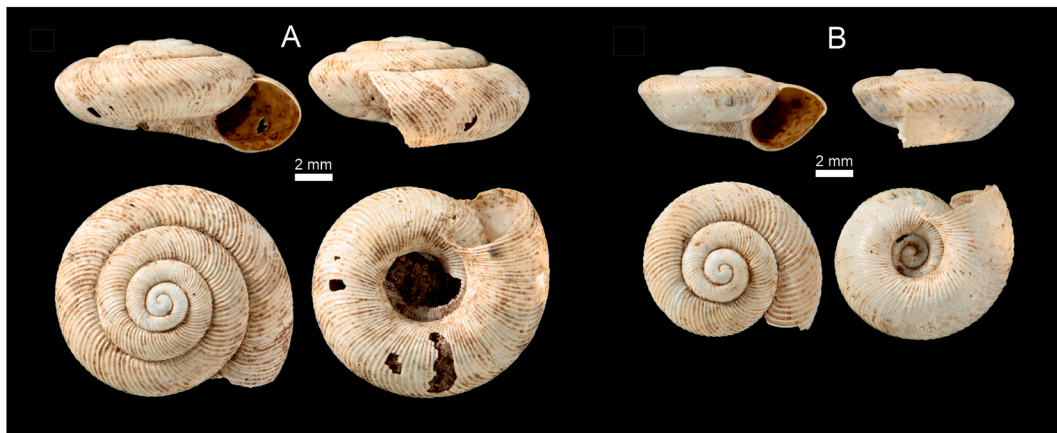


Fig. 8. Specimens of *Discus ruderatus* from Krasniy Yar XI, depth 60–70 cm: (A) adult; (B) juvenile.

species of *Sorex* was recovered from 145 to 155 cm (Fig. 10a). Dimensions of the mandible (coronoid height = 3.2 mm) fall within the range of both *Sorex minutus* and *Sorex minutissimus* (Eurasian least shrew). Both of these small shrews occur sympatrically in the region around Lake Baikal today (Henttonen et al., 2016; Hutterer et al., 2016). The mandible is typical of *S. minutus* in having the mental foramen below the anterior half of the first lower molar; in *S. minutissimus* the foramen is generally situated below the buccal re-entrant valley of the M_1 (Maul and Parfitt, 2010). The pygmy shrew is widely adaptable and occupies a broad range of habitats across much of continental Europe

from the British Isles and Portugal to European Russia and Siberia, reaching Lake Baikal in the east. It lives in a variety of habitats provided that low ground cover and an ample supply of invertebrates is available. Its highest densities are often found in moist habitats, such as swamps and peat bogs (Hutterer, 1990; Hutterer et al., 2016).

4.3.1.2. *Lepus timidus*, mountain hare. A hare (*Lepus*) is represented by a lower incisor (mesio-distal length = 1.39 mm, bucco-lingual width = 1.07 mm) of a young individual from 135 to 145 cm and a deciduous cheek tooth from 130 to 135 cm. Two species of *Lepus* occur today in

Table 4

Small mammals from the Krasniy Yar XI profile with number of identified specimens (NSIP) and minimum number of individuals (MNI).

| Unit | 2 | | 3 | | | 4 | | | |
|---|---------|---------|---------|---------|---------|-------|-------|-------|-------|
| | 155–165 | 145–155 | 135–145 | 130–135 | 100–110 | 80–90 | 70–80 | 60–70 | 40–50 |
| Insectivores | | | | | | | | | |
| <i>Sorex minutus</i> Linn., 1766, pygmy shrew | - | 1 | - | - | - | - | - | - | - |
| <i>Sorex</i> sp., shrew (small species) | - | - | - | - | - | - | - | 1 | - |
| Soricidae gen. et sp. indet., shrew | - | - | - | 1 | - | - | - | - | - |
| Lagomorphs | | | | | | | | | |
| <i>Lepus timidus</i> Linn., 1758, mountain hare | - | - | 1 | - | - | - | - | - | - |
| <i>Lepus</i> sp., hare | - | - | - | 1 | - | - | - | - | - |
| Rodents | | | | | | | | | |
| <i>Sicista subtilis</i> (Pallas, 1773), southern birch mouse | - | - | - | - | 2 (1) | 1 | 1 | - | - |
| cf. <i>Myopus schisticolor</i> (Lilljeborg, 1844), wood lemming | - | 2 (1) | - | - | - | - | - | - | - |
| <i>Clethrionomys rutilus</i> (Pallas, 1779), northern red-backed vole | - | 1 | - | - | - | - | - | - | - |
| <i>Arvicola amphibius</i> (Linn., 1758), water vole | - | - | 1 | - | - | - | - | - | - |
| <i>Microtus agrestis</i> (Linn. 1761), field vole | - | - | - | - | - | - | - | - | 2 (1) |
| <i>Microtus</i> sp., vole | - | - | - | - | - | - | - | - | 1 |
| Microtinae gen. et sp. indet., vole | 3 | - | - | - | - | - | - | - | - |

