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Living environments and diet of the Mongochen mammoth, Gydan Peninsula, Russia

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ABSTRACT

Remains of a male woolly mammoth (*Mammuthus primigenius* Blumenbach, 1799), radiocarbon dated to cal. 18,370 ^{14}C BP, were discovered in perennially frozen deposits in northern West Siberia (Gydan Peninsula, 72°10′ N, 79°35′ E). Microfossil and macrofossil samples from the inner part of the mammoth intestinal content, samples of the coat and skull taken from the mammoth carcass and samples of frozen deposits enclosing the carcass were studied for the purpose of reconstructing the mammoth's diet, season of death, and its living environments. Pollen, biomorphs and plant macrofossils indicate that grasses and sedges were the main food items, supplemented with small amounts of dwarf birch and larch twigs and a variety of herbs and mosses. The plant remains found in the intestines indicate that the animal died in the middle of summer. The mammoth lived in a cold tundra-like environment with sedge-grass and dwarf shrub communities and scattered larch stands.

1. Introduction

Frozen remains of the mammoth assemblage members appear to be a source of integrated information on the Pleistocene ecosystems (Guthrie, 1990). At present, more than 15 remains of the animals belonging to the mammoth fauna, with soft tissues preserved, are known scattered over the vast territory of Arctic. Of the greatest interest are those with stomach or intestines preserved and containing partly digested food. Most such finds are remains of mammoths (Sukachev, 1914; Ukraintseva, 1993; van Geel et al., 2008), although analogous remains of horse (Ukraintseva, 1977) and wooly rhinoceros (Garut et al., 1970; Lazarev, 1977; Boeskorov et al., 2011) are also known. Comparable to those in importance are fecal segments recovered from permafrost (van Geel et al., 2010) and dung found in some localities in arid zones (Mead et al., 1986). Studies of those remains provide the most reliable basis for reconstructing vegetation of the region at a certain time – the time when the animals lived and died, as well as the animals' diet. The intestinal content may shed light on the animals' ecological requirements. All those data would enable tracing the vegetation changes in different regions through the Late Pleistocene. Variations in the animal ecology may be related to changes in the ecosystems or in the biology of the animals themselves. The investigations are performed as a part of integrated studies of the "mammoth ecosystem" extinction (Guthrie, 2001, 2006).

One of the most recent finds was that of mammoth remains (*Mammuthus primigenius* Blumenbach, 1799) on the Gydan Peninsula (West Siberia), in the Mongocha-Yakha drainage basin (72°10′ N, 79°35′ E) at 60 m above sea level (Fig. 1). The find is known as "Mongocha mammoth", or "Yaptunay's mammoth" (after the name of Stepan Yaptunay – the Nenets who found it). According to the finder's statement, it was an entire carcass lacking tusks and teeth; later, some bones were removed.

Hair samples of the Mongochen mammoth have already been used for analyses of ancient DNA (Gilbert et al., 2007) and ^{13}C and ^{15}N isotopes (Mazepa et al., 2010). This paper presents the results of plant remain studies, both micro- and macro-remains recovered from the intestinal content, coat, head and sediments enclosing the mammoth carcass. Some paleoecological implications of the data are also considered.

2. Study area

Presently, a harsh arctic climate dominates the Gydan Peninsula. The mean January temperature is about −26 to −28 °C (−26.7 °C), and the mean July temperature ranges from 6 to 8 °C (6.6 °C). The mean annual precipitation is 300–400 (328) mm (Treshnikov, 1985; http://wcatlas.iwmi.org, New et al., 2002).

