A Holocene molluscan succession from floodplain sediments of the upper Lena River (Lake Baikal region), Siberia

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Abstract

Floodplain sediments of the upper Lena River near Basovo in south-central Siberia have yielded the most detailed Holocene molluscan succession yet reported from the entire eastern Palaearctic. Over 72,500 shells from at least 28 species of terrestrial and 23 species of freshwater mollusc have been recovered, an abundance and diversity far higher than previously reported from the region. The molluscan assemblages are dominated by land snails, especially members of the genus Vallonia, represented by five species including Vallonia tenuilabris and two poorly known species Vallonia kamtschatica and Vallonia cf. chinensis. Other noteworthy species recovered include Gastrocopta theeli, Carychium pessimum, Vertigo extima (southernmost record), Vertigo microsphaera and the first Asian records of three other taxa (Vertigo geyerti, Vertigo genesii and Vertigo parcedentata). Illustrations are provided for the critical species, since opinions differ about the status of various taxa and the correct names that should be used. The molluscan assemblages show clear successional trends during the early to mid-Holocene, reflecting episodes of dryness/wetness on the floodplain. Drier conditions at ca 6350 14C yr BP coincide with major changes in the archaeological record seen at other sites in the region but it remains unclear whether the two are linked. A prominent charcoal-rich horizon dated to ca 2800 14C yr BP marks a burning event in the catchment, which resulted in a two-fold increase in sediment accumulation rate. Remains of small mammals occurred throughout the sequence including a tooth of Microtus cf. maximowiczii, possibly the first occurrence of Ungar vole west of Lake Baikal. The faunal analyses have been integrated with a detailed pedological study of the sedimentary profile and a chronology was obtained by means of 12 AMS radiocarbon dates. This study provides the first detailed palaeoecological information relating to Holocene molluscan assemblages from the Cis-Baikal region and lays the foundation for future work in the eastern Palaearctic.

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1. Introduction

There is enormous disparity in the degree to which faunas from the western and eastern Palaearctic regions have been studied. This imbalance varies between taxonomic groups but in the case of non-marine molluscs, which are the main subject of this paper, it is very marked indeed. A number of factors contribute to this problem. Compared to the western Palaearctic, the eastern Palaearctic is far less populated and consists of vast expanses of remote terrain that is often both difficult to access and available for study for only a brief period during the summer months. In the past, the political situation has also made fieldwork in some areas difficult and even today fieldwork in remote uninhabited areas poses logistical challenges. Another serious problem confronting anyone attempting to view the fauna of the Palaearctic region as a whole is the different taxonomic traditions practiced in the
West and by some Russian scientists in the East, who often
have a greater tendency to ‘split’ species (Reischütz, 1994;
Korniushin, 1998). There are also disagreements about the
correct names that should be used even for species that
both groups consider valid. This limits a complete under-
standing of the biogeographical composition of the region
and leads to uncertainty about precise distributional ranges
of many taxa.

Most of the research documenting molluscan successions
during the Holocene (and earlier episodes of the Quatern-
ary) has been undertaken in western and central Europe
(e.g. Ložek, 1964, 1982; Evans, 1972; Puisségur, 1976;
Kerney et al., 1980; Meyrick, 2001, 2003). In contrast,
virtually no such detailed information exists for the entire
eastern Palaeartic. Apart from simple faunal lists obtained
from certain sites, the most detailed studies in Asia are
those undertaken on loess sequences in China (e.g.
Rousseau and Wu, 1999; Rousseau et al., 2000; Wu
et al., 2007), where the main focus of interest is the
Pleistocene rather than the Holocene.

During the last decade the Baikal Archaeology Project
(BAP) has been conducting multidisciplinary investigations
surrounding long-term culture change and continuity seen
in hunter–gatherer communities in the Lake Baikal region
of south-central Siberia (Weber et al., 2002, 2005; Weber
and Bettinger, n.d.). Early results from this international
research programme have demonstrated an intriguing
millennium-long ‘biocultural discontinuity’ separating
two distinct periods of emergent social complexity. Before
this hiatus, spanning the seventh millennium BP, relatively
large formal cemeteries were used by the early Neolithic
Kitoi culture but this mortuary tradition was apparently
abandoned for about 1000 years prior to the appearance
of Serovo-Glazkovo groups during the late Neolithic–Bronze
Age. Archaeological data further suggested that the
 cultural groups on either side of this middle Neolithic
hiatus differed in their subsistence, diet, mobility, genetic
affiliation and social relations. The causes of the abandon-
ment of mortuary tradition, and the archaeological
changes seen on either side of it, are not known although
they have been attributed primarily to cultural reasons,
rather than resulting from any climatic or environmental
change. These, however, remain distinct possibilities and
provided the impetus for the instigation of a series of
palaeoenvironmental investigations in the region (White,
2006; White and Bush, n.d.). The present study formed part
of one of these. Although its initial objectives were to
furnish environmental data to address the critical archaeo-
logical issue mentioned above, it also provided data of
relevance to a broader community of biogeographers and
Quaternary scientists.

This paper examines the palaeoecological significance of
a well-dated Holocene molluscan succession from flood-
plain sediments of the upper Lena River, west of Lake
Baikal in Siberia. Shells of land and freshwater molluscs
are abundant in a range of Quaternary sediments,
especially those that have accumulated in base-rich

conditions. Unlike plants and insects, mollusc shells are
not preserved in acidic environments but they are able to
resist strong oxidation, which is frequently responsible for
the loss of all organic fossils, including pollen, plant
macrofossils and beetle remains. They are therefore an
important group potentially able to provide much addi-
tional information about Quaternary environments. In
common with beetles and plant macrofossils, the shells of
molluscs can, with a few notable exceptions, also be
identified to species level enabling palaeoenvironmental
reconstructions to be made with far greater precision and
providing the opportunity to establish how and when
particular communities developed during the recent past.

Site selection in summer 1999 followed a 5-week
reconnaissance by boat during a geoarchaeological survey
of the upper Lena River valley between the towns of
Zhigalovo (54°48’N, 105°10’E) and Ust-Kut (56°48’N,
105°48’E), a stretch of river about 340 km in length
(Fig. 1). A floodplain sequence near the settlement of
Basovo was identified as a promising site since the
sediments there were clearly stratified, reasonably thick
and contained abundant shells and charcoal. In addition to
its record of the environmental history of the local area,
the site also had the potential to shed light on just how rich
and diverse the molluscan assemblages are in this region
and how they developed during the Holocene. Given their
geographical context within the boreal forest biome, these data may also be relevant to our understanding of interstadial faunas of the Pleistocene. In order to undertake this investigation in a satisfactory way, it is necessary to address a number of taxonomic and nomenclatural issues. Discussion and illustrations are therefore provided of a number of critical taxa, especially those that are either poorly known or which are the subject of taxonomic uncertainty. Remains of small mammals, including several noteworthy records, were recovered from the sequence and these are also discussed. The faunal analyses have been integrated with a detailed pedological study of the sedimentary profile and a radiocarbon chronology provided by means of 12 AMS dates.

2. Regional setting

The site near Basovo (55°52′30.4″N, 105°47′01.7″E; 345 m a.s.l.) is located within the upper Lena River valley of south-central Siberia, about 240 km west of the northern tip of Lake Baikal, the world’s most voluminous (23,015 km³) and deepest (1642 m) freshwater lake (Fig. 1). This area is part of the Lena-Angara foothills of the southern Central Siberian Plateau, with maximum elevations of surrounding hilly terrain reaching 1500 m a.s.l. (Boyarkin, 1973). Regional topography is formed primarily from bedded subhorizontal terrigenous carbon-bearing rocks of Cambrian and Ordovician age (Maslov, 1947; Kuznetsov and Zharkov, 1964). Cambrian rocks are represented by thin argillites interbedded (up to 1.5-m thick) with aleurolites, fine-grained sandstone, marl and limestone. Ordovician deposits are more widespread, forming the valley divides and upper valley slopes. Rocks of this age occur as parallel- and obliquely laminated, fine- and medium-grained sandstone, dolomites and limestone, with some aleurolites and argillites. Quaternary deposits occur as thin mantles of colluvium on valley slopes and as alluvial sediments of the Lena River terrace complex and its tributaries. Modern soil cover in the area includes loamy-skeletal Eutric Brunisols (Cryeutoic Cambisols) and Dystric Brunisols (Cryodytic Cambisols) on well-drained plateaus and slopes, together with clayey Gleyic Brunisols (Cryogleyic Cambisols) in poorly drained areas and Organic Cryosols (Cryic Histosols) in depressions (Dobrovolsky and Urusevskaya, 1984). Along river valley bottoms, Gleyed Cumulic Regosols (Gleyic Fluvisols) dominate.

The climate of the region is distinctly continental, characterised by long, cold, dry winters and short, warm and moderately wet summers (Irkutsk Meteorological Agency, 2002; Reference Book for Climatology of the USSR, 1949). These conditions result primarily from the dominance of the Siberian anticyclone (i.e. high pressure) in winter and the Inner Asiatic depression (i.e. low pressure) in summer. Average annual air temperature in the area is −4.3 °C. January is the coldest month, averaging −26 °C, with minimum air temperatures reaching down to −50 °C during winter. Average temperatures below 0 °C occur for 195–200 days annually, with continuous frosts lasting for 140–160 days. Frosts first occur by early September and last until mid-May. Warmest annual air temperatures are recorded during July (average temperature 17 °C) with daily highs averaging 22–24 °C but reaching a maximum of up to 36 °C. Average daily air temperatures over 0 and 10 °C are 160–165 and 70–80 days, respectively. Humidity patterns also follow a distinct seasonal regime, with two-thirds of annual precipitation accumulating between June and August. Annual precipitation totals in the river valleys range between 300 and 400 mm and reach up to 600 mm at higher elevations. Maximum rainfall generally occurs during July and August, with a combined average of 150 mm. Snow cover is formed by mid-October and lasts until late April to early May. Average snow depth in open areas during February is 40–47 cm, and 50–55 cm in sheltered areas during the first half of March.

The upper Lena River is characteristic of many rivers in eastern Siberia, with a well-defined cycle of spring flooding associated with the rapid rise of water levels (averaging 3–5 m). Approximately 80% of drainage occurs during the spring and summer months and more than 90% of suspended sediment/drift is deposited during the spring high water period (Romanchenko, 1990). During disintegration, drift-ice build-up is common and can lead to rapid catastrophic rises in water levels (up to 7 m). River ice generally forms in mid-November with annual ice breakup occurring in mid-April to early May.

Vegetation complexes in the vicinity of Basovo are characteristic of mountain-taiga forest, consisting of mature stands of pine (Pinus sylvestris), larch (Larix sibirica) and spruce (Picea obovata), together with birch (Betula alba), aspen (Populus), willow (Salix) and alder (Alnus) underbrush and forest herbage (Dobrovolsky and Urusevskaya, 1984). The floodplain and part of the lower slopes near Basovo are abandoned arable land that has acquired steppic features characterised by the dominance of grasses, wormwood (Artemisia) and herbs, including meadow foxtail (Alopecurus pratensis), milfoil (Achillea), plantain (Plantago) and chamomile (Matricaria). Red clover (Trifolium pratense) and shade horsetail (Equisetum pratense) occur in moist depressions along the floodplain. Abandoned farmland and historical clearance of forest along valley slopes adjacent to the site indicates the former occurrence of more intensive local land-use strategies.