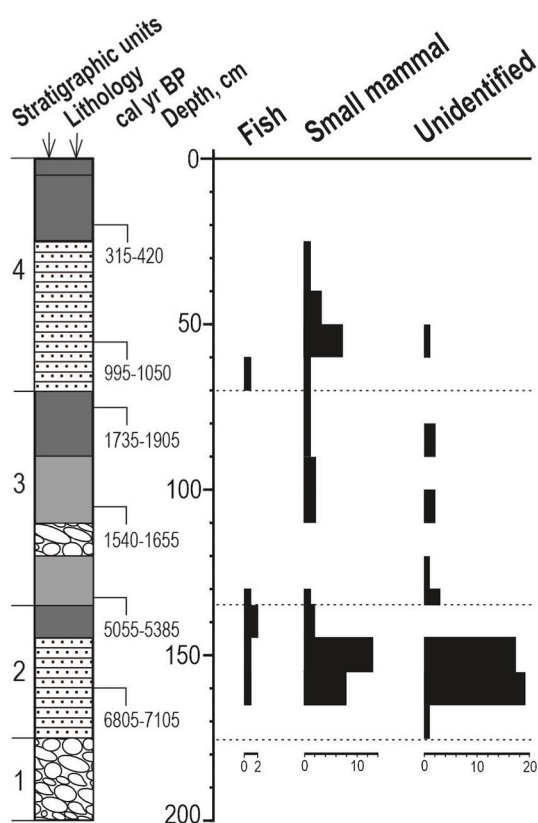


Fig. 9. Frequency of fish and small mammals through the Krasniy Yar XI samples, showing number of vertebrate bones in each 2.0 L sample.

eastern Russia: mountain hare, *Lepus timidus*, occupying an extensive range encompassing much of northern Eurasia; and brown hare *L. europaeus*, which occurs widely in temperate and boreal forest and grasslands and has a more westerly range, with some overlap between the two species in the west Siberian lowlands (Smith and Johnston, 2008; Hacklander and Schai-Braun, 2019). Despite the small size and juvenile state of the Krasniy Yar XI incisor, it can be referred unambiguously to *L. timidus* from its distinctive cross-sectional shape (Fig. 11; cf Maul, 2014). *L. timidus* occurs mainly in the tundra, taiga and steppes. In southern Russia, it inhabits lowland forest and scrub-steppe but also occurs in reed beds bordering lakes and rivers (Smith and Johnston, 2008); it lives mainly on grasses and other herbs, as well as browse and bark in the winter.

4.3.1.3. *Sicista subtilis*, southern birch mouse. Remains of birch mice are generally extremely rare in Quaternary sequences (Parfitt, 1999; Oppliger and Becker, 2010; Royer, 2016; Van Kolfschoten, 2014; Parfitt and Preece, 2022) and they are only occasionally recovered in modern bird of prey accumulations (Cserkés and Gubány, 2008; Cserkés et al., 2009). An unusual feature of the Krasniy Yar XI sequence is the presence of birch mice remains in at least three samples between 70 and 110 cm. Two isolated molars (Fig. 10c and d) may belong to a single individual as they exhibit very similar stages of wear and were recovered from adjacent sample levels. A further individual is represented by left and right mandibular rami from 100 to 110 cm (molars illustrated in Fig. 10b).

The taxonomy of *Sicista* is difficult and confused. The genus is thought to include between 14 and 17 species, with five major lineages recognizable (Lebedev et al., 2019): ‘tianschanica’ (*S. tianschanica*); ‘concolor’ (*S. concolor*); ‘caudata’ (*S. caudata*); ‘betulina’ (*S. pseudonapaea*; *S. betulina* species group (*S. betulina*, *S. strandi*); *S. subtilis* species group (*S. loriger*, *S. trizona*, *S. subtilis*), ‘caucasica’ (*S. armenica*, *S. caucasica*, *S. kazbegica*, *S. kluchorica*) and *S. napaea* of unknown taxonomic status. The taxonomy of the *S. subtilis* groups is currently unresolved with the number of recognized species ranging from three (Cserkés et al., 2016) to six (Kovalskaya and Fedorovich, 1997; Kovalskaya et al., 2011; Cserkés et al., 2019); formerly (e.g., Pucek, 1982a, 1999b), these were all subsumed within a single species, *S. subtilis*. Although detailed cranial measurements and molar size have been shown to separate *S. trizona* and *S. loriger* (Cserkés et al., 2009), relatively little is known about the skeletal and dental characteristics of eastern populations in the *S. subtilis* species group. In the absence of such a study, the Krasniy Yar XI specimens have been compared with the western Nordmann’s birch mouse *S. loriger* (using data in Pucek, 1982a, 1999b), and with our measurements of eastern *S. subtilis*.