In regard to the present-day vegetation, the studied area, according to Yurtsev (1994), belongs to the Yamal-Gydan (West

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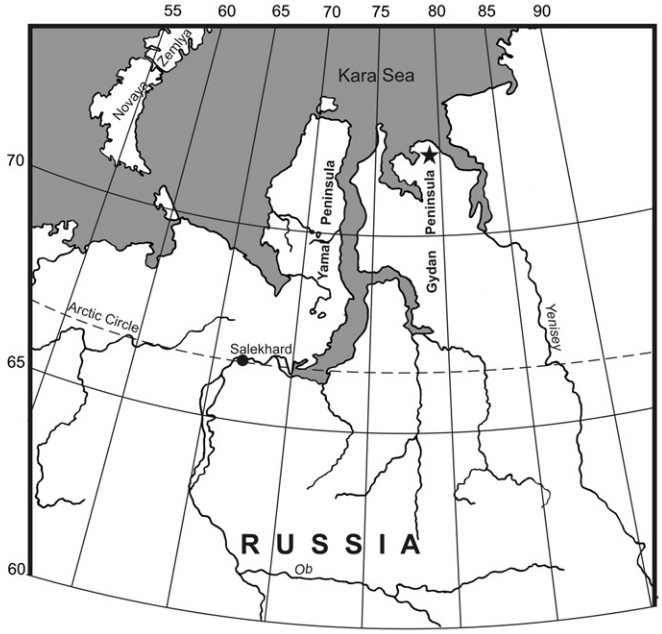

Fig. 1. Location map.

Siberian) subprovince of the European-West Siberian province, the northern variant of the Arctic tundra subzone. The subprovince under consideration features an impoverished flora marked by certain "negative" characteristics, resulting from the fact that many montane species (mostly East Siberian ones) have disjunct (fragmented) ranges (and therefore are not found in the region), and from the absence of most of eastern (occurring east of the Enisei) and western (European and amphi-Atlantic) species with the range reaching to the Urals. Many western elements are typically found in the southern regions, whereas the eastern elements gain in importance northward. Scarcely any endemic species are found in the region (Yurtsev et al., 1978; Yurtsev, 1994).

There are no shrubs in the modern vegetation of the studied site. The vegetation communities are dominated by herb and grass species such as *Alopecurus alpinus* Smith., *Deschampsia brevifolia* R. Br., *Carex arctisibirica* (Jurtz) Czer., *Carex concolor* R. Br., *Dryas punctata* Juz., *Bistorta vivipara* (L.) S.F. Gray, *Luzula confuse* Lindeb., *Saxifraga cernua* L., *Minuartia arctica* (Stev. ex Ser.) Graebn., *Valeriana capitata* Pall. ex Link., *Artemisia tilesii* Ledeb., as well as mosses *Hylocomium alaskanum*, *Tomenthypnum nitens*, *Aulacomnium turgidum*, and *Ptilidium ciliare* (Aleksandrova, 1977).

3. Material and methods

3.1. Taphonomic setting

The locality is situated at the interfluve of two small streams (Fig. 2). The mammoth remains occurred at a depth of 60–100 cm from the surface. Anatomically undisturbed remains include most of the spine (thoracic, lumbar and caudal parts) and the right-side ribs (Fig. 3a). The skull is destroyed. Spinous processes of all the vertebrae are directed vertically downward.

The sediments in proximity to the carcass display a sequence as follows (from the bottom upwards):

1. Below 110 cm – frozen silts, bluish-gray;
2. Bluish-gray silts, 15 cm thick;
3. Ice layer 10 cm thick, with a 1 cm interlayer of wool in the upper part;
4. Gray-blue silt 15 cm thick; the uppermost part includes an interlayer of wool ~ 1 cm thick;
5. Bluish-gray silts, 10 cm thick;
6. Gray silts, with traces of ferrugination along fissures; thickness 55 cm;
7. Turf, 5 cm thick.

The sediments overlying the skeleton and those occurring between the two interlayers of wool are seen in the section (Fig. 4). The mammoth remains are buried in subaerial silts.

Fig. 2. Locality of the Mongochen mammoth remains.

