Palaeoecological investigations of the landscape inhabited by the early Middle Pleistocene mammoth *Archidiskodon trogontherii* from Chembakchino, western Siberia

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Abstract

A practically complete skeleton of Archidiskodon trogontherii, *of the form with molar teeth characterised by thin enamel, was found in situ in the lower part of the deposits of the Semeikian Suit in the lower reaches of the Irtysh River near the Chembakchino site. The remains of small mammals, insects and plants have been found here associated with the vertebrate find. The nature of the deposits indicates that a large freshwater basin existed in the northern and central areas of the West-Siberian Plain. This lake froze in winter. Small mammals found included* Dicrostonyx ex *gi* renidens-simplicior, Lemmus *cf.* sibiricus *and* Microtus *exgr.* oeconomus. *Their morphology supports the date of 650± "110 Ka years BP obtained by the thermoluminescence method. Palaeomagnetic measurements on the deposits indicate that the remains are of early Brunhes Epoch age. According to results of palaeontological investigations including palaeocarpology, palaeoentomology and the vertebrate fauna, the riverside environment comprised a boggy floodplain with meadow vegetation, shrubs and areas of birch-spruce forest. This environment differs from both the periglacial and modern boreal ecosystems.*

Introduction

A comparison of the results of carpological and palaeoentomological analyses with the evidence of the associated vertebrate fauna allows detailed, objective reconstruction of Pleistocene ecosystems. Plants, insects, large and small mammals characterize the various energy levels in the structure of ecosystems, and, therefore, their distribution is limited by different ecological factors. In taphonomic terms these organisms characterize different processes in the formation of deposits (Borodin,1995). The present work deals with the results of investigation of fossil plants and animals from the Semeikian Suite Formation in the cliff outcrops of Chembakchino Yar. This site is one of the key Quaternary sites in the West-Siberian Plain (Volkova, 1966, Kaplyanskaya & Tarnagradsky, 1974) and is situated on the right bank of the Irtysh River, at 60°N latitude. The section is about 10 km long; the cliff being over 40 m high (Figure 1).

In 1993 an almost complete skeleton of a proboscidean was found in the deposits of the lower part of section, at a point 7 km from Chembakchino, on the right bank of the Irtysh river. It was found in a sand-silt lens within a thick bed of grey clay and was accompanied by the remains of small mammals, fossil insects and plant fragments. The following year additional material was obtained from a similar lens, located approximately 20 m upstream from the site where the elephant was found (Site Chembakchino-94 A). These lenses were at the same stratigraphical level in both exposures and belonged to the lower part of the basal unit of the Semeikian Suite (Kaplyanskaya & Tarnagradsky, 1974). These deposits have been dated by thethermoluminescence (TL) method to 650,000±110,000 years BP in the regional stratigraphical scheme for West Siberia. The strata are normally magnetized, which indicates that they represent the early part of Brunhes magnetic Epoch time (Arkhipov, 1987).

The data obtained allow the definition of the biostratigraphic characteristics of the Semeikian Suite and the reconstruction of the contemporaneous biotopes.