3. Materials and methods

3.1. Sedimentology

Following site descriptions, samples for various sedimentological analyses were collected from cleaned sections at consecutive 5cm intervals, respecting stratigraphic boundaries, from 2.60 m up to the modern surface. Finer sampling intervals were used for thin horizons and/or near
stratigraphic boundaries. Samples varied between 150 and 250 g dry sediment weight. For granulometric analyses, dried sediment was sieved through a 2000 µm diameter mesh to separate the fine fraction from larger particles, followed by hydrometer measurements of the sand (2000–50 µm), silt (50–2 µm) and clay (<2 µm) fractions (Sheldrick and Wang, 1993). Subsequent analyses included ultrasonic sieving of the sand fraction into very coarse (2000–1000 µm), coarse (1000–500 µm), medium (500–250 µm), fine (250–100 µm) and very fine (100–50 µm) components (Gee and Bauder, 1986). Due to the limited occurrence of coarse sediments, the 2000–500 µm sand fractions are combined for graphical presentation. Carbon content was measured by wet-oxidation digestion using a Carlo-Erba NA 1500 CNS Elemental Analyzer to determine total carbon and total organic carbon, with the inorganic component derived by subtraction (Ellert and Jansen, 1996). Soil colour was described with reference to the Munsell soil chart. Micromorphology samples were collected in 10 cm × 6 cm × 4 cm reinforced aluminium frames at selected contact points across stratigraphic boundaries and in vertical sequence along the lower half of the study section. Thin sections (ca 30 µm thick) of 14 undisturbed oriented samples were analysed for mineralogy, microstructure and pedogenic features using a petrographic microscope at magnifications up to ×720. Preparation techniques and micromorphological terminology follow Murphy (1986) and Bullock et al. (1985), respectively. The delineation of stratigraphic units is based on principles of lithostratigraphy and pedostratigraphy outlined in the North American Commission on Stratigraphic Nomenclature (1983) and Morrison (1998). Textural classes and soil classifications are based on the Canadian System of Soil Classification (Soil Classification Working Group, 1998), with the WRB international classification equivalents provided in brackets (International Society of Soil Science, 1998).

3.2. Fossils

Macrofossils (i.e. molluses, vertebrate remains and charcoal) were extracted from 50 samples, each volumetrically measured to 2.5 l of moist sediment, collected from the High Floodplain Section 2 (HFS2) at consecutive 5 cm intervals from 2.50 m up to the modern surface. To ensure systematic recovery of fossils, each sample was first wet-screened through a 500 µm mesh at laboratories of the Russian Academy of Sciences in Irkutsk. Screened samples were then air-dried and transported back to Canada and the United Kingdom where they were examined under a binocular microscope at variable magnifications (×6 – ×50) to extract all identifiable fossils using fine forceps and paint-brushes. Land and freshwater molluscs were the most abundant group of fossils recovered from the sequence at Basovo. Minimum totals for each species were determined by counting shell apices for all identifiable adults and juveniles (Ložek, 1986). In samples where diagnostic apertural fragments outnumbered apices for a given species (e.g. Pupilla and Vertigo), then the totals were based on these. Counts for bivalves were rounded up to the nearest even number and then halved to give the minimum number of individuals for each species. The results are presented as both frequency histograms and plots of the number of species, number of individuals and terrestrial/aquatic ratios. For the frequency histograms, all samples with more than 200 specimens of land snail are plotted as a percentage of the total terrestrial sum. In those samples containing fewer than 200 individuals, percentage calculations were not deemed statistically adequate and are therefore indicated by absolute numbers. The aquatic taxa are plotted as a separate frequency histogram but in this case all samples containing >50 specimens were calculated as a percentage of the total terrestrial sum in order to illustrate the dominant trends, despite the greater statistical uncertainty.

Vertebrate fossils (i.e. small mammals, amphibians and fish) were also recovered in 40 of the 50 samples analysed. Individual skeletal elements were recorded, but Minimum Numbers of Individuals were not calculated due to the generally low yield in most samples. No attempt was made to quantify the abundance of charcoal recovered since this is prone to fragmentation during sieving. However, the larger fragments were carefully picked and identified. Samples for pollen analyses were collected in 50 ml polypropylene containers at consecutive 3 cm intervals from 2.50 m up to the modern surface but as the sediments were generally oxidised, little or no meaningful pollen was recovered.

3.3. Radiocarbon dating

Charcoal preserved in stratified contexts was used to construct a detailed radiocarbon age model for the site. Discrete individual pieces of charcoal were selected for dating rather than using a mixture of smaller fragments. These specimens were not identified prior to submission, but charcoal from the same (and adjacent) levels has been identified (Supplementary Table 1). The 12 AMS 14C dates obtained provide a chronology for the Basovo section (Table 1).

4. Results and interpretations

4.1. Geomorphic setting and stratigraphy

Floodplain sediments on the left bank of the Lena River near Basovo were the focus of detailed study. Stratigraphic sequences are exposed along an actively eroding bank composed of fine-grained alluvial sediments containing multiple buried soils. Downstream (north) from the outlet of Domashnii Creek, the valley contains an older high terrace (T-2) and a high (T-1) and low (T-0) floodplain (Fig. 2). The high terrace rises 7–10 m above the Lena
River and occurs intermittently at several sites between Zhigalovo and Ust-Kut. Previous studies in the upper Lena River valley have reported a late Pleistocene age (QIII) for this terrace based on the occurrence of Coelodonta antiquitatis Fich., Mammuthus primigenius Blum. and Cervus sp. (Obruchev, 1892; Pavlovskiy, 1929). Near Basovo, the high terrace runs parallel to the Lena River to the north of Domashnii Creek for a distance of ca 750 m, where it intersects the floodplain with gently sloping topography. At its widest point, the floodplain extends up to ca 800 m from the eastern edge of the present river channel to the base of the adjacent valley slopes, continuing downstream for about 2.5 km. This landform can be divided into at least two components, an older high floodplain and a younger low floodplain. Given the research focus on reconstructing the Holocene environmental history at the site, the high floodplain section was selected for detailed study.

The exposed section of the high floodplain is about 220 m in length and 3–5 m in height and composed of loamy alluvial sediments with multiple buried soils, which formed during periods of relative floodplain stability. Sections were described and sampled at selected exposures designated as High Floodplain Sections 1, 2, and 3, hereafter referred to as HFS1, HFS2, and HFS3. The dotted line delineates a former channel of the Lena River separating the high (Lateglacial-Holocene) and low (late Holocene) floodplains. Note the elevation gradient of the floodplain in photo (B).

**Table 1**

<table>
<thead>
<tr>
<th>Unit</th>
<th>Depth (cm)</th>
<th>$^{14}$C yr BP</th>
<th>Calibrated yr BP 68% c.i. (1σ)</th>
<th>Calibrated yr BP 95% c.i. (2σ)</th>
<th>Lab ref. no.</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>30–35</td>
<td>1630±90</td>
<td>1415–1615</td>
<td>1330–1720</td>
<td>TO-10557</td>
</tr>
<tr>
<td>7</td>
<td>40–45</td>
<td>1410±60</td>
<td>1290–1350</td>
<td>1260–1415</td>
<td>TO-10556</td>
</tr>
<tr>
<td>6</td>
<td>82</td>
<td>2780±360</td>
<td>2430–3360</td>
<td>2040–3780</td>
<td>TO-9431</td>
</tr>
<tr>
<td>5</td>
<td>97</td>
<td>2620±90</td>
<td>2710–2780</td>
<td>2465–2880</td>
<td>TO-9436</td>
</tr>
<tr>
<td>4</td>
<td>95–100</td>
<td>2910±60</td>
<td>2950–3080</td>
<td>2915–3215</td>
<td>TO-10555</td>
</tr>
<tr>
<td>4</td>
<td>100–105</td>
<td>2790±60</td>
<td>2840–2950</td>
<td>2765–3005</td>
<td>TO-10554</td>
</tr>
<tr>
<td>4</td>
<td>105</td>
<td>3380±80</td>
<td>3550–3695</td>
<td>3445–3785</td>
<td>TO-9433</td>
</tr>
<tr>
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<td>130–135</td>
<td>6350±120</td>
<td>7200–7420</td>
<td>6985–7475</td>
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<tr>
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<td>170–175</td>
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<td>9025–9430</td>
<td>8985–9530</td>
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<tr>
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<td>8770±100</td>
<td>9595–9915</td>
<td>9535–10,185</td>
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<tr>
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<td>11,195–11,260</td>
<td>11,165–11,440</td>
<td>TO-9435</td>
</tr>
</tbody>
</table>

All samples were pre-treated and measured at IsoTrace Laboratory, Toronto, Canada and calibrated using INTCAL98 (Stuiver et al., 1998).
the course of floodplain development. HFS1 is located along the slightly elevated southern end of the high floodplain where stratigraphic sequences, particularly in the lower portion of the section, exhibit both fewer laminations and other microstratigraphic detail that characterise HFS2 and HFS3, located ca 45 m and ca 53 m to the north, respectively, and at slightly lower elevations (Figs. 2 and 3). Generally, pedogenic sequences consist of Gleyed Cumulic and Gleyed Cumulic Humic Regosols (Gleyic Fluvisols). Site stratigraphy is illustrated in Figs. 3 and 4 and described in detail below. Micromorphological descriptions and illustrations are presented in Supplementary Data.

Unit 1

Lithology. Unit 1 consists of a bedded, clast-supported gravel composed of well-rounded pebbles, cobbles and boulders of mixed lithology.

Interpretation. These sediments were deposited under high-energy fluvial conditions and represent a gravel bar of the upper Lena River.

Unit 2

Lithology. Unit 2 is a weakly stratified sequence of fine loamy sediments with very low organic carbon (<0.5%) content. These deposits overlie Unit 1 and occur as the basal fine-textured unit along the entire high floodplain section. Sediments are highly calcareous, yellowish red (5YR 4/6) loams with generally poorly defined parallel horizontal bedding. Occasionally, the bedding undulates slightly and exhibits small changes in texture resulting from weak alluvial sorting. Molluscs become increasingly abundant near the top of this unit. The base of Unit 2 and nature of contact with underlying coarse alluvial material were not directly observed at the excavated sections.

Interpretation. Unit 2 represents the accumulation of fine alluvium along the bank of the upper Lena River during the late Pleistocene. Accelerated erosion in the upper watershed is indicated with subsequent aggradation downstream.