Several *Sicista* species have restricted (often endemic) ranges, but those of the southern birch mouse *S. subtilis* and northern birch mouse *S. betulina* are much more extensive (Fig. 12). These species are generally allopatric, with the southern birch mouse occupying steppe and semi-steppe zones. The ‘core’ range of *S. subtilis* species group is more southern than that of *S. betulina* and extends from eastern Europe through southern Russia and northern Kazakhstan to northwestern China and the Altai Mountains in Mongolia (Pucek, 1999b; Cserkés et al., 2014; Cserkés and Kennerley, 2017). Two significant relict populations of *S. subtilis* occur further east; the first is located in the upper reaches of the Yenisey River (south of Krasnoyarsk), and the second outlier occurs in the region bordering the southern tip of Lake Baikal and extends into the headwaters of the Angara River (Shenbrot et al., 1995; 2008). *Sicista betulina* is a much more widespread species, its range encompassing the conifer-mixed woodland and steppe-forest zones, and mountain forests of Europe and Asia. It ranges from Lake

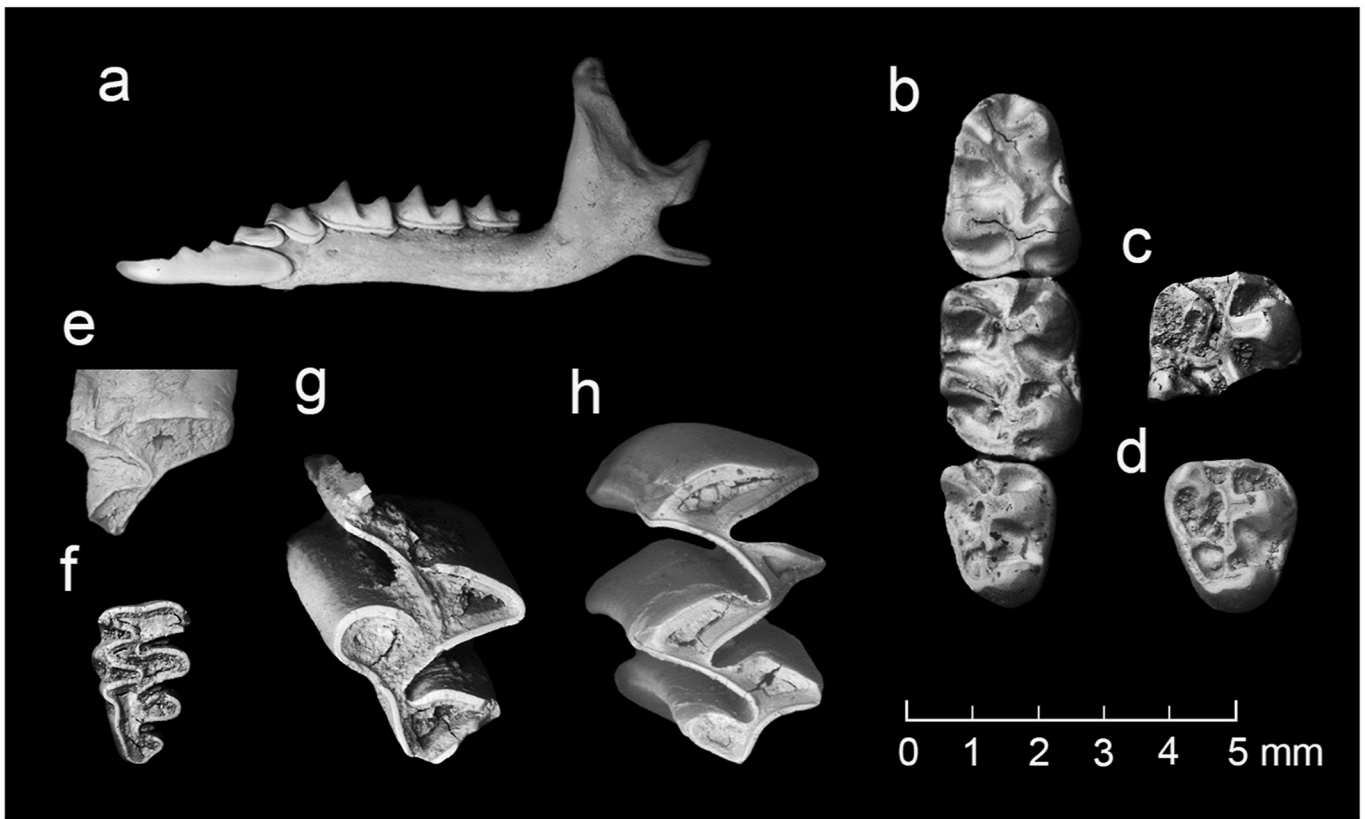


Fig. 10. Small mammal remains from Krasniy Yar XI: (a) *Sorex minutus* left mandible, 145–155 cm; (b–d) *Sicista subtilis*, (b) right M_{1-3} , 100–110 cm; (c) right M_2 , 80–90 cm; (d) right M_3 , 70–80 cm; (e) *Myopus schisticolor* left M^1 , 145–155 cm; (f) *Clethrionomys rutilus* right M^3 , 145–155 cm; (g) *Arvicola amphibius* left M^2 , 135–145 cm; (h) *Microtus agrestis* left M^2 (digested), 40–50 cm. (a) buccal view and (b–h) occlusal view.