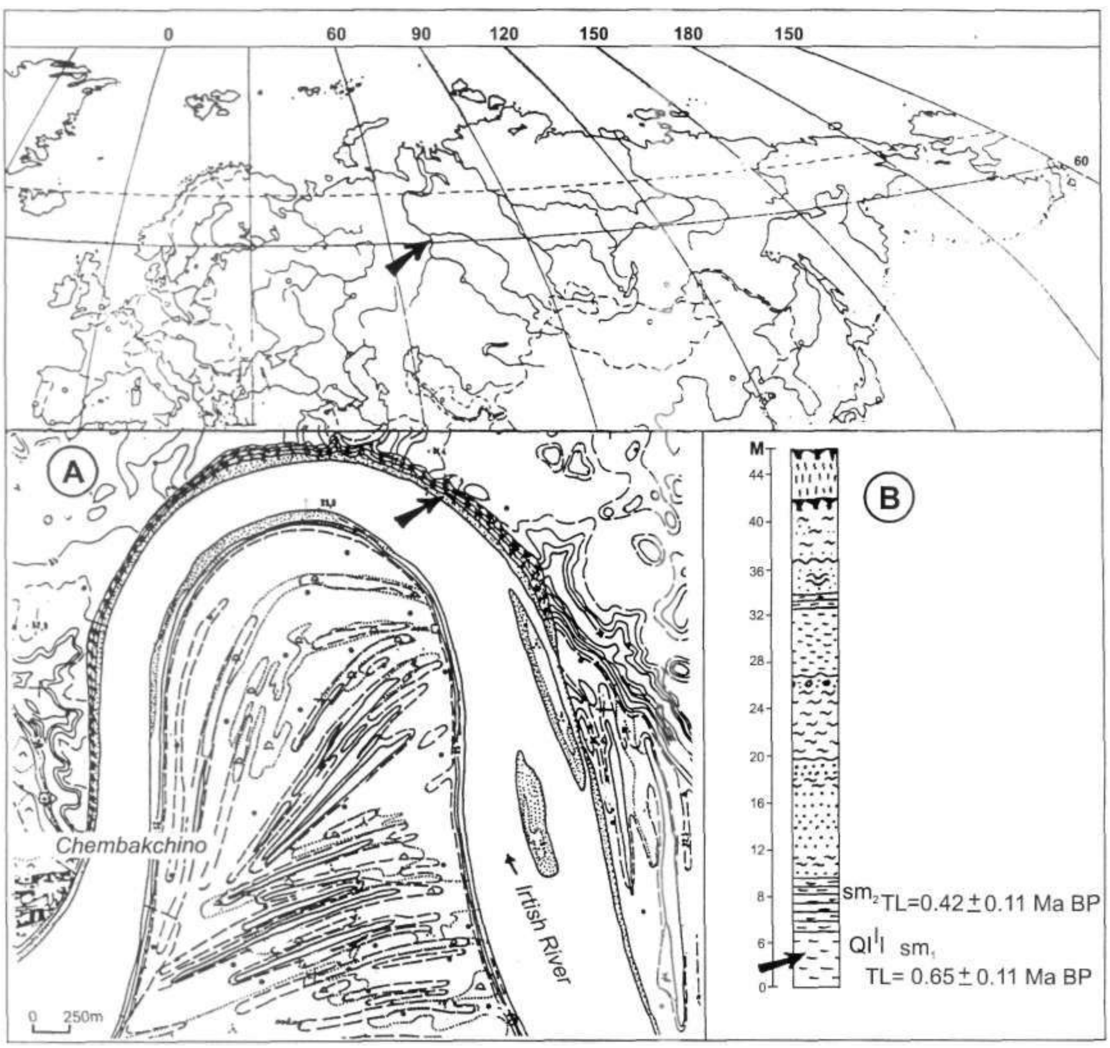

Figure 1
The geographical position ol the cliffs at Chembakchino Yar:
A - the plan of the cliffs;
B - Stratigraphical section showing the beds from which materials were collected. The arrow marks the site where the Archidiskodon trogontherii *skeleton was found.*

Results and discussion

The lens from which the main part of the vertebrate, insect and plant assemblages was collected was 430 cm in length and 35 cm in thickness and formed a lenticular stratified body. In the lower part of the lens the deposits consisted largely of thin layers of clayey gravel and sand, whereas in the upper part they were predominantly silty. Samples of material for analysis were collected from the different layers, which could be distinguished on lithology and colour. In general there was no difference in the composition of the flora and fauna between the different layers, but the concentration of fossil remains varied with the lithology and grain size. The lower layers contained the highest concentration of organic material. As well as the bones of fish and small mammals, some bird bones were found. The remains of insects and plant macrofossils were recovered from all layers of the lens. A comparison of the list of plant and animal species, together with their relative abundance, found in the different layers of this exposure and that from the lens where the elephant was found, further confirms that they belonged to the same stratigraphical level.

Additional information about the age of formation of the deposits was obtained from the morphological analysis of the molar teeth of the vole fossils. These appear to be in accordance with the suggested TL date. *Dicrostonyx* molars showed characteristics intermediate between *D. renidens* Zazhigin, 1974 and *D. simplicior* Fejfar, 1966 (Figure 2). This implies that the faunas are at least older than the Okian Stage (i.e. older than the Elsterian). The presence of the archaic morphotypes of *Microtus* ex.gr. *oeconomus* M/1 also indicates an age in the early part of the Tiraspolian.