Unit 3

Lithology. Unit 3 ranges between 15 and 30 cm in thickness and is composed of very fine loamy sediments overprinted by a weakly developed cumulic soil profile (buried soil E). Due to slight elevation differences and their associated effects on landform development, this unit varies in composition along the high floodplain. At Section HFS1, Unit 3 is ca 15 cm thick and occurs ca 1.60 m below the modern surface, consisting of dark reddish brown (5YR 2.5/2) silty clay loam. Cryogenic features are absent and the lower boundary of this unit is clear and wavy. Northward along the section (i.e. with decreasing elevation) at HFS2 and HFS3, stratigraphical features of Unit 3 become more complex due to increased sedimentation during pedogenesis, more frequent water-table fluctuations and pronounced cryogenic deformation. At these sections, Unit 3 is predominantly a dark reddish brown (5YR 2.5/2 to 5YR 3/2) silty clay loam between 25 and 30 cm thick.
occurring ca 1.75 m and ca 2.05 m below the modern surface, respectively. Few well-rounded to rounded pebbles, gravels and cobbles occur near the base of this unit at HFS2. This coarse layer is both limited and irregular in its occurrence along the high floodplain. Molluscs become increasingly abundant and species-rich. At HFS2, wood charcoal recovered from the lower pedogenic horizon returned ages of $8770 \pm 780$ 14C yr BP (1.95 m below surface), $9490 \pm 780$ 14C yr BP (1.95 m below surface) and $9880 \pm 100$ 14C yr BP (1.97 m below surface). Near the upper boundary of Unit 3, wood charcoal was dated to $8260 \pm 130$ 14C yr BP (1.70–1.75 m below surface).

**Buried soil E.** At HFS1, Unit 3 includes a moderately developed calcareous buried soil with subangular blocky macrostructure that grades downward to minimally altered silty clay loam and loamy parent materials. At HFS2 and HFS3, multiple incipient soils are evident as very thin (<5 cm), dark and discontinuous layers with relatively high organic carbon content (1.15–1.45%). Soil horizon boundaries for this cumulic and cryoturbated unit are irregular and broken.

**Interpretation.** Unit 3 is a silty clay loam floodplain alluvium overprinted by a cryogenically altered immature cumulic soil profile (Gleyed Cumulic Regosol (Gleyic Fluvisol)). Sedimentation generally occurred under low-energy conditions relative to other deposits represented along the high floodplain. Weak soil genesis occurred in an accretionary matrix with intervening overbank sedimentation of fine silts. Pedogenic features are indicated by darker colours, increased organic carbon content and development of soil structure. At HFS2, the base of this unit contains discontinuous and poorly sorted coarse materials including sand, pebbles and cobbles, the origin tentatively attributed to the melt-out of ice-rafted debris washed onto the floodplain. AMS radiocarbon dates provide bracketing ages with a mean pooled average (based on three dates) of $9450 \pm 14$C yr BP (cf. Stuiver and Reimer, 2005) for the lower pedogenic horizon and $8260 \pm 14$C yr BP for the uppermost soil horizon. The pedogenic sequence indicates relative floodplain stability at Basovo for the first time during the Holocene.

**Unit 4**

**Lithology.** Unit 4 is 70–90 cm thick and consists predominantly of clayey and silty loams with weakly developed soils (buried soils D1 and D2) in its upper part. At HFS1, it extends from 0.90–1.60 m below the surface and is composed of a black (10YR 2/1) calcareous silt loam fining downward to a dark grey (10YR 4/1) clay loam, with a relatively homogenous reddish brown (5YR 4/3) clay loam in its lower half. At HFS2, Unit 4 extends from 1.00–1.80 m below the surface and is represented in the lower portion by cryoturbated alluvium, differentiated primarily by texture, with an overlying pedogenic sequence. The basal sediments of this unit at HFS2 and HFS3 consist of a thin (<10 cm), reddish brown (5YR 4/4) loam underlying a thicker (ca 35 cm) reddish brown (5YR 4/3) clay loam. Total organic carbon content is relatively low (0.40–0.75%), whereas the total inorganic carbon fraction reaches a maximum for the entire sequence (up to 3.87%). Shells attain their greatest abundance in Unit 4.
The upper portion of Unit 4 is composed of organic-rich, calcareous black (10YR 2/1) silt loam and dark grey (10YR 4/1) clay loam pedogenic horizons. At HFS2 and HFS3, this sequence is approximately twice as thick as at HFS1. Cryogenic features are prominent throughout this unit. AMS radiocarbon dating of charcoal from Unit 4 produced ages of 6350 ± 60 14C yr BP (1.30–1.35 m below surface) near the middle of the unit, 3380 ± 80 14C yr BP (1.05 m below surface) near the top, and 2790 ± 60 14C yr BP (1.00–1.05 m below surface) at the upper boundary.

**Buried soil D2.** A complex pedogenic sequence overprints the alluvial sediments comprising Unit 4. Buried soil D2 consists of a gleyed, weakly developed, dark grey clay loam with relatively high total organic carbon content (1.15–1.60%) and platy macrostructure. At HFS1, this soil horizon is 10–15 cm thick with a clear and wavy lower boundary. At HFS2, this soil horizon is ca 20 cm thick with an abrupt and irregular lower boundary. Post-pedogenic modification of soil structure (i.e. repeated wetting and drying cycles or ice-lensing) may account for its moderately developed platy character.

Buried soil D1. The upper portion of this pedogenic sequence consists of a moderately developed and weakly gleyed black silt loam with high total organic carbon content (1.90–3.40%). At HFS1, this soil horizon is ca 25 cm thick with a clear and wavy lower boundary, and at HFS2 the horizon is 15–20 cm thick with a clear and irregular lower boundary. A distinct stratigraphical marker occurs within the high floodplain as a thin (1–3 cm), charcoal-rich layer at the top of Unit 4. Only faint traces of charcoal could be identified at HFS1, whereas a more continuous, although still irregular, lens was observable at both HFS2 and HFS3.

**Interpretation.** Unit 5 is an alluvial loam weakly altered by a thin, incipient soil (Orthic Regosol (Haplic Fluvisol)). Sedimentation probably occurred immediately after the burn event mentioned previously, which marks the onset of increased erosion and aggradation on the floodplain during the late Holocene. This unit is variable in thickness across the high floodplain, represented by sediments up to ca 15 cm thick along the northern section (i.e. HFS2 and HFS3) and becoming increasingly thin and intermittent near HFS1. The uniformity of the radiocarbon dates indicates that the abundant charcoal scattered throughout Units 5 and 6 is the product of the same burning event. The pooled mean of four AMS radiocarbon dates on material attributed to this forest fire is 2800 14C yr BP (cf. Stuiver and Reimer, 2005).

**Unit 6.** Lithology. Unit 6 is variable in composition along the high floodplain. At HFS1, it is ca 30 cm thick and consists of a dark brown loam that directly overlies the thin (1–3 cm) and discontinuous Unit 5. Further north, at HFS2 and HFS3, it is also ca 30 cm thick but is composed of poorly defined horizontally stratified reddish brown (5YR 4/4), calcareous loamy sands in its lower part, with an overlying calcareous cumulic soil profile (buried soil B). The basal alluvial sediments of this unit at HFS2 and HFS3 have low organic carbon content (0.50%). Shells are moderately abundant in Unit 6.

Buried soil B. Overprinting of this parent material by pedogenic processes is indicated by dark colours, high organic carbon content (1.92–3.07%) and subangular blocky macrostructure. Soil development is represented by a moderately developed, dark brown (7.5YR 3/2) loamy horizon 15–20 cm thick with overlying sandy laminations acting to modify pedogenic processes and thus creating a thin (<10 cm), dark brown (7.5YR 3/4) sandy loam transitional layer at the upper boundary.
Interpretation. Unit 6 is interpreted as alluvial loam weakly altered by pedogenesis (Cumulic Regosol (Haplic Fluvisol)). This sequence represents a renewed period of floodplain instability indicated by the deposition of sandy loam followed by a period of relative surface stability that fostered pedogenic development on the floodplain. Soil development, however, was at times interrupted by the deposition of fine sandy lenses from periodic flood events or from wind-blown sediments transported from exposed local sandbars. Wood charcoal from the moderately well-developed soil horizon in the middle of Unit 6 returned an age of 2780 ± 14C yr BP, consistent with the interpretation of local sandbars. Wood charcoal from the moderately well-

formed modern surface soil. Two charcoal samples from the top of the buried soil horizon average 1520 ± 14C yr BP, consistent with the interpretation of reworking.

Unit 7

Lithology. Unit 7 ranges between 60 and 65 cm in thickness and exhibits a consistent stratigraphical expression across the entire high floodplain section, characterised by calcareous, yellowish red (5YR 3/6), fine sandy loam sediments (ca 10 cm thick) in its lower part (directly above Unit 6) with an overlying pedogenic sequence (buried soil A and the modern surface soil). The basal sediments from this unit have low organic carbon content (0.40-0.55%) and contain the highest percentage of sand in the entire record. Upward fining of particles coincides with increased organic carbon content. These organic-rich horizons are very dark greyish brown (10YR 3/2-10YR 3/3). Shells are generally sparse in this upper unit. Wood charcoal from the buried soil horizon of Unit 7 at HFS2 returned inverted ages of 1630 ± 90 and 1410 ± 60 ± 14C yr BP from depths of 30-35 and 40-45 cm below the modern surface, respectively.

Buried soil A and modern surface soil. The buried sandy loam soil horizon associated with Unit 7 is ca 25 cm thick with subangular blocky macrostructure and high total organic carbon content (2.60-3.20%). The thin (<10 cm), weakly developed modern surface soil formed in the upper part of the unit is also distinguished by a sandy loam texture, subangular blocky to granular macrostructure and high total organic carbon content (1.65-3.35%). The modern surface horizon appears to have been left relatively unaltered by human activities, apart from the seasonal grazing of domestic livestock. Several small burrows were also present.

Interpretation. Unit 7 is a loamy floodplain alluvium weakly altered by two separate pedogenic profiles (Cumulic Regosol (Haplic Fluvisol)), indicating a continuation of alternating cycles of floodplain activity. The uppermost horizon is the modern surface soil. Two charcoal samples from the top of the buried soil horizon average 1520 ± 14C yr BP.

4.2. Molluscs

4.2.1. Identification problems

During the analyses, a number of identification problems were encountered. Moreover, a few of the names used here are at odds with usage in Russia (cf. Likharev and Rammel’meier, 1962; Zhadin, 1965). These issues are discussed briefly as follows.

Vallonia. This genus constituted the most abundant group of molluscs at Basovo, representing over 70% of the entire fauna. Following consultation with Dr. Jochen Gerber, who has made a comprehensive study of this genus (Gerber, 1996), five species of Vallonia were recognised (Fig. 5). Vallonia tenuilibris is readily separable from the others by virtue of its much larger size and more loosely coiled apex. Vallonia pulchella can be distinguished from the other species by its relatively smooth, unribbed shell. Vallonia costata has a shell with regular, widely spaced, coarse ribs on both the upper and lower surfaces and has a more depressed, flattened spire with a distinctly shouldered whorl profile. The real problem at Basovo was the separation of the other two taxa attributed to Vallonia kamtschatica and Vallonia cf. chinensis. Both have shells covered with closely spaced fine ribbing, but in V. kamtschatica, the apertural lip is thin and the spire more depressed. Vallonia chinensis is poorly known (see Section 4.2.3) and attribution to this species is tentative. The juveniles were counted separately (Supplementary Table 2) and for graphical presentation divided in proportion to the number of securely identified adults.