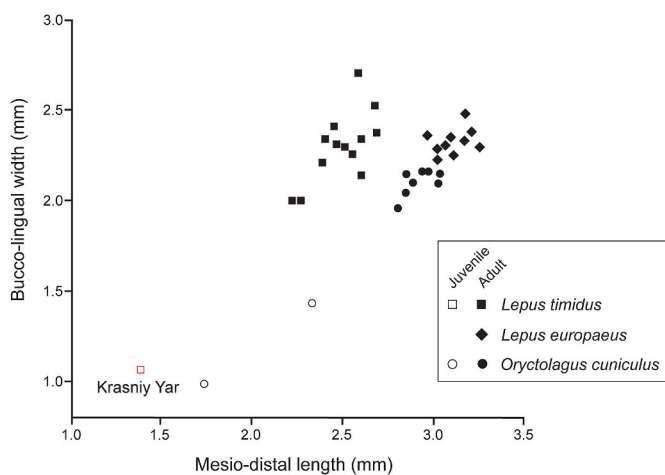


Fig. 11. Bivariate plots of the dimensions of lower incisors of *Lepus timidus*, *L. europaeus* and *Oryctolagus cuniculus*. The Krasniy Yar XI incisor tapers towards the occlusal surface and is clearly from a very young individual; measurements of juvenile rabbit (*O. cuniculus*) incisors are plotted to illustrate the similarity in cross-sectional shape in adult and very young individuals, despite the much smaller size of the juvenile incisors. Unworn incisors, and incisors in early wear, are shown by open symbols.

Baikal to the eastern Baltic coast with scattered outposts in Norway, Sweden, Denmark, southwest Germany, the Alps and Carpathians. These provide evidence for the relict character of its current range in central and northern Europe (Pucek, 1999a; Cserkés and Kennerley, 2017).

The dentitions of *S. betulina* and the *S. subtilis* species group differ chiefly in size and complexity of the ridges and spurs on the molars

(Mayhew, 1978; Oppliger and Becker, 2010). Cheek teeth of *S. betulina* have a complicated occlusal structure with additional spurs and ridges. The cheek teeth of *S. subtilis* are generally larger and relatively broader in comparison to their equivalents in *S. betulina*. They also exhibit a simpler occlusal pattern with fewer additional spurs and ridges. In terms of size, proportions and occlusal morphology, the Krasniy Yar XI molars are indistinguishable from those of extant *S. subtilis* species group (Table 5, Fig. 13).

The southern birch mouse is a valuable ecological indicator. It is closely tied to steppes and rough grassland in scrub and lightly-wooded country, in particular birch woodland with dense cover of herbaceous vegetation. The record of *S. subtilis* is of particular interest, as it is the only small mammal from Krasniy Yar XI that appears to be absent from the region today. Currently, the nearest known outpost *S. subtilis* is some 400 km to the southwest (Fig. 12).

4.3.1.4. *cf. Myopus schisticolor*, wood lemming. Two fragmentary lemming molars were recovered from 145 to 155 cm (Fig. 10e). They match the characteristic pattern of *Lemmus* (Norway lemming and its allies) and *Myopus schisticolor* (wood lemming). No morphological or size distinction between these two genera can be made from the fragmentary Krasniy Yar XI specimens. Because *Lemmus* is confined to arctic and subarctic tundra, an attribution to *Lemmus* is doubtful, making *Myopus schisticolor* more likely. The wood lemming is an inhabitant of taiga forest. It has a modern distribution that extends across the entire boreal forest zone from Scandinavia to the Pacific coast. It prefers wet habitats with secondary growth, pine-bogs and mossy spruce forests. An essential habitat requirement is a thick moss layer in which it constructs burrows and runways; moss also provides a critical winter food source (Henttonen, 2016).

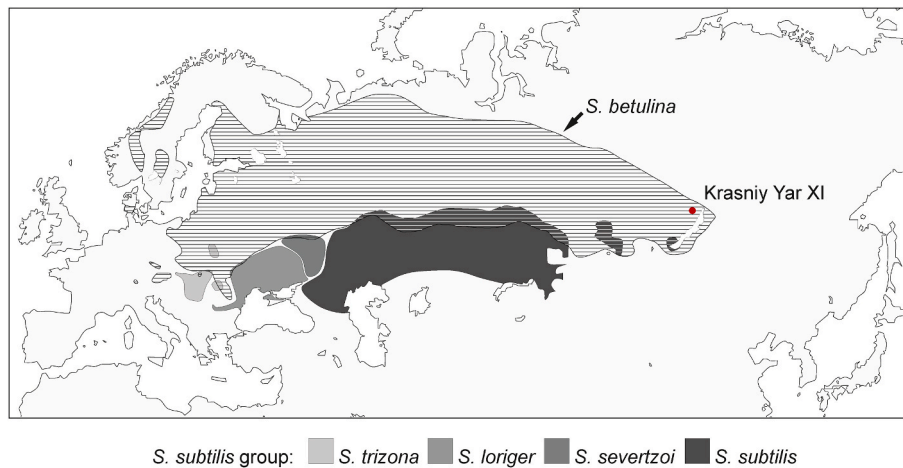


Fig. 12. Map showing the present-day distributions of *Sicista betulina* and *S. subtilis* species group (*S. trizona*, *S. loriger*, *S. severtzoi*, *S. subtilis*).