The elephant skeleton was embedded in a layer of brown clayey silt with fine light-grey sand; the space between elephant bones being filled with organic detritus, the largest amount of this being beneath the skeleton. Outside the skeleton the organic detritus was absent.

Comparison of the Lower M3 and the postcranial skeleton of the elephant from the Chembakchino site with various published information (Table 1) showed that it was similar in its characteristics to Early Tiraspolian proboscideans from Sussenborn, Germany, and should be identified as *Archidiskodon trogontherii* (Pohling, 1881). As the upper and lower M3 are slightly worn, its AEY (African Elephant Years) age must be over 30 years, and the narrow M/3 and the rostrum mentale probably suggests a female individual.

The peculiar features of the Chembakchino elephant M/3 are a relatively high and narrow crown and the thin enamel. Its hypsodont index is close to the maximum and the crown width to the minimum values. According to the classification of I.V. Foronova and A.N. Zudin, this elephant relates to the group characterized by molar teeth with thin enamel, showing specialized adaptation to periglacial conditions (Foronova & Zudin,1986). These authors assumed that Siberia was the centre of the origin of such a periglacial specialization found in elephant teeth from Northern Eurasia. This specialization had already taken place in early *A. trogontherii.* Thus, the molar structure of the Chembakchino elephant supports the assumption that this elephant and its ancestors might have inhabited steppe (periglacial) landscapes.

Before the ecological conditions under which the elephant lived are reconstructed, the contemporaneous palaeogeographical situation of the West-Siberian Plain requires description. One reconstruction (Arkhipov, 1965, 1987) suggests that Semeikian Suite was deposited during a marine incursion along the low-lying river valleys. Another opinion (Zubakov & Borzenkova, 1983) is that these deposits were laid down in a large lake basin, which formed the south of an ice-sheet margin. Figure 3 shows the possible palaeogeographical conditions at the time of deposition of the Semeikian Suite deposits, according to Arkhipov (1965). There are considerable differences from the modern geographical situation. The nature of the varved clays in the Semeikian Suite suggests that they

Table 1
The sizes of the Archidiskodon trogontherii *IPohlig 1881) M/3. Min Max (mean) values are presented (the number of talons in our case - 4)*

	Localities			
Teeth characteristics	Chembakino, Semeikian suite	Tiraspol (Dubrovo, 1971)	Süssenborn (Dubrovo, 1975)	Data from Garutt & Foronova, 1976
1 Crown length	320	300-410 (351)	225-383 (320)	200-470 (330)
2 Crown width	85	79-115 (95.9)	71-114 (94.8)	82.5-120 (90)
3 Crown height	145	130-173 (153.3)	127-167 (144.6)	125-220 (140)
4 Number of lamellae	20	16-21 (18.8)	16-21 (18.8)	17-23 (20)
5 Lamellae frequency	6.4	4-7 (5.38)	4-8.25 (5.39)	4-9.9 (5.9)
6 Lamellae length	16.2	-	-	11-25 (17)
7 Enamel thickness	2.0	2-3 (2.6)	2-3.3 (2.7)	1.5-3.0 (2.0)
8 Crown height: length ratio	45.3	37-43	38.65-47	42.4
9 Crown width: length ratio	26.6	23.8-29.9	25.2-30.5	27.3
10 Crown width: height ratiio	58.6	59.7-67.5	56.71.7	64.3