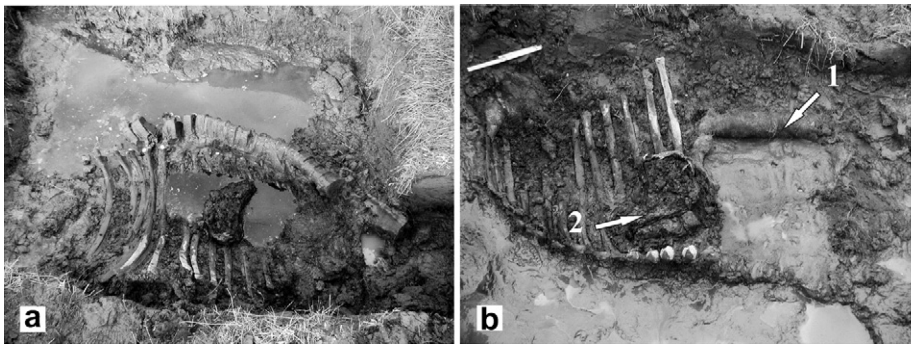

Fig. 3. Part of the Mongochen mammoth skeleton arranged in anatomical order (a) and part of the intestine contents and hair of the Mongochen mammoth (b). 1: hair of the Mongochen mammoth; 2: part of the content of the large gut and rectum with already formed dung.

3.2. Methods

In the course of field work, the large gut contents were cleaned from the enclosing sediments and sampled for paleobotanical studies. Samples were taken for pollen analysis and phytolith analysis (1 sample for each). As well, 8 l of the intestine contents (sampled in various parts of the guts) and 1 kg of wool were taken for plant macrofossil analysis (seed and fruit studies). The enclosing sediments were sampled for pollen and phytolith analyses (12 samples for each) and for seed studies (9 samples). One sample was taken from the sediments infilling the skull.

The plant macrofossil samples were washed through sieves with mesh sizes of 250 μm. Both the floating and the settled fractions were examined. A Carl Zeiss stereomicroscope with a 7× to 56× magnification was used for the analysis. Twigs, leaf remains, fruits, seeds, mosses and a variety of unidentified vegetative remains were picked from the sample following Nikitin (1969).

Samples for pollen analysis were prepared using standard techniques according to Faegri and Iversen (1989). Microfossil remains were analyzed with an Olympus BX 51 microscope at 100×, 400× and 1000× magnification. At least 300 pollen grains and spores were counted in every sample. The percentage of AP and NAP pollen is based on the pollen sum. The percentage of spores and obviously reworked pollen is based on the pollen sum. The pollen data were illustrated in a graph, drawn using TILIAGRAPH.

The identification of micro- and macrofossils based on reference collections of pollen, seeds, and plant remains at the Institute of Plant and Animal Ecology (Yekaterinburg, Russia). Additionally, various keys were used (Dobrokhotov, 1961; Kats et al., 1965; Kuprianova, 1965; Kuprianova and Alyoshina, 1972; Velichkevich and Zastawniak, 2009).

Biomorphs were extracted from contents of the large intestines using standard wet oxidation and heavy flotation techniques (Golyeva, 2001). Thereafter the phytoliths were examined on slides in glycerine using Carl Zeiss HBO 50 (AC) optical microscope at 200×–400× magnification. Pictures of paleofossils taken at 400× magnification with phase contrast (ph2). The terms describing phytolith morphologies follow anatomical terminology, and otherwise they describe the geometrical characteristics of the phytoliths. The International Code for Phytolith Nomenclature was also followed where possible (Madella et al., 2005).

Samples of wool were dated by a continuous-flow isotope-ratio-monitoring mass spectrometer (Europa Geo 20/20) at the Research Laboratory for Archaeology and the History of Art, University of Oxford, and by the Groningen AMS facility at the Centre for Isotope Research, Groningen University. One sample of the intestinal contents was dated at the Radiocarbon Laboratory of the Institute of the History of Material Culture of the Russian Academy of Sciences.