Vertigo. Eight species of Vertigo have been recognised at Basovo (Fig. 6a–h). These can be identified relatively easily from adult shells on the basis of their apertural barriers (or lack of them). The main problem concerns the juveniles, which form the greatest proportion of specimens. Apart from juvenile shells of Vertigo microsphaera, which are ribbed (as strongly as Vertigo substriata), immature specimens of Vertigo cannot be identified to species. For graphical presentation, the procedure adopted was to divide the immature apices in proportion to the number of securely identified adults for each species present in that sample. Further problem concerns the use of names. Following consultation with Dr. Beata Pokrzyżko, who is a specialist on this family, many specimens recovered in this study have been attributed to V. extima. This is a newly recognised species (Waldén, 1986) that is not mentioned in many standard textbooks. In Russia, these specimens would probably be listed incorrectly as a form of Vertigo modesta. Indeed, the name ’modesta’ appears to be used for five further species: Vertigo arctica, Vertigo genesii, Vertigo geyeri, Vertigo rotnebyensis and even Vertigo alpestris, which some regard as a subspecies (Schileyko, 1984, p. 211); these taxa are readily distinguishable (cf. Fig. 6a–h). Vertigo parcedentata is another species not regularly recognised in either western or Russian literature, except as a synonym of V. genesii, but these two taxa are clearly distinct (Pokrzyżko, 1993, 2003).

Nesovitrea. All specimens were examined by Dr. A. Reidel, who confirmed that only Nesovitrea hammonis was present.

Gyraulus. Many species of Gyraulus have been described from Russia, a recent review listing no less than 32 different
Fig. 5. Species of *Vallonia* represented at Basovo: (1a–d) *V. tenuilabris*; (2a–d) *V. cf. chinensis*; (3a–d) *V. pulchella*; (4a–d) *V. costata*; (5a–d) *V. kamtschatica*.

Fig. 6. The species of *Vertigo*, *Gastrocopta* and *Carychium* represented at Basovo: (a) *Vertigo genesii*, (b) *V. pygmaea*, (c) *V. geyeri*, (d) *V. alpestris*, (e) *V. microsphaera*, (f) *V. antivertigo*, (g) *V. extima*, (h) *V. parcedentata*, (i) *Gastrocopta theeli*, (j) *Carychium pessimum*. 
species as occurring there (Prozorova, 2003), rather more than recognised in earlier studies (Meier-Brook, 1983). At Basovo, three species of *Gyraulus* appear to occur. The first, represented by occasional shells, has strong spiral sculpture and appears to be *G. albus* (Müller). The identity of the remaining two taxa proved somewhat problematic. One has rather rapidly expanding whorls, a slight angulation on the periphery and a relatively smooth shell (Figs. 7, 1a–d). In the other species, the whorls expand more slowly, the periphery is rounded and the shell is ornamented by distinct fine ribbing (Figs. 7, 2a–d). The former has been identified as *G. acronicus* (Férussac) and the latter *G. rossmaessleri* (Auerswald), which may have been recorded as *G. kruglowiae* Johansen in the Russian literature.

*Lymnaeidae*. Reliable identification of immature specimens belonging to this family is a common problem and the recent recognition of a number of cryptic species in the modern European fauna has made the matter worse. In the present study, the problem is exacerbated further by the fact that a number of regional forms have been given names and it is still unclear which of these represent valid taxa (cf. Kruglov and Starobogatov, 1993a, b). Attribution to particular genera (i.e. *Stagnicola*, *Radix*, *Galba* or *Lymnaea*) is relatively straightforward but finer taxonomic distinctions are tentative. Illustrations are given of the tall form of *Galba truncatula* and other lymnaeid taxa left in open nomenclature (Fig. 8a–c).

*Succineidae*. A notorious group to identify without anatomical characters. At least three species of succineid are present at Basovo. Shells attributed to *Succinella oblonga* are distinguished by their more elongate shells with relatively taller spires. Two other species are present, one with tight coiling and a more pointed apex (Fig. 8f–i) and another that has a distinctly bulbous apex (Fig. 8j and k). These are not distinguished in the graphs or tables, where they are both listed as cf. *Oxyloma/Succinea*; identification to species requires further work.

Fig. 7. Two species of *Gyraulus* from Basovo: (1a–d) *G. acronicus*; (2a–d) *G. rossmaessleri*. 
Pisidium. All the specimens were identified by Dr. J.G.J. Kuiper.

4.2.2. Analysis of the molluscan succession

The floodplain sequence at Basovo contains abundant shells throughout much of the profile, which appears to span the entire Holocene (Fig. 9). The 50 (2.5 l) sediment samples processed yielded over 72,500 specimens belonging to at least 28 terrestrial and 23 aquatic taxa. All of the samples were fossiliferous, 17 of which provided $>200$ shells, 15 contained 200–1000 shells and 18 samples furnished $>1000$ shells; the richest sample yielded ca 7500 shells. *Vallonia* dominates the record, represented by over 51,000 specimens or 72.5% of the entire assemblage. The extraordinarily high shell counts bestow great confidence in the data, allowing the recognition of clear trends that have real ecological meaning, rather than the result of statistical artefacts. The large sample sizes also facilitated the consistent recovery of rare species that occur at frequencies of $<1\%$.

The molluscan succession (Figs. 10 and 11) can be divided into six local mollusc zones (Bsv1–Bsv6). The zone boundaries were initially drawn by eye but the data were subsequently subjected to a Two-Way Indicator Species Analysis (TWINSPAN; Hill, 1979), which produced reassuringly similar results. The principal difference observed between these so-called ‘subjective’ and ‘objective’ zonation techniques is found in Zone Bsv6, where several samples were grouped within other zones delineated by TWINSPAN. Low shell abundance in some of the samples from Zone Bsv6 may account for this discrepancy. The assemblages are thought to reflect communities that lived on the floodplain, rather than including significant elements carried downstream. The faunal fluctuations are therefore regarded as reliable indicators of local floodplain ecology. The molluscan zones at Basovo are characterised as follows.

**Zone Bsv1: 200–250 cm ($>10,000^{14}C$ yr BP).** This represents the earliest molluscan assemblage recovered at Basovo. The lowermost levels yielded few shells, so the...
character of the assemblage is defined by its upper part, where some 25 taxa are represented. Dominant land snails include *Vallonia tenuilabris* (ca 25%), *V. cf. chinensis* (declining to ca 5% from values of ca 40%), *V. kamtschatica* (showing a steady increase from about 5% to ca 50%), *Punctum pygmaeum* (up to ca 20%) and *Vertigo extima* (ca 8%). Subordinate terrestrial taxa (ca 5%) include *Oxyloma/Succinea*, *Pupilla muscorum*, *Succinella oblonga* and *Vertigo alpestris*, together with catholic species such as *Cochlicopa cf. lubrica*, *Nesovitrea hammonis*, *Euconulus fulvus* agg. and *Deroceras/Limax*. Aquatic taxa are less common although they increase in relative frequency in the upper 10 cm of this zone. *Galba truncatula*, *Radix* sp. *A. Gyraulus acronicus*, *G. crista*, *Musculium lacustre*, *Pisidium henslowanum*, *P. subtruncatum*, *P. nitidum*, *Sphaerium* sp., *Valvata aliena* and *V. macrostoma* were represented. Most of these species belong to the ‘slum group’, as defined by Sparks (1961), and suggest the presence of pools on the floodplain. The molluscan assemblage on the whole is characteristic of cool and moist conditions, with open-ground and marsh habitats. No radiocarbon dates are available from this zone but from its context it appears to date from the Late glacial (>10,000 14C yr BP).

**Zone Bsv2: 170–200 cm (9450–8260 14C yr BP).** Major changes occur within this zone, which is the most species-rich of any in the entire sequence. At least 38 species have been recovered, which is overwhelmingly dominated by terrestrial taxa (>95%); aquatic taxa are rare (Fig. 9). The base of the zone is defined where values of *V. kamtschatica* exceed 55% and those of *V. cf. chinensis* fall below 5%. At or near the lower boundary, significant declines are also seen in *Vertigo extima*, *P. pygmaeum* and *Deroceras/Limax*, whereas the decrease in the relative frequency of *Vallonia tenuilabris* does not occur until the middle of the zone. Conversely, a number of new species appear or expand at or towards the base. These include *V. costata*, and a little later *V. pulchella*, *C. cf. lubrica*, *N. hammonis*, *E. fulvus* agg., *S. oblonga*, *Vertigo microsphaera* and *Discus ruderatus*. A range of other species make their first, or in some cases only, appearance in this zone but at much lower frequencies. These include *Vertigo parcedentata* and *Columella columella* (only appearances), *Vertigo geyeri*, *Gastrocopta theeli* and *Bradysbaena cf. schrencki*. These faunal changes indicate a shift towards drier conditions from the base to the middle of the zone but a reversion to wetter conditions is evident towards the top. This is reflected most clearly by the changing frequencies of the *Vallonia*, especially the antipathetic behaviour of *V. costata* and *V. pulchella*, the sharp rise of *V. cf. chinensis* to values of >60% and the corresponding decline in *V. kamtschatica* from about 55% to less than 5%. AMS radiocarbon dates provide bracketing ages for this zone, with a mean pooled average of ca 9450 14C yr BP (based on three dates) near the lower boundary and 8260 14C yr BP at the upper boundary.

**Zone Bsv3: 135–170 cm (<8260 to >6350 14C yr BP).** Shell abundance reaches a maximum in the middle of this zone (>6000 shells/2.51 sample) but the number of species falls progressively from at least 37 at its base to 24 at the top (Fig. 9). Compositional changes within the genus *Vallonia* are again prominent features defining zonal boundaries. The lower boundary is defined by the abrupt rise in the frequency of *V. pulchella* to values above 25%. However, it is *V. cf. chinensis* that continues to dominate the assemblage, particularly early on, where it occurs at frequencies of about 40%, declining to half these values
towards the top of the zone. *Vallonia tenuilabris* undergoes more modest but sustained rises (up to 5%), whereas *V. kamtschatica* and *V. costata* now only occur at relatively low frequencies. Other species of dry-ground, such as *Vertigo alpestris* and apparently *V. microsphaera*, also decline or disappear. These changes indicate the development of a wetter environment, a conclusion strengthened by the increases in marshland taxa such as *Oxyloma/Succinea* and *V. extima*, especially towards the top of the zone. The transient occurrence of the hygrophilous species *Zonitoides nitidus*, near the lower zonal boundary, pinpoints a period when conditions became particularly wet. Two other hygrophiles, *Carychium pessimum* and *Vertigo genesii*, also appear in low numbers near the lower boundary of the zone and *Vertigo antivertigo* persists at low frequency. A number of other terrestrial taxa found in the underlying sequence are either no longer present (*S. oblonga*, *Vertigo alpestris*, *V. geyeri*, *V. parcedentata* and *C. columella*) or occur only as occasional shells in the lower part of this zone (*V. microsphaera*, *B. cf. schrencki* and *G. theeli*). Aquatic taxa are relatively abundant and comprise ca 30% of the total assemblage near the top of the zone. The dominant aquatic species are members of the slum group, especially *Anisus leucostoma*, *Aplexa hypnorum* and *Pisidium casertanum*. These slum taxa, which typically inhabit small water bodies subject to stagnation and considerable temperature variations (Sparks, 1961), suggest the existence of small ephemeral pools on the floodplain and support other evidence of relatively wet conditions. Other aquatic taxa include *Stagnicola* sp., *Radix* sp. B and *Gyraulus rosmasaetzleri*. Bracketing AMS radiocarbon dates provide a maximum age of $<8260^{14} \text{Cyr BP}$ at the lower boundary of the zone and a minimum age of $>6350^{14} \text{Cyr BP}$ at the upper boundary.