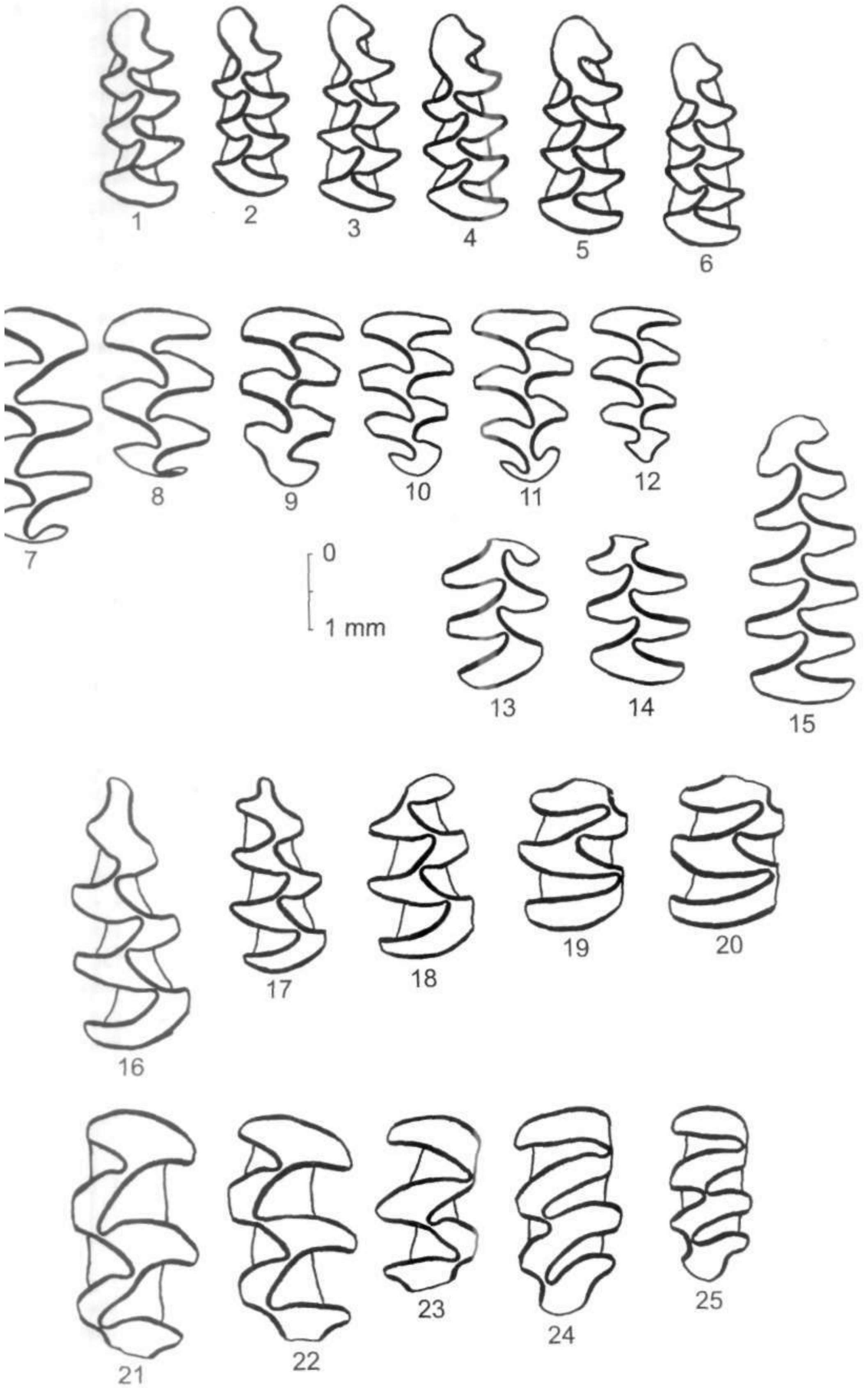

Figure 2
Rodent molar teeth from the Chembakchino - 94 A site: 1-6 - МП Microtus ex *gr.* oeconomus; 7-75- Dicrostonyx *exgr.* renidens-simplicior *(7 -* Ш / , 8 *- M2/6, 9-12-M3/, 13-M/3, 14-M/2, 15 -Щ1);* 16- *25* -Lemmus *cf.* sibiricus *(16, 17-МП, 18-M/2, 19, 20 - M/3,21, 22-Mil, 23 - M2I, 24, 25 - M3I)*

were formed within or on the edge of a lake basin, under conditions characterised by distinct seasonal changes in sedimentation and freezing in winter (Kaplianskaya & Tarnagradsky, 1974).