4. Results and discussion

4.1. Anatomic studies

The excavations yielded an almost complete mammoth skeleton (except for tusks, the upper teeth, the left half of the pelvic bone, left femur and parts of bones of the sternum, palm and foot); the entire right hand (*manus*) with skin and muscles was

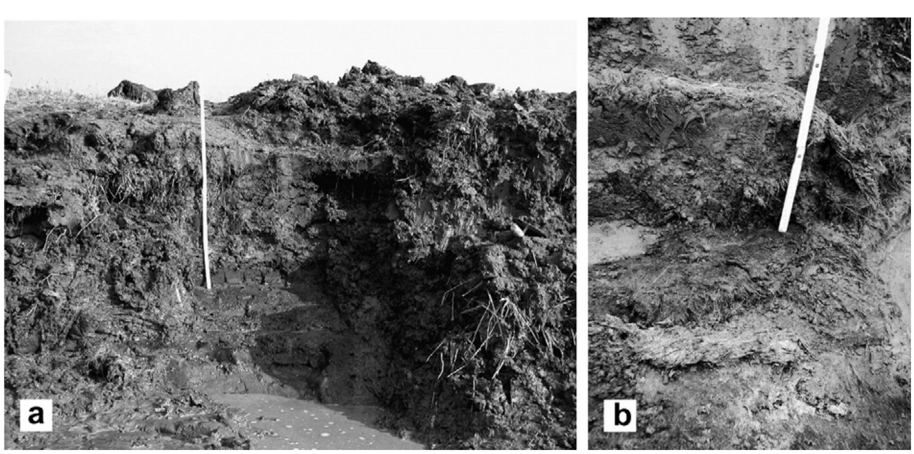

Fig. 4. Section of deposits from the Mongochen mammoth site. a: the excavated sediment sequence; b: the two interlayers of wool in sediments.

Table 1
Macrofossils of various samples from the Mongochen mammoth site.

Taxon	Sample of mammoth wool	Sample of mammoth colon contents	Sediments										Ecology
			Turf	Gray silts						Bluish-gray silts			
			Depth, cm										
			0–5	5–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	
Daphniidae													
Daphnia sp.		4		1		3	6	1	5	1	3		
Bryophyta gen. indet.	≈200V	VV	10V		1V	1V		3V	6V	≈200V	2V	2V	
Selaginellaceae													
Selaginella selaginoides				3		3 + 3*	1		1	4	1		Mesohydrophyte, moist but drained habitats
Pinaceae													
Larix sibirica	1V	V								1*V			Mesophyte, boreal
Poaceae													
Alopecurus cf. *glaucus*	3												Mesohydrophyte, boreal
Phleum sp.			2		3								
Poa sp.	1												Open slopes, tundra, streambanks
Poaceae gen. indet.	1	9		1	1	70	67	50	130	163	200	230	
Cyperaceae													
Carex cf. *acuta*		4											Hydrophyte, boreal
Carex aquatilis		5											Hydrophyte, water-swamp, boreal
Carex rostrata		1											Hydrophyte, water-swamp, boreal
Carex sp.	1	3		1						2			Commonly moist substrates, streamsides, shorelines, meadows
Eleocharis sp.						1*	1						
Juncaceae													
Luzula sp.			12										
Juncus sp.									1	1			Wet meadows, arctic-alpine, river flats, borders of ponds, lakes, streams
Melanthiaceae													
Tofieldia pusilla						1				1	1		Mesohydrophyte, typical arctic
Salicaceae													
Salix glauca	1V												Circumpolar, shrub communities
Salix sp.			10*V										
Betulaceae													
Betula nana	1V						1*						Subarctic, shrub communities
Betula sect. Betula		3							1	1	2		Boreal
Betula sp.										1*	1*		
Alnus fruticosa		1*											Subarctic, shrub communities
Polygonaceae													
Bistorta viviparum	2	1	11								1		Circumpolar, arctic-alpine, turfy, rocky, moist grassy herbmats, manured places
Rumex sp.			1										

Table 1 (*continued*)