**Zone Bsv4: 100–135 cm (6350–3380^{14} \text{Cyr BP})**. Compositional changes continue in this zone, which has high species richness but only moderate abundance (Fig. 9). Again, *Vallonia* is dominant, represented by the sustained presence of *V. pulchella* (up to ca 20%) together with increases in both *V. kamtschatica* (up to ca 40%) and *V. costata* (up to ca 20%). *Vallonia cf. chinensis* continues at moderate frequencies (up to ca 25%), but *V. tenuilabris* declines abruptly and is absent for most of the zone. Particularly noteworthy is the recurrence of *V. costata*, which indicates a renewed period of drier conditions. *Vallonia pulchella*, however, continues in relatively high numbers, suggesting the persistence of some moister habitats on the floodplain. These changes in proportions of *Vallonia* coincide with marked decreases in *Oxyloma/Succinea* and *Vertigo extima*, taxa associated with wet conditions. It is interesting to note that *Pupilla muscorum*, which is here represented by a large form, also shows a decrease, behaving in sympathy with marshland taxa. *Zonitoides nitidus* again makes a transient appearance at
the base of this zone, just preceding the *V. costata* rise. Catholic species show minor increases, and greater species richness is accounted for by the recurrence of *D. ruderatus*, *B. cf. schrencki*, *G. theeli*, *V. microsphaera*, *V. antivertigo* and *V. pygmaea*, as well as the first sustained presence of *C. pessimum*. Aquatic taxa show a significant reduction in the dominance of slum species but *G. truncatula* increases, as does *G. acronicus*. The assemblage indicates moderately dry conditions, although still moist enough for wet-ground species such as *V. pulchella*. Bracketing AMS radiocarbon dates provide an age of 6350 14C yr BP for the lower boundary and an upper age of 338014C yr BP. Towards the upper boundary, the number of shells falls dramatically, possibly a result of acidification of the sediment by percolating water from the overlying charcoal layer.

**Zone Bsv5: 65–100 cm (−2800 to >1520 14C yr BP).** This zone represents a period of increased instability and marks a trend towards reduced shell abundance and species richness (Fig. 9). In the terrestrial component, *V. kamtschatica* (30–40%) and *V. pulchella* (ca 20%) occur in relatively high numbers, whereas *V. cf. chinensis* and *V. costata* become increasingly rare. *Vallonia tenuilabris* percentages increase throughout this zone (up to ca 35%). Other terrestrial species, such as *Oxyloma/Succinea* (10–18%), *V. extima* (10–17%), *N. hammonis* (up to 10%), *E. fulvus agg.* (5–10%) and *D. ruderatus*, also show increases, but *B. cf. schrencki*, *S. oblonga*, *C. pessimum*, *V. microsphaera*, *V. pygmaea* and *V. geyeri* only occur sporadically. The aquatic fauna is dominated by *G. rossmaessleri*, *A. hypnorum*, *G. truncatula* and *Stagnicola* sp. The greatest number of aquatic species occurs in the lower part of this unit, which includes *Gyraulus acronicus* and *G. crista*, *Valvata macrostoma*, *Anisus leucostoma*, *Radix* sp. B, *Musculium lacustre* and *Pisidium* spp.
The dominance of wet-ground taxa indicates the presence of moist, open meadows and marsh habitats on the floodplain. Bracketing AMS radiocarbon dates provide a maximum age of <2800 ¹⁴C yr BP (mean pooled average of four dates) for the lower boundary and an age of >1520 ¹⁴C yr BP (average of two dates) for the upper boundary of this zone.

Zone Bsv6, sub-zones A and B: 0–65 cm (1520 ¹⁴C yr BP to the present). Zone Bsv6 is divided into two sub-zones given the limited shell abundance in the upper (A) portion. The lower (B) component is represented by comparatively low numbers of molluscs and variable species richness (Fig. 9). The terrestrial fauna is again dominated by Vallonia, including V. kamtschatica (up to 70%) and V. costata (up to 30%) and to a much lesser extent V. tenuilabris (up to 7%). Vallonia pulchella and V. cf. chinensis become increasingly rare or absent, providing further evidence of increasingly drier habitats on the floodplain. Catholic species such as Deroceras/Limax, P. pygmaeum, C. cf. lubrica, N. hammonis and E. fulvus agg., as well as Oxyloma/Succinea, V. extima and P. muscorum, also occur in this sub-zone. The aquatic fauna is poorly represented, occurring primarily in the lower portion of sub-zone B and including Gyraulus spp., A. hypnorum, A. leucoostoma, G. truncatula, M. lacustre and Pisidium spp. Valvata macrostoma occurs at the top of this sub-zone. The few terrestrial species from sub-zone A include V. kamtschatica, V. costata, V. tenuilabris and V. pulchella, Deroceras/Limax, P. pygmaeum, Vertigo spp. and C. pessimum. An apparently high aquatic percentage for sub-zone A is explained by very low mollusc totals in some samples. Aquatic taxa from sub-zone A include G. truncatula, Gyraulus spp., V. macrostoma, A. leucoostoma, Radix sp. B, M. lacustre and Pisidium spp. Despite the decline in shell numbers, the species in this zone appear to impart an ecological signature, perhaps indicating a return to increasingly drier conditions from ca. 1520 ¹⁴C yr BP until the present. Alternatively, greater anthropogenic activity on the floodplain in historic times could have altered the natural composition of the molluscan population in Zone Bsv6.

4.2.3. Species of particular taxonomic, ecological and biogeographical interest

A number of noteworthy species encountered at Basovo deserve special mention.

Vallonia tenuilabris (A. Braun, 1843). This species (Figs. 5, 1a–d) reached western Europe during cold stages of the Pleistocene, where it is said to be typical of cold, dry and open habitats, forming the so-called ‘cold steppes’ (Ložek, 1964). Today, it is extinct in Europe but is widespread throughout northern Asia, from northern India, Tibet and Kazakhstan, eastwards to China and northwards into Mongolia and Russia as far as northern Siberia (Gerber, 1996). Its Pleistocene occurrences in Europe suggest an association with cold treeless landscapes and it now certainly extends into treeless tundra as well as montane steppe, where it inhabits grassland and lives under stones. It also has a broad altitudinal range, extending from lowland habitats to over 4500 m in the Central Asian mountains. However, in southern Siberia it also occurs in mixed forest of the taiga biome (Schileyko, 1984, pp. 169), and we have found it living at high frequencies in woodland consisting of pine, larch, willow and poplar at several sites to the east and west of Lake Baikal.

Vallonia kamtschatica Likharev, 1963. This species (Fig. 5a–d), originally described as a subspecies of V. cyclophorella, is apparently known from the Miocene of China but otherwise only as modern shells (Gerber, 1996). It is confined to Asia and has a modern distribution stretching from the Yenisei River in the west, through central and eastern Siberia to the Pacific Coast, including Kamchatka, the Kuril Islands and Hokkaido, as well as Mongolia and northern China (Gerber, 1996). Little is known about the ecology of V. kamtschatica, having only been described as associated with sparse birch and poplar forests, as well as with grassy vegetation and in rocky environments (Gerber, 1996). In the upper Lena valley, we found it living in dry habitats, including scree and grassland. Its behaviour in the sequence at Basovo, where it fluctuates broadly in sympathy with V. costata, likewise indicates a xerophilous preference.

Vallonia cf. chinensis Suzuki, 1944. This species (Figs. 5, 2a–d) was originally described from Middle Pleistocene sediments (Kuhsiangtung Formation) at Harbin, China (Suzuki, 1944). Unfortunately, the type series was destroyed during World War II, leaving only Suzuki’s description and illustrations. Gerber (1996) subsequently used these to identify 12 specimens from China (South Gansu, ‘near Saksagir River’) and one from the Amur region of the Russian Far East as V. chinensis, the only known examples of this species before the recovery of those described here. Since it has not been possible to make direct comparisons with specimens from the type locality, the identification of those from Basovo must remain tentative. At Basovo, 3735 adult specimens of Vallonia were attributed by Dr. Jochen Gerber to V. cf. chinensis, making it by far the largest sample of this species known. If correctly identified, these constitute the most westerly records of this species within northern Asia, suggesting that V. chinensis has a much wider range than previously supposed. There is no direct ecological information known for this species but its behaviour at Basovo, where it fluctuates in sympathy with V. pulchella, suggests that it likes damp open-ground.

Vertigo extima (Westerlund, 1877). This species (Fig. 6g) was originally described as a variety of V. arctica (Wallenberg, 1858) from Baklanowskii in Siberia. Until recently, it was only known from its type locality and was overlooked by most workers. Waldén (1986) demonstrated the validity of this species and gave details of additional
scattered localities in montane regions of northern Scandinavia, Arctic and sub-Arctic Siberia and westernmost Alaska (from where it had been described as *Vertigo modesta ultima* Pilsbry). *Vertigo extima* favours wetlands and humid stream valleys with a rich vegetation of herbs; it also occurs in *Salix* scrub and in moist parts of birch woodland (Waldén, 1986; Pokryszko, 2003; von Proschart, 2003). These habitat preferences accord well with its behaviour at Basovo, where it occurred throughout most of the Holocene, often at relatively high frequencies (ca 10% of the assemblage), showing a sympathetic relationship to the Succineidae. We found living populations of *V. extima* in a calcareous fen in the Maloe More region of western-central Baikal and in damp grassland habitats bordering birch woodland with larch and pine near Burdukovo (Fig. 1). We also found Holocene fossils of *V. extima* in nearby floodplain sediments of the Selenga River. These occurrences constitute the most southerly yet recorded for this species. It is likely to be more widely distributed in the region; the lack of previous records certainly results from its conflation with *Vertigo modesta*.

*Vertigo genesii* (Gredler, 1856), *V. geyeri* Lindholm, 1925 and *V. parcedentata* (A. Braun, 1847). These three species (Fig. 6a, c and h, respectively) are all typical of wetlands, especially those of high base status, such as calcareous fens or flushes formed in the vicinity of springs. According to Pokryszko (2003), none of these species has hitherto been found outside Europe, so these fossil records represent their first representation in Asia and an enormous extension of their known range. We have also recently found *V. genesii* living at several sites in the upper Lena River valley and in the Maloe More region. Living populations of *V. genesii* have also just been reported from the Russian Altai (Pokryszko and Horsák, 2007). In several Russian textbooks (e.g. Likharev and Rammel’meier, 1962), *V. geyeri* is regarded as merely a form of *V. genesii*, which itself is often thought to be a synonym of *V. modesta* (e.g. Schileyko, 1984). Even greater confusion has surrounded the differentiation of *V. genesii* and *V. parcedentata*, which have also been regarded as synonyms. They are, however, clearly different but this distinction has yet to be made in any identification manual, either in eastern or western literature. Older published records of *V. parcedentata* must therefore be treated with great caution. In Europe, genuine *V. parcedentata* is known as a fossil (Late Weichselian or early Holocene) from central Europe (Ložek, 1964) and southernmost Sweden (von Proschart, 2003). However, it is known living from only four sites in Dovrefjell in southern Norway, each of which are open fens of soligenous or mixed character lying between 990 and 1210 m a.s.l. (Pokryszko, 1993). The vegetation at each of these sites varied, the common feature being the abundance of plants indicative of rich conditions, together with luxuriant moss cover. Even in these optimum habitats, *V. parcedentata* occurred at extremely low densities (together with *V. genesii*), a feature it shares with its occurrence at Basovo. Indeed, had not such large samples been processed, it is likely that this species would have remained undetected. We have yet to find *V. parcedentata* living in the Baikal region although more extensive fieldwork may eventually demonstrate its presence. However, it has recently been reported living in the Altai Mountains, about 1300 km to the southwest (Pokryszko and Horsák, 2007).