On the basis of the fish fauna, notably, *Lota lota* L, *Esox lucius* L and members of the Salmonidae and Cyprinidae families, the basin was a freshwater one at least at this latitude. The point of deposition of the sites investigated was probably close to the shoreline. This is particularly suggested by the abundance of beetle remains. Nazarov (1984) records similar mass accumulations of insect material, usually relating to the margin of basins or rivers, where insect remains and detritus are concentrated. At such a point the plant and insect assemblages might consist of material accumulated over a period of several years. The large number of intact insect remains indicates that this fossil material was not re-deposited. The virtual completeness of the elephant skeleton demonstrates that the sand-silt lens in which it was entombed was almost immediately buried by fine sediments, otherwise it would have been washed away. Thus the fossil material from the Chembakchino site virtually represents an intact ecosystem assemblage. The abundant plant macrofossil remains found have been identified to reconstruct local contemporaneous plant communities. Plant macrofossil assemblages from lacustrine environments into which streams carry detritus from a wide area provide evidence not only of plant communities of riverside and fringing marsh, but also of dry-land vegetation (e.g. Krivonogov, 1988).

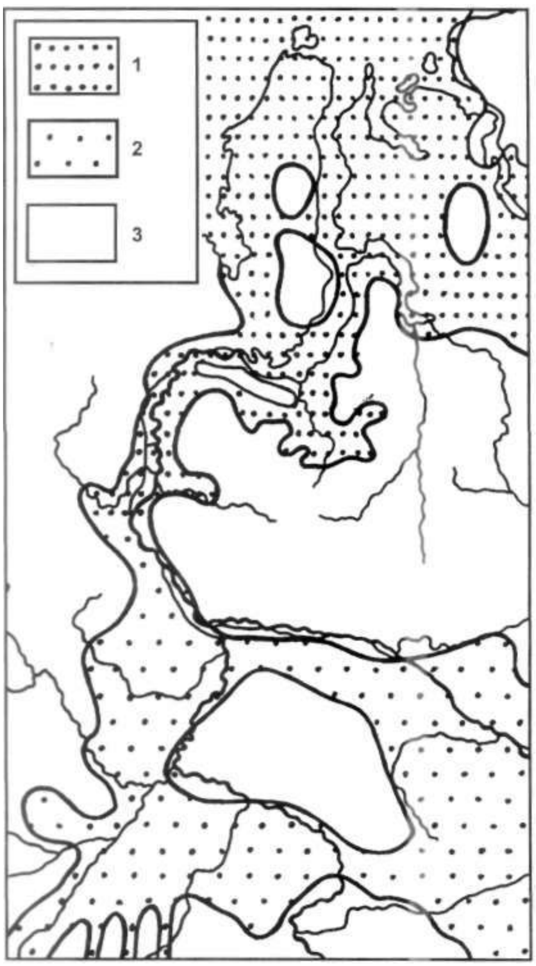

Figure 3
The palaeogeographical situation of the central and northern parts of the West-Siberian Plain at the end of the Early and beginning of the Middle Pleistocene (according to Arkhipov, 1963). 1: marine deposits; 2: lake-alluvial deposits; 3: (dry) land.

The plant assemblages recovered from the Chembakchino site contained the fruits of tree birches *Betula* sect. *Albae,* and of willows *Salix* spp., and also some needles of the spruce *Picea obovata.* Other shrubs were represented by occasional finds of dwarf birch fruits *Betula nana* and seeds of crowberry *Empetrum nigrum,* and elder *Sambucus* sp. Among the herbs and grasses identified the remains of marsh, aquatic and riverside species dominated. Various species of Ranunculaceae were present, and taxa characteristic of disturbed ground were numerous, including Polygonaceae, *Potentilla* spp. and *Chenopodium* spp. All the samples contained the remains of Pliocene and Early Pleistocene species, believed to be reworked.

The list of species obtained (Table 2) resembles the floras of the grey clay silt deposits from the Irtysh and Ob basins, described by Nikitin (1940). However, some differences occur, for example a greater number of woody plants (birches, in particular) were found and there were no specifically arctic plants, such as *Andromeda polifolia, Chamaedaphne calyculata, Cochlearia arctica* or *Rubus arcticus.* By analogy with the modern zonal distribution of vegetation, the species composition of the samples studied corresponds to the middle taiga vegetation of the West-Siberian Plain. At present the region under investigation, the Ob-Irtysh floodplain occurs in the southern taiga zone with forest-shrub-meadow plant communities. These upland sites are characterised by closed coniferous forest with *Pinus sibiricus, Picea* and *Abies* and typical forest herbs. The floodplain forests comprise fir-spruce-birch and pine-birch associations. The plant macrofossil assemblages indicate the vegetation of the region was a boggy floodplain within an area of birch-spruce forest.