Table 5

Measurements of molar teeth of the *Sicista subtilis* species group (*S. loriger*, eastern Romania and *S. subtilis*, Russia) and *S. betulina* compared with those from Krasniy Yar XI. Measurements of modern samples from Pucek (1982a, b) and Tesakov (unpublished).

| | Length | Width |
|-----------------------------|---------------------|---------------------|
| | Min.–Mean–Max. (n) | Min.–Mean–Max. (n) |
| M ₁ | | |
| <i>S. betulina</i> (Poland) | 0.96–1.03–1.07 (21) | 0.71–0.74–0.79 (21) |
| <i>S. loriger</i> (Romania) | 1.08–1.13–1.18 (19) | 0.80–0.89–0.94 (19) |
| <i>S. subtilis</i> (Russia) | 1.1–1.15–1.2 (6) | 0.85–0.87–0.9 (6) |
| Krasniy Yar (100–110 cm) | 1.05 | 0.80 |
| M ₂ | | |
| <i>S. betulina</i> (Poland) | 0.94–1.03–1.10 (22) | 0.73–0.79–0.86 (22) |
| <i>S. loriger</i> (Romania) | 1.03–1.11–1.20 (19) | 0.83–0.89–0.98 (19) |
| Krasniy Yar (100–110 cm) | 1.05 | 0.84 |
| <i>S. subtilis</i> (Russia) | 1.1–1.13–1.2 (6) | 0.85–0.89–0.95 (6) |
| Krasniy Yar (80–90 cm) | – | 0.83 |
| M ₃ | | |
| <i>S. betulina</i> (Poland) | 0.70–0.77–0.84 (22) | 0.58–0.65–0.73 (22) |
| <i>S. loriger</i> (Romania) | 0.70–0.78–0.86 (19) | 0.64–0.72–0.78 (19) |
| <i>S. subtilis</i> (Russia) | 0.75–0.78–0.8 (5) | 0.7–0.74–0.8 (5) |
| Krasniy Yar (100–110 cm) | 0.82 | 0.68 |
| Krasniy Yar (70–80 cm) | 0.80 | 0.72 |

4.3.1.5. *Clethrionomys rutilus*, northern red-backed vole. An upper third molar (length = 1.50 mm) of this species was recovered from 135 to 145 cm (Fig. 10f). *Clethrionomys rutilus* is one of the most common small mammals in the taiga and occurs throughout the northern Holarctic, from Scandinavia through Siberia to the Pacific coast and northern parts of North America. In Siberian coniferous forest, it is particularly numerous in areas with fallen trees and clearings supporting a mix of dense scrub and rich herbaceous ground cover. It is also common in willow scrub and open birch woodland (Linzey et al., 2016).

4.3.1.6. *Arvicola amphibius*, water vole. A fragmentary second upper molar of water vole *Arvicola amphibius* was also recovered from 135 to 145 cm (Fig. 10g). In Russia the species is semi-aquatic and may be locally abundant in marshes and reedbeds on the banks of rivers, streams and lakes. The Lena Basin and Lake Baikal are located at the eastern limit of its extensive range, which covers much of continental Russia and Europe with a latitudinal range from Iran and Israel to the Arctic coast (Batsaikhan et al., 2016). There is considerable variability in different populations, some having molars with the enamel thicker on the concave side of the triangles and others with thicker enamel on the convex side, as in *Mimomys savini*, the early Middle Pleistocene ancestor of *Arvicola* (Röttger, 1987). Although the enamel structure of *Arvicola* in the Lake Baikal region has not been studied in detail, it may be

significant that the Krasniy Yar XI molar retains the ancestral condition with thicker enamel on the convex side of the triangles.

4.3.1.7. *Microtus agrestis*, field vole. A single specimen, a digested second upper molar (M₂) from 135 to 145 cm is referred to *Microtus agrestis*. This attribution is based on the presence of a small additional posterior lingual angle (Fig. 10h), which distinguishes *M. agrestis* from all other Palearctic *Microtus* species. Although widespread throughout the Palearctic temperate forest, taiga and tundra zones from western Europe to Lake Baikal, the field vole is primarily a grassland species that reaches its highest densities in damp situations supporting rough tussocky grasses and sedges (Kryštufek et al., 2016).