**Vertigo microsphaera** Schileyko, 1984. This species (Fig. 6e) resembles *V. substriata* from which it can be distinguished by its smaller size (holotype: 1.8 mm in height, 1.1 mm in breadth), presence of only one parietal tooth and stronger ribbing on the body-whorl (Schileyko, 1984). The original description was based on just two specimens from the North Pacific: the holotype from the vicinity of Podutesnaya Bay, Bering Island, where it occurred in rock crevices with *V. modesta*, and a paratype from a bamboo thicket on Shikotan Island, where it occurred with *V. hirasei* (Schileyko, 1984). It has subsequently been found living among forest leaf-litter and bamboo (*Sasa kurilensis*) covering slopes in the southern Kuril Islands (Prozorova, 2002) and commonly at high elevations in the Altai Mountains (Pokryszko and Horsák, 2007). We have also found *V. microsphaera* living at several sites to the west and southeast of Lake Baikal, where it occurred in a variety of habitats including wetland, damp grassland bordering coniferous forest and leaf-litter in birch–hazel woodland. Prior to its fossil discovery at Basovo, it had never previously been found in Siberia. In addition, we have found it in Holocene sediments in the Kirenga valley, about 125 km due east of Basovo, and near Burdukovo in Trans-Baikal (Fig. 1).

**Gastrocopta theeli** (Westerlund, 1877). According to Likharev and Rammel’meier (1962), this species (Fig. 6i) occurs in three distinct parts of the former USSR, namely the southern Maritime Territory, near the city of Yeniseysk, Siberia and in the tributaries of the Rion River (Transcaucasia). Schileyko (1984) lists records from the southern Primorye (Primorskiy Kray), Yeniseysk, Chelabinsk, the southern Altai, the high mountains of Daghistan and the northern Caucasus. It is also known from Korea, China and Pakistan, where it occurs at numerous sites in FANA, NW Frontier, Baluchistan and Punjab Provinces (B. Pokryszko, unpublished data). Ecologically, it prefers wooded, shady and humid places but seems to be indifferent to the substratum, which may range from limestone to granite. During the Pleistocene, it occurred in eastern Siberia and had a range that extended into western Europe (Ložek, 1964) but it is unknown there in later deposits. Particularly relevant to the present study is the recent reporting of *G. theeli* from other Holocene sequences in a wide area from the Muya-Kuanda and Tunka depressions in the Baikal Rift Zone, through the Cis-Baikal Trough near Irkutsk, to the Lena River valley within the high Upper Lena Plateau (Filippov et al., 2000).
At a site near Urik (Fig. 1) above the floodplain of the Urik River (Angara River drainage basin), it occurred in a rich molluscan assemblage of 37 species and represented 4.4% of the total shells. This frequency is far higher than its occurrence at Basovo, where it never exceeds 1% of the assemblage, but the sample size is far lower and it is likely that juvenile shells from Urik were not counted exhaustively. In the Lena River valley, G. theeli was previously found in late Holocene sediments of the low (3.5 m high) floodplain terrace near the Elovka River mouth, 55 km downstream of Ust-Kut (Fig. 1). Here the assemblage was dominated by bivalves and G. theeli represented only 1% (Filippov et al., 2000). We have found G. theeli at similarly low frequencies in Holocene floodplain sediments in the Kirenga valley and in the Selenga valley near Burdukovo (Fig. 1) but this species has yet to be found living in the Baikal region.

_Pupilla muscorum_ (Linnaeus, 1758). The specimens from Basovo were relatively large, with tumid whorls and an aperture generally lacking teeth. Such forms are typical of marshes and moist grassland, a conclusion supported by its behaviour at Basovo, where its highest frequencies coincide with wetland phases. _Pupilla_ is notoriously variable and several varietal names have been proposed for what are often regarded as ecophenotypes. One of these, which differs from typical _muscorum_ by virtue of its broader and thinner shell, has recently been shown on the basis of molecular (and other) data to be specifically distinct (von Proschwitz et al., 2007, n.d.). They assign such forms from calcareous fens to _Pupilla pratensis_ (Clessin), which occurs in central Europe and Scandinavia, and we have found it living in scattered localities across the Baikal region. However, the Basovo specimens appear to belong to _P. muscorum_, despite their breadth.

_Carychium pessimum_ Pilsbury, 1901. This species was formerly regarded as a form of _C. sibiricum_ Westerlund but its shell is narrower and more slender (Fig. 6j). According to Likharev and Rammel’meier (1962), it occurs in the southern Maritime Territory of the Russian Far East, as well as in Japan and Korea. At Basovo, it was present only after ca 8260^{14}C yr BP and generally occurred in low numbers. Near Burdukovo, we found it living in damp habitats, including some with heavy shade but always in relatively low numbers. It was also present in the uppermost level at Basovo, suggesting that it probably still lives at the site today.

_Discus ruderatus_ (Férussac, 1821). This boreo-montane species lives in coniferous woods, marshes and moist grassland. It has an enormous range extending east from central Europe and Scandinavia right across the Palaearctic region as far as the Pacific coast. Forms in North America may be conspecific, so its range may eventually prove to be Holarctic. Throughout much of the western part of its range, _D. ruderatus_ shows little variation in shell form but in the east it becomes extremely variable, particularly with respect to the height of the spire and the extent of angulation of the periphery. This has resulted in the description of a number of subspecies, the validity of which has still to be satisfactorily resolved (cf. Umiński, 1962). Most of the specimens from Basovo have a smooth apical microsculpture and a rounded whorl periphery although a few had slight angulation.

_Bradybaena cf. schrencki_ (Middendorff, 1851). Only immature and broken shells of _Bradybaena_ were recovered as fossils at Basovo, rendering the attribution to this species somewhat tentative. However, adult modern shells were also found near the site resembling _B. schrencki_. According to Schileyko (1978), _B. schrencki_ occurs in northeastern Europe, Siberia, the Altai and Kamchatka where it lives in humid forest areas and open spaces not far from water with high grass and bushes.

### 4.3. Vertebrates

Although not common, small vertebrate remains were recovered from much of the sequence at Basovo. Preservation of the bone material was generally good, with some physical breakage, but little sign of soil corrosion, rounding or weathering. Several bones were leached by root action and affected by manganese concretions, which form a coating on surfaces, implying burial under damp conditions. Good preservation of some particularly fragile specimens indicates lack of transport or post-mortem breakage, suggesting that the bones were buried rapidly in a low-energy depositional environment. A number of the microtine molars show evidence of corrosion by gastric juices, indicating that some remains were deposited at the site by predators, probably in the form of regurgitated pellets of birds of prey or in the faeces of mammalian carnivores. Digested bones occur throughout the section with no concentration at any particular level. This suggests that although predators brought some of the bones to the site, not all the remains were necessarily introduced in this way. The most abundant bones are of small mammals, representing at least seven species (Table 2; Fig. 12).

The earliest identifiable vertebrate records are from Unit 3, dated between ca 9450 and 8260^{14}C yr BP, and include the flat-skulled shrew _Sorex roboratus_ and a tooth resembling that of the Ungar vole _Microtus maximowiczii_. _Sorex roboratus_ occurs throughout Siberia, extending from the Pacific Coast west as far as the Ob River and south to Vladivostok, Lake Baikal and Mongolia, although its associated habitats are still poorly documented (Corbet, 1978). Hoffmann (1985) describes the holotype as having been captured in dense pine forest near the Kolyma River mouth in northeast Siberia. The occurrence of the _M_. _cf._ _maximowiczii_ is noteworthy since its modern range is apparently restricted to an area extending from the eastern shore of Lake Baikal to the upper Amur Basin (Corbet, 1978; Gromov and Polyakov, 1992). _M. maximowiczii_ is
known from only a few localities in that region, the closest of which is over 200 km east of Basovo. Previously, it had never been found west of Lake Baikal.

The identification of the Basovo specimen is somewhat tentative because the dentition of *M. maximowiczii* is only distinguishable by size from its sibling species, the Manchurian reed vole *Microtus fortis* (Orlov et al., 1974). Nothing is known about possible size differences that may have existed between these two taxa during the early Holocene and a larger sample from Basovo is needed to