The type of plant communities and the plant species present largely determine the nature of the insect fauna. The entomological data allow an amplification of the conclusions based on plant macrofossil analysis and a more accurate reconstruction of the climatic conditions, especially temperature. The insect faunas have been analysed both in terms of their zoogeography and habitat type (Figure 4). The different groups were selected according to the geographical distribution and habitat characteristics of recent species.

The principal group represented is that of subarctic species (74%). In the samples this group is dominated by species of ground beetles: *Amara interstitialis* Chd. (9% of the total insect faunal assemblage), *Elaphrus angusticollis*

Species	Total	L. 1-2	L.3	L.4	L.5
Picea obovata	V	V	6V	3V	V
? Pinus sp.	-	-	-	V	-
Betula sect.Albae	12	3	18+V	31+V	25+V
Salix sp.	1	4	-	4	-
Betula nana	1	-	4	18	4
Empetrum nigrum	2	1	-	1	-
Hypericum sp.	-	-	-	-	1
Fragaria vesca	-	-	1	-	-
Potentilla supina	2	7	17	11	18
Potentilla anserina	15	4	20	8	6
Potentilla spp.	-	2	1	7	4
Ranunculus sceleratus	150	*	*	*	*
R. reptans	50	3	-	50	22
Menyanthes trifoliata	10	1	14	3	3
Eleocharis palustris	**	**	**	**	**
? Eleocharis acicularis	-	40	43	4	25
Polygonum aviculare	180	22	162	80	37
Rumex cf. *sibiricus*	12V+15	4V+6	45V+43	40	2V+10
Rumex cf. *ucrainica*	V	-	-	-	-
Rumex sp.	2	-	-	+	+
Rumex maritimus	-	-	-	-	V
Scirpus lacustris	1	-	-	-	-
Stellaria palustris	8	-	3	2	3
Carex spp.	120	47	166	340	140
Rorippa sg. *Nasturtium* sp.	2	-	2	7	-
Rorippa palustris	-	7	30	10	7
Alisma sp.	-	-	3	16	-
Sagittaria sagittifolia	-	-	12	-	-
Ranunculus sg. *Batrachium* spp.	14	180	300	250	200
Hippuris vulgaris	9	7	9	17	2
Myriophyllum verticillatum	1	-	-	1	-
Sparganium sp.	2	-	-	-	-
Typha spp.	-	6	32	3	17
Potamogetonaceae	*	**	**	**	**
Ranunculaceae	76	12	86	43	31
Polygonaceae	60	100	100	00	50
Cyperaceae	2	2	-	-	3
Rosaceae	-	1	-	2	-
Alismataceae	4	-	-	11	4
Chenopodiaceae	-	-	1	1	5
Asteraceae	-	-	2	6	-
Characeae	-	1	11	-	1
Azolla spp.	2	3	28	1	4
Azolla interglacialica	3	-	0	-	1
Selaginella selaginoides	-	-	-	-	2
Najas tenuissima	-	-	-	-	1
Najas sp.	-	-	1	-	-
Decodon sp.	-	-	2	-	1
Comptonia sp.	-	-		-	1
Epipremnum sp.	1	-	-	1	-
Hartzia rosenkjaeri	-	-	1	-	-
Aracispermum cf. *canaliculatum*	1	-	-	-	-
Scirpus sp.	-	-	-	1	-
Sambucus sp.	1	-	-	-	-

* 300 to 1000 specimens

** more than 1000 specimens

Table 2: Species list of plant macrofossil remains from the Chembakchino-94a site (layer U.