5. Discussion

5.1. Synthesis of multi-proxy data from Krasniy Yar XI

The stratigraphical sequence at Krasniy Yar XI adds to the growing number of Holocene landscape and environmental change studies in the Lake Baikal region. The site preserves floodplain sedimentation and cycles of pedogenesis, incorporating a relatively rich record of terrestrial and aquatic macrofossils, spanning ~7000 years. Overlying a coarse gravelly substrate (Unit 1), the deposition of fine loamy alluvium marks the onset of floodplain development at the site during the early Holocene, followed by a sustained period of soil formation and hence relative landform stability (Unit 2) prior to ~5220 cal yr BP. The corresponding terrestrial mollusc assemblage (Zone KY1) was both shell- and species-rich, initially dominated by *Vallonia pulchella*, commonly found in wet meadow and marshland habitats, being gradually replaced by *V. costata*, which is more shade-tolerant and generally occurs in drier, better-drained, environments. Aquatic molluscs also comprised a significant component of the assemblage in this part of the sequence, particularly *Pisidium nitidum*, which suggests that at least some of the fauna from Zone KY1 may reflect redeposited elements. Remains of *Sorex minutus*, *Lepus timidus*, cf. *Myopus schisticolor*, *Clethrionomys rutilus* and *Arvicola amphibius* were also found in Unit 2, also suggesting open riparian habitats and more shaded environments.

A relatively prolonged interval of weak floodplain pedogenesis (Unit 3) ensued from ~5220 to ~1820 cal yr BP, punctuated by the deposition of a thin layer of very coarse sediment derived from a high-energy fluvial event. The associated mollusc record (Zone KY2) contained fewer shells than adjacent zones, with aquatic molluscs now occurring in much lower frequencies. Open conditions persisted on the floodplain with habitats dry enough to support *V. costata*, which dominated the assemblage along with increased percentages of *Perpolita petronella* and *Cochlicopa lubrica*. The occurrence of southern birch mouse (*Sicista subtilis*) in the upper

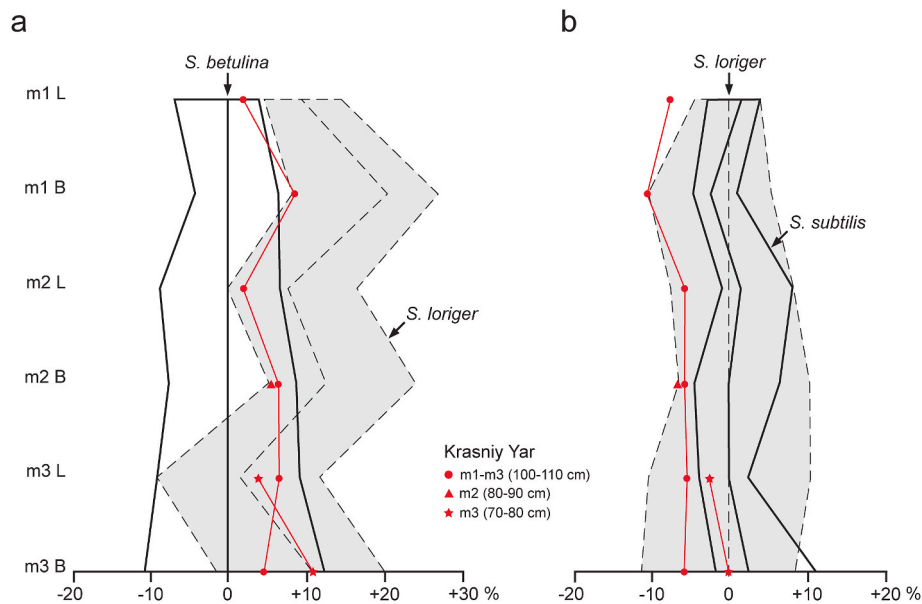


Fig. 13. Ratio diagrams showing relative lengths (L) and breadths (B) of molars in samples of *Sicista subtilis* species group (*S. loriger*, eastern Romania and *S. subtilis* from Russia) and *S. betulina*. The standards of comparison (zero line) are the mean of the *S. betulina* sample (a) and *S. loriger* (b). The other measurements are plotted in units of percentage deviation from that mean. Minimum, maximum and mean dimensions of modern *Sicista* samples are derived from Pucek (1982a, b).

part of Unit 3 is noteworthy as it is rare as a Quaternary fossil. Its presence is typically associated with steppe and semi-steppe habitats comprised of grassland scrub and lightly wooded environments with dense herbaceous vegetation. As current forest density in the Kirenga Valley is estimated at ~97–98% (Batuev, 2004b), this suggests that this species can live along open floodplains in otherwise dense boreal forest. It is interesting to speculate that *S. subtilis* survived the demise of mammoth-steppe in the Baikal region in such riparian open grasslands. Moreover, the associated age determinations of <2000 cal yr BP suggest that habitats suitable for *S. subtilis* persisted in the Kirenga Valley for several millennia after the Pleistocene-Holocene transition.

Overlying Unit 4, which comprised the uppermost part of the stratigraphical record, includes initially a generally less active interval of floodplain pedogenesis and increasing deposition of fine sand. This part of the sequence dates to ~1025 cal yr BP. Over the last ~400 years, however, enhanced floodplain surface stability and soil development is evident up to the present. Associated mollusc abundance and species richness (Zone KY3) showed marked increases compared to underlying Zone KY2. *V. costata* continued to dominate the assemblage together with increased frequencies of *Carychium pessimum* and *Vitrina pellucida*, perhaps suggesting a more humid and better vegetated habitat. In addition, slightly higher frequencies of aquatic specimens in this part of the record indicate the periodic invasion of flood waters on the aggrading landform. Remains of *Microtus agrestis* and *Sorex* sp. were also found in Unit 4.