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**Table 2**

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Fish</th>
<th>Amphibian</th>
<th>Small mammal</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–5</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>5–10</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>Rodent: mandible frag.</td>
</tr>
<tr>
<td>10–15</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>?Fish: tooth.</td>
</tr>
<tr>
<td>15–20</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>Indet.</td>
</tr>
<tr>
<td>20–25</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>Microtinae: upper incisor.</td>
</tr>
<tr>
<td>25–30</td>
<td>2</td>
<td>–</td>
<td>1</td>
<td>Microtinae: molar frag, RC.</td>
</tr>
<tr>
<td>30–35</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>Microtinae, upper incisor.</td>
</tr>
<tr>
<td>35–40</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Indet.</td>
</tr>
<tr>
<td>40–45</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>Femur (prox).</td>
</tr>
<tr>
<td>45–50</td>
<td>–</td>
<td>–</td>
<td>2</td>
<td><em>Aredolca terrestris</em>: LM1; Microtinae: lower incisor (juv).</td>
</tr>
<tr>
<td>50–55</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>Microtinae: upper molar frag.</td>
</tr>
<tr>
<td>55–60</td>
<td>1</td>
<td>–</td>
<td>2</td>
<td>Fish: vertebrate; Microtinae: lower incisor, RC; Small mammal: phalanx.</td>
</tr>
<tr>
<td>60–65</td>
<td>–</td>
<td>–</td>
<td>9</td>
<td>Soricidae: humerus (distal); <em>Sicista betulina</em>: LM3; small mammal: phalanx, metapodial (x3), caudal vertebra, ulna, radius (shaft &amp; prox).</td>
</tr>
<tr>
<td>65–70</td>
<td>–</td>
<td>–</td>
<td>73</td>
<td><em>Sorex minutus</em>: L lower incisor, R lower incisor, L &amp; R mandible frags (ascending ramus), L mandible with M1 (M2 and unicuspid isolated), probably all from the same individual; <em>Sicista betulina</em>: 5 including 2 molars in maxilla frag; Small mammal: ulna frag, rib (x5); mandible frags. (x2), humerus (prox epiph), skull frag., metapodial (x8), astragalus (x3), calcaneus (x3), vertebra (x8), phalanges (x23), tibia (x2 distal &amp; most of shaft), humerus (x2), radius (complete), innominate frag, incisor frags (x7).</td>
</tr>
<tr>
<td>70–75</td>
<td>9</td>
<td>–</td>
<td>2</td>
<td><em>Sicista betulina</em>: maxilla with LM5; Small mammal: incisor frag (rodent).</td>
</tr>
<tr>
<td>75–80</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>Indet small vertebrate.</td>
</tr>
<tr>
<td>80–85</td>
<td>–</td>
<td>–</td>
<td>5</td>
<td>Small mammal: scapula frag, tibia (shaft), astragalus.</td>
</tr>
<tr>
<td>85–90</td>
<td>2</td>
<td>–</td>
<td>4</td>
<td>Soricidae: upper molar; Small mammal: vertebra frag, phalanx, metapodial.</td>
</tr>
<tr>
<td>90–95</td>
<td>3</td>
<td>2</td>
<td>4</td>
<td>Microtinae: molar frag; Small mammal: vertebra, metapodial, upper incisor frag.</td>
</tr>
<tr>
<td>95–100</td>
<td>–</td>
<td>–</td>
<td>2</td>
<td>Small mammal: tibia (shaft &amp; dist), humerus (prox epiph).</td>
</tr>
<tr>
<td>100–105</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>105–110</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>Muridae?: upper incisor (rootlet corrosion).</td>
</tr>
<tr>
<td>110–115</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Indet small vertebrate.</td>
</tr>
<tr>
<td>115–120</td>
<td>1</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>120–125</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>Fish: vertebrate; Anuran: 1; Microtinae: upper incisor frag.</td>
</tr>
<tr>
<td>125–130</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td><em>Clethrionomys rufocanus</em>: LM1 (digested, juvenile); Indet small vertebrate.</td>
</tr>
<tr>
<td>130–135</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Indet small vertebrate.</td>
</tr>
<tr>
<td>135–140</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>Indet small mammal: phalanx.</td>
</tr>
<tr>
<td>140–145</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Indet small vertebrate.</td>
</tr>
<tr>
<td>150–155</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Indet small vertebrate.</td>
</tr>
<tr>
<td>155–160</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>Anuran: ilium frag; <em>Apodemus</em> sp.: M1, Indet small mammal: ?caudal vertebra.</td>
</tr>
<tr>
<td>160–165</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td><em>Apodemus peninsulae</em>: M1,</td>
</tr>
<tr>
<td>165–170</td>
<td>–</td>
<td>–</td>
<td>4</td>
<td>Microtinae: molar frags (x3); Indet small mammal: metapodial frag.</td>
</tr>
<tr>
<td>170–175</td>
<td>1</td>
<td>11</td>
<td>1</td>
<td>Fish: cyprinid tooth; Amphibian: bone frags (including ilium); Many small frags probably also anuran (not identifiable to element); <em>Microtus</em> sp.: M2.</td>
</tr>
<tr>
<td>175–180</td>
<td>1</td>
<td>–</td>
<td>4</td>
<td>Fish: vertebrate; Microtinae: molar frags (x4).</td>
</tr>
<tr>
<td>180–185</td>
<td>1</td>
<td>11</td>
<td>6</td>
<td>Amphibian (includes anuran ilium); Indet small mammal: metapodial, vertebrae (2), radius (proximal); Microtinae: incisor frag; Soricidae: L. upper incisor, unicuspid.</td>
</tr>
<tr>
<td>185–190</td>
<td>6</td>
<td>10</td>
<td>15</td>
<td>Indet small mammal: femur (shaft with distal end, distal epiphysis), vertebrae frags (2), metapodial, phalanx (2), mandible (2); Microtinae: upper and lower incisor; <em>Microtus</em> sp.: M2 (light digestion), molar frags (2); <em>Microtus cf. maximowiczii</em>: LM1,</td>
</tr>
<tr>
<td>190–195</td>
<td>2</td>
<td>11</td>
<td>11</td>
<td>Indet small mammal: radius (prox), ulna frag, rib frag, caudal vertebra, phalanx (?burned), lower incisor frag, molar frag; <em>Sorex roboratus</em>: L upper incisor; <em>Clethrionomys</em> sp.: molar frag (heavily digested); <em>Microtus</em> sp.: M2,</td>
</tr>
<tr>
<td>195–200</td>
<td>–</td>
<td>–</td>
<td>4</td>
<td>Indet small mammal: femur (prox shaft), upper incisor frag; <em>Microtus</em> sp.: M2, M3,</td>
</tr>
<tr>
<td>200–205</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Indet small vertebrate.</td>
</tr>
<tr>
<td>205–210</td>
<td>1</td>
<td>–</td>
<td>1</td>
<td>Microtinae: molar frag.</td>
</tr>
<tr>
<td>210–215</td>
<td>1</td>
<td>–</td>
<td>1</td>
<td>Fish: vertebrate; Small mammal: ?rub.</td>
</tr>
</tbody>
</table>
confirm that the specimen recovered there is typical. *Microtus fortis* is larger than *M. maximowiczii* and this disparity in body size is reflected in dimensions of the teeth (Gromov and Polyakov, 1992). The Basovo first lower molar can be distinguished from that of *M. fortis* on the basis of its small size (3.02 mm), smaller than that of *M. fortis* (length M1: range 3.3–4.0 mm, mean 3.5 mm), but within the range of *M. maximowiczii* (length M1: range 2.6–3.2 mm, mean 2.9 mm). Ecologically, the Manchurian reed vole and Ungar vole inhabit similar environments with a preference for marshes and riparian areas bordering streams and rivers. *Microtus fortis* is strongly associated with marsh meadow and floodplain meadow along the banks of streams, lakes and marshes. It prefers bushy banks, especially those with abundant fallen logs, and moist meadows overgrown with trees and bushes. According to Ognev (1966), it was found in all locations examined except stoney-strewn steppe, bare mountains and typical taiga. *M. maximowiczii* lives in birch woodland and in tussock-covered marshes and bush thickets along river-banks, but it avoids steppe (Ognev, 1966).

Vertebrate fossils recovered from the lower portion of Unit 4 (<8260 to >6350 14C yr BP) include those of the Korean field mouse *Apodemus peninsulae*, a species typically associated with woodland or scrub, as well as numerous amphibian remains. Those from the upper portion of this unit (<6350 to >2800 14C yr BP) include the grey-sided vole *Clethrionomys rufocanus*, a species that commonly inhabits wet coniferous forests (Kaneko et al., 1998). Remains of northern birch mouse *Sicista betulina* and Eurasian pygmy shrew *Sorex minutus* cluster around the small mammal ‘peak’ near the boundary of Units 6 and 7 (<2800 to >1520 14C yr BP); the bones of *S. minutus* appear to be from the same individual. This species occurs in a wide variety of habitats including woodland, grassland, dunes and heath, and is also tolerant of damper conditions. *Sicista betulina* is typically found in woodland or scrub habitats. Approximately 10 cm above this vertebrate ‘peak’, remains of water vole *Arvicola terrestris* were found. This species indicates more open vegetation and favours wet meadow, marsh and banks of rivers and lakes with sedges and reeds.

The small mammal fauna therefore provides evidence of woodland and riparian grassland or marsh at the edge of the river. The presence of *M. maximowiczii* at Basovo indicates a westwards extension of its range in the early Holocene. The small-scale concentrations of small mammal specimens centred on 65–70 cm and 185–190 cm do not coincide with peaks in the number of digested bones. These can probably be taken to reflect the accumulation of animals that were not items of prey. Sparse remains of fishes and amphibians are also present throughout the sequence at Basovo, although the identification of these specimens is still unresolved.

5. Discussion and conclusions

5.1. Environmental reconstruction of the Basovo site

The results presented above provide a multi-proxy record of floodplain development at Basovo and allow the first relatively high temporal resolution reconstruction of Holocene environmental change in the upper Lena River valley. At the end of the late Pleistocene, gravel (Unit 1) and fine sandy alluvium (Unit 2) accumulated, providing the basal parent materials for the initiation of floodplain
aggradation. The upper portion of these sediments (top of Unit 2) contains a land snail assemblage (Zone Bsv1) dominated by Vallonia tenulabris, V. cf. chinensis, Punctum pygmaeum and Vertigo extima, species characteristic of cool conditions with associated open-ground and marshland habitats.

Sedimentation of Unit 3 occurred in a comparatively low-energy depositional environment, reflected by the fine texture of the loams, with intervening periods of floodplain stability allowing incipient pedogenic horizons (buried soil E) to develop. This cumulic pedogenic sequence was initiated by ca 9450 14C yr BP and although episodically interrupted by the deposition of fine alluvium during low-energy flood events, soil formation processes and hence relative floodplain surface stability continued until 8260 14C yr BP. The malacofauna from this unit (Zone Bsv2) is both abundant and species-rich, dominated by three species of Vallonia, (V. kamtschatica, V. cf. chinensis and V. costata). While the autecology of the former two species remains poorly documented, the last species inhabits open and moderately dry environments. Low frequencies of V. pulchella, Oxyloma/Succinea and V. extima, species associated with wetter conditions, as well as the general absence of aquatic taxa, also point to relatively dry habitats on the floodplain. Of particular interest is the occurrence of V. microsphaera, the first fossil record of this distinctive but poorly known species, as well as V. geyeri and V. parcedentata, which represent the first documented occurrences of these taxa in Asia (cf. Pokryszko, 2003; Pokryszko and Horsák, 2007). In addition, the presence of Ungar vole M. cf. maximowiczii, which is now restricted to the drier Trans-Baikal region, may indicate more extensive forest-steppe during the early Holocene. Wood charcoal (Pinus/Larix/Picea) from Unit 3 suggests the presence of coniferous forests. The data from the early Holocene indicate that the floodplain at Basovo was relatively stable, although subject to episodic low-energy overbank deposition, which allowed pedogenesis to occur in moderately dry and open conditions with nearby coniferous forest.

Increased landscape instability following this period of early Holocene floodplain pedogenic development is indicated by the deposition of relatively coarse alluvium forming the lower part of Unit 4. The malacofauna (Zone Bsv3) is rich in species and is the most prolific in the entire sequence. Terrestrial taxa are again dominated by V. cf. chinensis, as well as V. pulchella, Oxyloma/Succinea and V. extima, the last three species all inhabit wet meadow and marsh habitats. The decline of V. costata to negligible levels supports this ecological interpretation of increasingly wetter conditions. The proliferation of aquatic species such as A. leucostoma and A. hypnorum near the top of this unit indicates the development of ephemeral pools on the floodplain surface. Amphibian remains dominate the vertebrate record from these levels. This interval of floodplain aggradation is bracketed by radiocarbon dates of <8260 and >6350 14C yr BP. These data indicate the development of wetter conditions at the end of the early Holocene and a cessation of pedogenic processes on the floodplain.

The uppermost portion of Unit 4 consists of a pedogenic sequence (buried soils D1 and D2) representing a renewed period of low deposition and relative floodplain stability. The malacofauna (Zone Bsv4) shows a substantial decrease in abundance but still relatively high species richness, except near the upper boundary. Terrestrial taxa are again dominated by open-ground, marsh and catholic species, especially by Vallonia. Of particular interest is the recurrence of V. costata, indicating a return to drier habitats. The abrupt decline in wet-ground taxa, such as Oxyloma/Succinea and V. extima, as well as aquatic species, also indicates a trend towards increasingly drier conditions. Vallonia pulchella, however, continues to exist in relatively high numbers, evidence of rather diverse habitats on the floodplain. Remains of Clethrionomys rufocanus may indicate the presence of moist coniferous forests. Wood charcoal also suggests greater botanical diversity near the site, including mixed coniferous (Pinus/Larix/Picea)-deciduous (Betula and Salicaceae) forest. Sediments from the upper part of this unit yielded pollen spectra indicative of pine forest with grassland. Radio-carbon-dated charcoal again provides bracketing ages for the above sequence (upper component of Unit 4 and Zone Bsv4). The lower boundary is dated at 6350 14C yr BP and the upper boundary to ca 2800 and 3380 14C yr BP, respectively. Thus site data spanning the middle Holocene indicate a period of relative floodplain stability, which promoted pedogenesis under increasingly drier conditions, although microhabitats in the surrounding area were still wet enough to support relatively diverse vegetation complexes and hygrophilous molluscan assemblages.