Sahib. (9%), *Bembidion* (? *Asioperyphus)* sp. (8%), *Pelophila borealis* Pk. (8%) and *Amara erratica* Chd. (6%). The second largest group included polyzonal insects (18%), particularly species of riverside habitats and phytophages. This group included the ground beetles *Notiophilus aquaticus* L, *Agonum gracile* Gyll., *A. 1 dolens* Sahib., *Bembidion ? varium* 01., *B.* cf. *infuscatum* Dej., *B. (Eupetodromus)* sp., 8. ? *assimile* Gyll., pill beetles *Morychus* sp. and *M.* cf. *aeneus,* road beetles of the genus *Olophrum* and a snout beetle *Notaris bimaculatus* F. The only tundra species was the ground beetle *Curtonotus alpinus* (4%). Some boreal species were also found. Their modern distribution is limited by the borders of the forest zone. Some of these species inhabited both forests and boggy meadows (e.g. the ground beetle *Pterostichus? diligens* Sturm.). Others are inhabitants of forest habitats and they need either woody plants (the powder-post beetle *Stephanophachys* sp.) or forest floor conditions (the ground beetle *Amara 1 brunnea* Gyll.). Of these three species only *Stephanophachys* can be considered as an indicator of the presence of woody plants near the site where the mammoth died.

On the evidence provided by the insect fauna, it is possible to conclude that during the formation of the layer studied there were plant communities similar to modern floodplain vegetation with some solitary trees. The sites lay close to the open shore with a clay substrate. This is deduced from the modern habitat distribution of the dominant beetle species (the ground beetles *Pelophila borealis, Amara interstitialis, A. erratica* and *Elaphrus angusticollis).* The remains of cryophilous insects (the ground beetle *Curtonotus alpinus* and the road beetles *Tachinus* sp. and 7! cf. *apterus)* suggest a colder climate in this region at that time in comparison to that today.

In spite of the scarcity of their remains the bird species recorded also give some indications of the character of this ecosystem. Two of the bones belonged to two different species of snipe, for which floodplain meadow would be an ideal habitat. One bone belonged to willow-ptarmigan *Lagopus lagopus.* Today these birds may inhabit a variety of different environments - tundra, open pine forest, birch woodland or forest-steppe, but the main condition is the availability of shrubs, such as willow and birch, that can be used as food in winter. In the middle taiga zone, this species usually inhabits 'riams' (moss-covered raised bogs colonised by pine) (Ravkin, 1984; Potapov, 1990) and raised bogs with pools and ridges.

Another bone comes from an owl. Unfortunately, it was impossible to be certain of the species, but it could be *Asio otus* or *A. flammeus.* At present the habitats of these