5.2. Floodplain environmental and biogeographical records in the Lake Baikal region

The initial aim of the study was to investigate whether floodplain sequences in the Baikal region could potentially shed any light on the environmental context and possible cause of the discontinuity seen in the regional Neolithic archaeological record. The results from Krasniy Yar XI, and the other floodplain sites previously investigated (White et al., 2008, 2013), show that the records are too discontinuous and the temporal resolution just too low to address causal issues in any meaningful way. Nevertheless, the radiocarbon-dated sequences have provided extremely valuable records of the molluscan and small mammal assemblages from the boreal region of southern Siberia and their history

throughout the last ~11,000 cal yr BP (White et al., 2008, 2013; see also regional summary by Khenzykhenova et al., 2021). These provide some of the best such records currently available.

Detailed information about modern land snail communities of the Baikal region is rather sketchy and no published quantitative data exists. This is not the case with land snail assemblages from the Altai region, ~1500 km to the west of Lake Baikal. Here quantitative data from vascular plants and co-occurring land snails have been obtained along transects covering a range of climatic and environmental gradients (Hoffmann et al., 2011). These data are very relevant to the present study because many species found there also occur in the Baikal region and appear in our floodplain sequences, including a few recently described as new (Nekola et al., 2018).

The Altai study included data from a range of habitats from dry steppe environments, through alpine meadows to forests of birch or larch (Hoffmann et al., 2011). Many of the species encountered had rather catholic ecological preferences and occurred in a broad range of different habitats. It is therefore not straightforward to estimate the extent of shade from these molluscan assemblages, although the dominance of *Vallonia* species at Krasniy Yar XI does suggest rather open conditions throughout (see Horsák et al. (2018) for a detailed study of forest snails from the Altai region and the factors influencing their diversity and abundance). The ecological successions of land snails from Siberia do not show an obvious replacement of open-ground communities by those of forest, such as those that characterise Holocene sequences from central and NW Europe (e.g., Ložek, 1964; Kerney et al., 1980; Preece and Bridgland, 1999).

Ecological studies in the Altai found that species such as *Fruticicola schrenkii*, *Gastrocopta theeli* and *Vallonia costata* typify assemblages at the dry end of the environmental gradient, whereas Succineidae, *Perpolita* spp., *Euconulus fulvus* and *Punctum pygmaeum* occurred towards the wet end (Hoffmann et al., 2011). This conforms well with our interpretations of the Krasniy Yar XI sequence, although *Vallonia tenuilabris* and *V. kamtschatica* occurred in the lower part of the sequence at Krasniy Yar XI where conditions appear to have been wetter.

An interesting observation concerns the relationship between intervals of local floodplain stability and the relative frequencies of certain land snails, particularly *Vallonia costata*, which dominates certain levels in the sequences studied in the upper Lena and lower Selenga regions, as

well as at Krasniy Yar XI. Periods of greater surface stability allow pedogenic processes to intensify, resulting in the development of organic-rich soil horizons (Ah, Ab, AC) on the floodplain surface. This is illustrated in the Krasniy Yar XI data, which showed increases in organic content coinciding with intervals of floodplain pedogenesis (Fig. 3). This pattern was also evident in the sedimentological records at Basovo (White et al., 2008, Fig. 4) and Burdukovo (White et al., 2013, Fig. 3) and is a widely recognized proxy for distinguishing periods of soil formation in stratigraphical sequences.

Detailed malacological comparisons with other sequences in the Baikal region are limited because few have the same level of detail, and they are hampered by the fact that until relatively recently there has not been standard taxonomic usage. Because of this it is not yet possible to show whether regional differentiation in faunal assemblages existed. It is interesting to note, however, that Holocene land snail assemblages from the Krasnosyarsk forest steppe region, about 900 km to the west of the Baikal region, were remarkably similar (Yamskikh et al., 2022), suggesting that they may indeed characterise large parts of southern Siberia.

From a biogeographical viewpoint, the molluscan assemblages that we report from Krasniy Yar XI contain no major surprises, but a few of the species recovered (e.g., *V. chytryi*) have never previously been found as fossils in the region. This is really just a reflection of our general lack of knowledge about the Holocene assemblages from this area. The Altai region was found to support a range of species (e.g., *Pupilla loessica*) known from the Pleistocene of Europe that had never previously been found living (Horsák et al., 2010, 2015). These communities appear to provide useful analogues of those that occurred in western Europe during full glacial conditions of the Pleistocene. None of these species have yet been found in the Baikal region, although most of the modern survey work undertaken here (such as our 2007 field survey) has been focused on lowland floodplains, rather than montane habitats.