At the top of Unit 4, a thin lens of charcoal dated to 2790 14C yr BP is thought to represent material redeposited onto the floodplain following a forest fire in the upper Lena River catchment. No evidence was found to indicate that this burning event is related to anthropogenic activity but it resulted in accelerated erosion and increased instability, leading to the downstream accumulation of charcoal-rich loamy sediments (Unit 5) on the floodplain near Basovo. Sediment accumulation rates during the late Holocene (<2800 14C yr BP to the present) are twice those that occurred during the early and middle Holocene (10,000–2800 14C yr BP). Weak pedogenic development then ensued leading to the formation of buried soil C within Unit 5. Radiocarbon dating of wood charcoal from Unit 5 returned ages of 2910 and 2620 14C yr BP, generally consistent with the age obtained from the charcoal layer at the top of Unit 4. The uniformity of these dates suggests that the abundant charcoal present in both Unit 5 and much of the overlying sequence is redeposited from the same burning event that occurred ca 2800 14C yr BP.

Immediately above Unit 5, a renewed period of landscape instability is marked by the deposition of fine sandy loam alluvium, which forms the basal sediments of Unit 6.
The overlying cumulic soil profile (buried soil B) indicates relatively greater floodplain stability but this pedogenic sequence was interrupted by the episodic deposition of fine sandy lenses from brief flood events, particularly near the upper boundary of this unit. Land snails return but only at relatively low frequencies, with V. kamtschatica, V. pulchella, Oxyloma/Succinea and V. extima dominant, indicating a return to wet, open meadow and marsh habitats. The relatively high numbers of aquatic taxa may reflect the periodic inundation of floodwaters. Wood charcoal from the pedogenic horizon in the middle of this unit was dated to 2780 $^{14}$C yr BP, suggesting that it is derived from the burning event reflected by the charcoal horizon at the top of Unit 4. The data indicate that the beginning of the late Holocene was marked by periods of floodplain stability and soil formation under increasingly wet conditions, interspersed with episodic flooding events and the deposition of fine sandy alluvium.

Unit 7 consists of fine sandy loam alluvium weakly altered by two distinct pedogenic profiles (buried soil A and the modern surface soil). The basal sediments from this unit contain the highest percentage of sand in the entire sequence and indicate a significant period of floodplain deposition. Vertebrate remains, especially Sicista betulina, Sorex minutus and Arvicola terrestris, are abundant in these sandy sediments, possibly reflecting a hydrological concentration. A weakly developed buried soil profile occurs above this unaltered alluvium and the overlying modern surface soil delineates the upper boundary of the high floodplain stratigraphic section. The molluscan assemblages (sub-zones Bsv6B and Bsv6A) decrease in both abundance and diversity. Wet-ground taxa, such as V. pulchella, Oxyloma/Succinea and V. extima, decline whereas V. costata becomes a dominant component. These data may suggest a return to drier conditions on the floodplain but anthropogenic activity and cattle grazing may also be factors influencing mollusc abundance and composition. Two charcoal samples from the buried soil horizon of Unit 7 average 1520 $^{14}$C yr BP.

5.2. Broader significance of the Basovo site

The investigation reported here constitutes the most detailed yet undertaken of a Holocene molluscan succession in the entire eastern Palaearctic region. A total of over 72,500 specimens have been analysed from 50 contiguous sampling levels. Previous studies in the Baikal region have essentially been based on the analyses of single or few samples from individual sites and even these have tended to sample using relatively coarse intervals and sieving techniques (i.e. 1 mm mesh), thus mixing sedimentary contexts and missing most of the juvenile specimens. There is virtually no published information and what little exists is often written in extremely obscure Russian reports. One exception is a short paper by Filippov et al. (2000) reporting the discovery of Gastrocopta at a number of Holocene sites in eastern Siberia. This paper provides lists of the associated molluscan faunas and details of the total number of shells counted, although little information about the methodology used and the relative frequencies of the component taxa. Nevertheless, it provides a useful baseline study with which to compare the data from Basovo. Their most productive site (2318 shells analysed) was located in the first (3 m) terrace above the floodplain of the Urik River (Angara drainage basin) at Urik itself (Fig. 1). Here, they recovered 14 species of terrestrial and 23 species of freshwater mollusc, which they state is “the richest thanatocoenosis that has ever been encountered in the Holocene of eastern Siberia” (Filippov et al., 2000, p. 466). The molluscan fauna from Basovo has yielded twice the number of land snail species, although the totals of aquatic taxa are identical. Most of the land snail species encountered at Urik were also present at Basovo, the two exceptions being Carychiium minimum and Vertigo modesta (probably a misidentification of V. genesii, which we found living near Urik). As at Basovo, Vallonia dominates and is said to account for 46% of the assemblage. There is apparently far less congruence when the aquatic faunas are compared but again this may simply reflect different taxonomic traditions, although it seems that their sample included more specimens derived from the river channel rather than its floodplain. These examples bring into sharp focus the urgent need for taxonomic standardisation. It is hoped that the discussion and illustrations of critical taxa provided here will be a step in this direction.

The molluscan assemblages at Basovo show clear successional trends, allowing the reconstruction of environmental conditions on the floodplain throughout most of the Holocene. Several of the taxa encountered are poorly known and little ecological information exists about their habitat preferences. However, these can be inferred from their behaviour in relation to other better-known species with which they are associated. These conclusions will be strengthened when detailed ecological data from Siberia become available for these species. There is always a possibility that the ecological ranges of some taxa may be different in peripheral regions of their distribution. The occurrence of V. tenulabris in woodland habitats in southern Siberia, although supposedly a species of ‘cold steppe’ (Ložek, 1964), serves to emphasise this point.

The molluscan assemblages indicate that conditions on the floodplain at Basovo became increasingly drier at ca 6350 $^{14}$C yr BP. This is clearly a local signal but, interestingly, it appears to coincide with a broader regional trend detected at a number of sites in the Lake Baikal area (Kataoka et al., 2003; Bezrukova et al., 2005a, b, n.d.; Demske et al., 2005; White, 2006; Tarasov et al., 2007; White and Bush, n.d.), Mongolia (Peck et al., 2002; Fowell et al., 2003; Prokopenko et al., 2005, 2007) and across northern China (An et al., 2000; He et al., 2004; Chen et al., 2006; Jiang et al., 2006; Huang et al., 2007), as well as in numerical climate modelling results for Inner Asia (Bush, 2005). It is also significant that this period of increased aridity coincides with major archaeological changes in the
Lake Baikal region (Weber et al., 2002, 2005). It remains unclear whether increasing aridity played a critical role in the abandonment of distinct mortuary traditions by early Neolithic hunter–gatherers and an ensuing ‘biocultural discontinuity’ spanning the seventh millennium BP.

The data from Basovo may also shed light on the extent to which modern animal and plant communities in northern latitudes provide realistic analogues for fossil assemblages from cold stages of the Pleistocene. This issue is of critical importance in climatic and environmental reconstructions of cold stages, which represent over 80% of the last 500 Ka. In mid-latitudes, biotic assemblages from Pleistocene cold stages are often described as ‘arctic’ or ‘arctic-alpine’, reflecting their supposed similarity to modern communities from northern latitudes or high elevations. Pollen analysis, the technique most widely used to reconstruct vegetational history, has inherent limitations as many plants found in northern regions cannot be identified below the level of genus or family (cf. Odgaard, 1999). Some comparative analyses have been undertaken using plant macrofossils (e.g. West, 2000) but virtually no quantitative information exists from many groups of invertebrates, even though invertebrate fossils are usually identifiable to species. The exception is, of course, beetles, which have been studied from a range of Quaternary cold stage deposits, as well as in modern arctic, arctic-alpine and boreal environments in both Eurasia and North and South America (Elias, 1994). The sheer diversity of beetle taxa, coupled with their often highly specific habitat preferences and climatic requirements, has made them particularly valuable palaeoenvironmental indicators.

The molluscan assemblages from Basovo may offer a similarly useful contribution in this regard. The site is located within the boreal forest biome (mountain-taiga) so that the most similar faunal assemblages from the Pleistocene might be expected to be represented by those from interstadial periods rather than the coldest episodes (stadials). Indeed some taxa with Asiatic modern ranges or affinities reached western Europe during cold stages of the Pleistocene, including mammals (e.g. Kahlke, 1994) and beetles (e.g. Coope, 1968), although most species are unlikely to have dispersed such vast distances. Molluscan faunas from stadial episodes in western Europe are generally rather similar and consist of a limited range of hardy species (Succineidae, Columella columella, Pupilla muscorum and Vertigo genesii) that mostly have modern ranges extending into the arctic. Land snail assemblages from interstadial periods are slightly more diverse and in addition include Cochlicopa lubrica, Vallonia pulchella, V. costata, Punctum pygmaeum and Trichia hispida (cf. Holyoak, 1982; Moine et al., 2005). At one early Devensian (Weischelian) site in central-southern England, the assemblage also contained Vertigo substria, Discus ruderatus and Nesovitrea hammonis (Bryant et al., 1983). Assemblages from the Lateglacial interstadial are far better known (e.g. Kerney, 1963; Ložek, 1964; Evans, 1972; Preece, 1998) both from dry-ground and wetland contexts. In wetlands similar to those at Basovo, other species of Vertigo (V. antvertigo, V. pygmaea, V. geyeri) occur together with Euconulus fulvus agg., Vitrina pellucida and Arianta arbustorum. Molluscan assemblages from interstadial episodes in Britain therefore share at least 16 of the 28 species of land snail known from Basovo. At continental sites further east, the similarity will increase, although central European faunas yield species absent from both Britain and Siberia (cf. Ložek, 1964; Moine et al., 2005). However, several of the most common species represented at Basovo are Asiatic forms that have never been found further west, so it would be unwise at present to push this analogy too far.

The Basovo assemblages also contain a number of unexpected species, previously known from only a few sites (V. cf. chinensis, V. microsphaera and V. extima) or else otherwise unknown in Asia altogether (V. geyeri, V. genesii and V. parcedentata) prior to this study. In part, this reflects the limited amount of work undertaken in the region but it must also result from taxonomic confusion. For example, V. genesii and V. extima are likely to be far more widespread than currently supposed and many existing records of Vertigo modesta will undoubtedly prove to be misidentifications of these species. Similarly, regional Asiatic forms of Vallonia (e.g. V. kamtschatica and V. chinensis) are also likely to be seriously under-recorded. Future work should establish whether other taxa, such as G. theeli, still live in the region. It remains to be seen whether the molluscan succession reported from Basovo is typical of the region in general. Nonetheless, this study has provided the first detailed account of the Holocene successional history of non-marine molluscs in the Lake Baikal region and laid the foundation for future work in the eastern Palaearctic.

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Appendix A. Supplementary Material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.quascirev.2008.01.010.

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