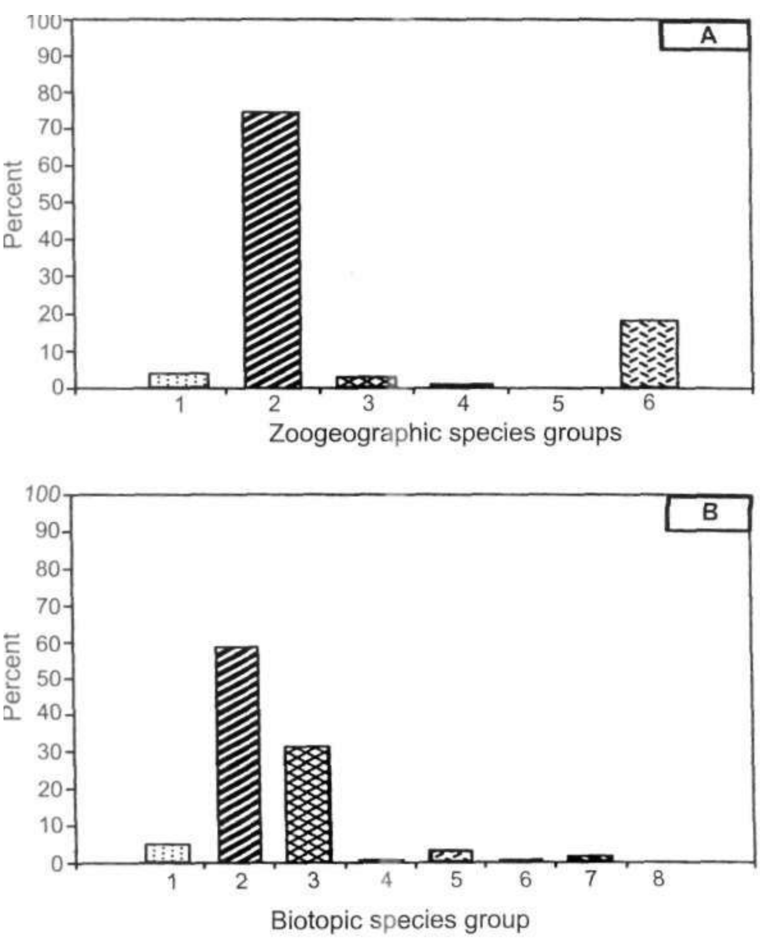

Figure 4
The proportion of zoogeographic (A) and habitat IB) groups of insect species from the Chembakchino-94 A site. (A): 1 - tundra species; 2 - subarctic species; J - boreal species not strictly limited by the presence of forest; 4 - forest species; 5 - xerophile species; 6 - polyzonal species; IB): 1 - hydrobionts, 2,3,4 - herpetobionts 12 - hydrophylic, 3 - mesophylic species of open spaces, 4 - soil inhabitants); 5 - herb and shrub inhabitants; 6 - dendrobionts; 7 - copro- and necrophiles; 8 - mycetophages and mycetobionts.

birds differ slightly. The long-eared owl *(Asio otus)* prefers to nest in tall forest trees with mixed but mainly coniferous tree species, but with some scrub, meadows and other open spaces. By contrast, Marsh owl *(Asio flammeus)* prefers open marshes, mown fields, clearings in pine forests and the floodplains of large rivers (Ivantchev, 1993).

Another faunal group present were small mammals. These have traditionally been used as biostratigraphical markers in the Pleistocene and in reconstructions of landscape and/or climatic conditions. In this material, small mammals were only represented by rodents, including collared lemming *Dicrostonyx* ex gr. *renidens-simplicior* (5%), brown lemming *Lemmus sibiricus* (18%), and tundra vole *Microtus* ex gr. *oeconomus* (77%).

The majority of small mammal remains in alluvial and lake deposits are believed to be derived from the pellets of birds of prey that have been washed into aquatic environments. In terms of species composition and relative abundance material from pellets gives a distorted picture of the actual fauna. There is usually overrepresentation of species from open habitats. Nevertheless, the faunal lists obtained, albeit derived from pellets, provide a characteristic picture of the landscape and climate. Modern *Microtus oeconomus* Pallas, 1778 inhabits boggy meadows and meadow-forest sites of tundra, forest and forest-steppe. *Lemmus sibiricus* Kerr, 1792, which at present inhabits tundra and forest-tundra in western Siberia, prefers wet sedge tundra habitats. The only species of this genus that inhabits the forest zone in eastern Siberia, *L. amurensis* Vinogradov, 1924, favours boggy open places. The modern distribution of the genus *Dicrostonyx* is restricted to the tundra and forest-tundra zones, where it prefers hummock tundra sites on hill slopes and floodplain surfaces with low bushes, but it avoids excessively moist places and also dry lichen tundra. The presence of these rodents in Pleistocene faunas is usually related to periglacial conditions.

Thus, all the small mammal species found can be considered as species of open habitats within the biome where forest vegetation was represented. However, one must take into account the possibility that the ecological requirements of Pleistocene species of the genera might differ from those of their modern representatives (Smirnov, 1992). They might possibly have lived in landscapes with a more developed forest vegetation, compared to their typical modern habitats.

Conclusions

The results of the analyses presented allow the reconstruction of a riverside ecosystem; a boggy floodplain with meadow vegetation, scrub and a fringe of birch-spruce woodland. The edge of the river was bordered by a zone of bare clay, up to several metres wide and lacking vegetation. Because the area under consideration was a low-lying plain within a large island (Arkhipov, 1965), the type of ecosystem described was probably also typical of sites away from the river. The data suggest the predominance of open landscapes with boggy-meadow vegetation or open woodlands. The list of animal species present suggests that the environment cannot be equated precisely either with modern periglacial or boreal types. The species content of both the insect and the small mammal faunas suggests more rigorous climatic conditions in this region at that time than today. Probably, the presence of a large freshwater body in the West-Siberian Plain, which froze in winter, considerably influenced the regional climate. At times of very cold climate, this huge water body, formed by damming of rivers from the south, might have rendered climatic conditions milder and prevented the formation of periglacial conditions locally. During warmer periods, late thawing of the water would have given rise locally to a more severe climate and prevented formation of a forest zone, even though the region lies within the modern forest belt. In both cases, global climatic changes could be modified by regional factors within the West-Siberian Plain, giving rise to the specific character of its local ecosystems.

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