The most surprising vertebrate discovery at Krasniy Yar XI was that of southern birch mouse (*Sicista subtilis*), previously unknown from the Baikal region despite numerous investigations of the small mammal assemblages from the Holocene (see review by Khenzykhenova et al., 2021). The teeth of this species are extremely small and might simply have been overlooked on that account but the absence at other sites could well be genuine. This is a species that prefers rather open environments and perhaps the riparian habitats along major river valleys provide the conditions necessary to support this species.

It remains speculative whether broader regional-scale Holocene climate signatures can be drawn from these local data as the stratigraphical records from Basovo, Burdukovo and Krasniy Yar XI document different time intervals, are discontinuous by nature, and display varying levels of temporal resolution. Other Holocene proxy records from the region, mostly derived from more continuous lake sediment cores, demonstrate a broadly temperate warm and humid climate with maximum forest expansion during the mid-Holocene (e.g., Bezrukova et al., 2005a, 2005b, 2010, 2013; Demske et al., 2005; Karabanov et al., 2000; Khenzykhenova et al., 2021; Kobe et al., 2022; Mackay et al., 2013; Shichi et al., 2009; Tarasov et al., 2009, 2013, 2017; White and Bush, 2010), although spatial variability is apparent and the reliability and resolution of reconstructed site age-models varies considerably. At Lake Ochaul, located only ~180 km south-west of Krasniy Yar XI, the entire middle Holocene period (8000–4200 cal yr BP) is characterised by a stable lake system associated with the maximal spread of taiga forests across the region, with a trend towards more open forests during the late Holocene (Kobe et al., 2022). This reconstruction would seem to support the presence of southern birch mouse (*Sicista subtilis*) in the upper part of the sequence at Krasniy Yar XI.

Results from new high-resolution palaeoenvironmental research across the Baikal area will ultimately enable observations from local Holocene archaeological sequences to be more meaningfully framed within the context of regional climate change (White and Bush, 2010; Tarasov et al. 2017; Weber, 2020). The latest research arising from the

Baikal Archaeological Project continues to identify a clear biocultural discontinuity reflected most obviously in differences in mortuary behaviour across the region. The reasons for these differences are likely to be multi-causal (see Weber (2020) for a recent synthesis of new data), although climate and environmental change has long been suspected as a significant contributing factor.

6. Conclusions

1. The floodplain sequence at the Krasniy Yar XI site in the remote Kirenga valley, like the other local records that we have previously described from the upper Lena and lower Selenga valleys, proved to be too discontinuous, and had insufficiently high temporal resolution, to address issues relating specifically to the cause of the cultural discontinuity recognized in the regional archaeological record.
2. The Krasniy Yar XI site nevertheless provided a valuable radiocarbon-dated record of a fossiliferous floodplain sequence covering much of the Holocene. Several buried pedogenic horizons occur in the sequence, reflecting periods of relative stability of the floodplain.
3. The shells of land and freshwater molluscs, which occur throughout the sequence, provide a record of changing local environmental conditions. Aquatic species and hygrophilous land snails are frequent in the early part of the sequence, whereas land snails of drier ground, particularly *Vallonia costata*, dominate the later horizons. The local river floodplains provide important habitats for both land snails and mammals that require open-country environments in an otherwise predominantly forested landscape.
4. The molluscan fauna is similar to other Holocene assemblages reported from the Baikal region but it contained several additional species including *Vertigo kushiorensis*, *V. chytryi* and *V. genesioides*, although the last species, described in 2018, has been reported under a variety of different names. *Vertigo genesioides* and *V. cf. kushiorensis botanicorum* have recently been reported from Holocene sequences in the Krasnosyarsk forest steppe region about 900 km to the west (Yamskikh et al., 2022). The associated molluscan assemblages from this area are remarkably similar to those reported from the Baikal region, suggesting that they may characterise large parts of southern Siberia. Further comparisons are hampered by inconsistency regarding taxonomic usage.
5. The molluscan sequence from Krasniy Yar XI is also noteworthy for the high frequency (mean 9.8%) of sinistral specimens of *Cochlicopa* that occurred in 12 of the 18 samples analysed. The occurrence of sinistral *Cochlicopa* at Krasniy Yar XI spans a period of ~7000 years.
6. Remains of small mammals, which were also frequent in the sequence, included southern birch mouse (*Sicista subtilis*) that is not known to inhabit this part of Siberia. Perhaps the increasingly open nature of the riparian habitats bordering large rivers during the late Holocene provided suitable conditions for its long-term survival.

Author contributions

Dustin White: Conceptualization, Fieldwork, Methodology, Investigation, Formal analysis, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization, Project administration, Funding acquisition. **Simon A. Parfitt:** Methodology, Formal analysis, Writing – Original Draft, Writing – Review & Editing, Visualization, Funding acquisition. **Alexander A. Shchetnikov:** Fieldwork, Investigation, Writing – Original Draft, Project administration. **Alexey S. Tesakov:** Resources. **Richard C. Preece:** Conceptualization, Formal analysis, Writing – Original Draft, Writing – Review & Editing.

Data availability

Datasets (Mollusca and vertebrates) related to this article are deposited in the collections at the University Museum of Zoology

Cambridge (UMZC), alongside those from Basovo and Burdukovko.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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