Taxon	Sample of mammoth wool	Sample of mammoth colon contents	Sediments										Ecology
			Turf	Gray silts						Bluish-gray silts			
			Depth, cm										
			0–5	5–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	
Caryophyllaceae													
Dianthus sp.									1				Gravelly, dry open slopes
Cerastium sp.	2	2											Rocky, gravelly or sandy, alpine tundra to heath to meadows
Minuartia spp.	14	2	8		2	52	22	1	37	49	37	5	Alpine tundra, snowbeds, gravelly, dry open slopes
Caryophyllaceae gen. indet.		5 + 3*	1				2		4	2	3		
Ranunculaceae													
Ranunculus hyperboreus		2											Circumpolar, hydrophyte, wetness indicator
Ranunculus sceleratus		1											Hydrophyte, wetness indicator
Ranunculus sp.		1 + 1*	1			1*							
Papaveraceae													
Papaver sp.	9	8	5	1		33	37	3	77	34	30	2	
Brassicaceae													
Draba spp.	23	1	6 + 1*		1	19	18	9 + 5*	29	25	5	11	Generally in dry to mesic tundra, often calcareous
Rorippa palustris						1							Hydrophyte, river flats, borders of ponds, lakes, streams
Brassicaceae gen. indet.		3 + 3*								8*	7		
Saxifragaceae													
Saxifraga sp.			7			2			1	2			Cryophytes
Rosaceae													
Comarum palustre										1			Hydrophyte, water-swamp
Dryas punctata	33V												Xeromesophyte, typical arctic
Dryas sp.		1V	200*V						1*V				
Potentilla nivea	5	60				3	20	18	39 + 10*	10	1	1	Mesoxerophyte, disturbance indicator
Rubus cf. *idaeus*						2*							Mesophyte, boreal
Violaceae													
Viola sp.				1									
Hippuridaceae													
Hippuris vulgaris											1		Hydrophyte, water-swamp
Asteraceae gen. indet.		4											
Sum of macrofossils (psc.)	97	124	275	7	8	192	169	89	338	508	292	251	

Symbols: * – fragment of macrofossils; V – vegetative parts of plants.

found, as well as the contents of the large intestines and a great amount of hair (Fig. 3). The alveolar socket of the task is about 150 mm in diameter, and m3 are only slightly worn. Judging from the data, the skeleton is of an adult mammoth male. There were no pathologies, nor traces of fractures on the bones. Hindguts were completely filled, up to and including rectum. The straight intestine contained some petrified faces (coprolites) (Fig. 3b).

4.2. Comments on taphonomy

Results of the anatomic studies permit reconstructing the process of the animal's death. Full large intestines suggest the mammoth had eaten a great volume of food not long before its death. This fact, along with the lack of bone pathologies and fractures, indicates that the animal was relatively healthy. How could an adult, relatively healthy and well-fed male meet his death? The cause may be inferred from the animal's posture at the time of his death. As has been noted above, the spinous processes of all the vertebrae were directed downward; so the animal must have been lying on its back when buried. That could be only in case it fell into a deep narrow fissure with its back down, so it could not get out and died. The death was not instant as indicated by the presence of coprolites in the rectum; the intestines continued functioning for some time. As a result of intestinal peristalsis, the large guts were filled and coprolites formed.

The absence of peat or mud in the sediments enclosing the mammoth disproves a suggestion that it found its death in a swamp or in a water body. Most likely the fissure was due to frost action or solifluction. It penetrates older sediments deposited before the mammoth's death. So the pollen, phytoliths and plant macrofossils recovered from the enclosing sediments are older than the animal and cannot characterize its living environments. It is only analysis of samples taken from the large intestine contents that may be used for reconstructing the mammoth habitat and diet.

4.3. Dating

The liquid-scintillation radiocarbon age of 18,370 ± 350 BP (LE-8664), obtained for the intestinal contents of the Mongochen mammoth corresponds to the middle of MIS 2 – the Late Weichselian period at the end of the Last Glacial Maximum (LGM). Some hair samples showed younger ages: 17,125 ± 70 BP (OXA-17116) and 16,690 ± 70 BP (GrA-35614). These data might indicate that the skin was contaminated with younger material, but the source of the contamination remains unclear.

4.4. Plant remains incorporated into the mammoth coat

The plant macrofossils incorporated into the mammoth wool were recovered from the right side on which the mammoth was lying. The sample included leaf fragments of *Dryas punctata*, *Betula nana*, and *Salix glauca*, fruit fragments of *Draba* spp., as well as single fruits and seeds of different herbs (*Potentilla* sp., *Minuartia* sp., *Cerastium* sp., *Carex* sp., Poaceae gen. indet., *Polygonum*

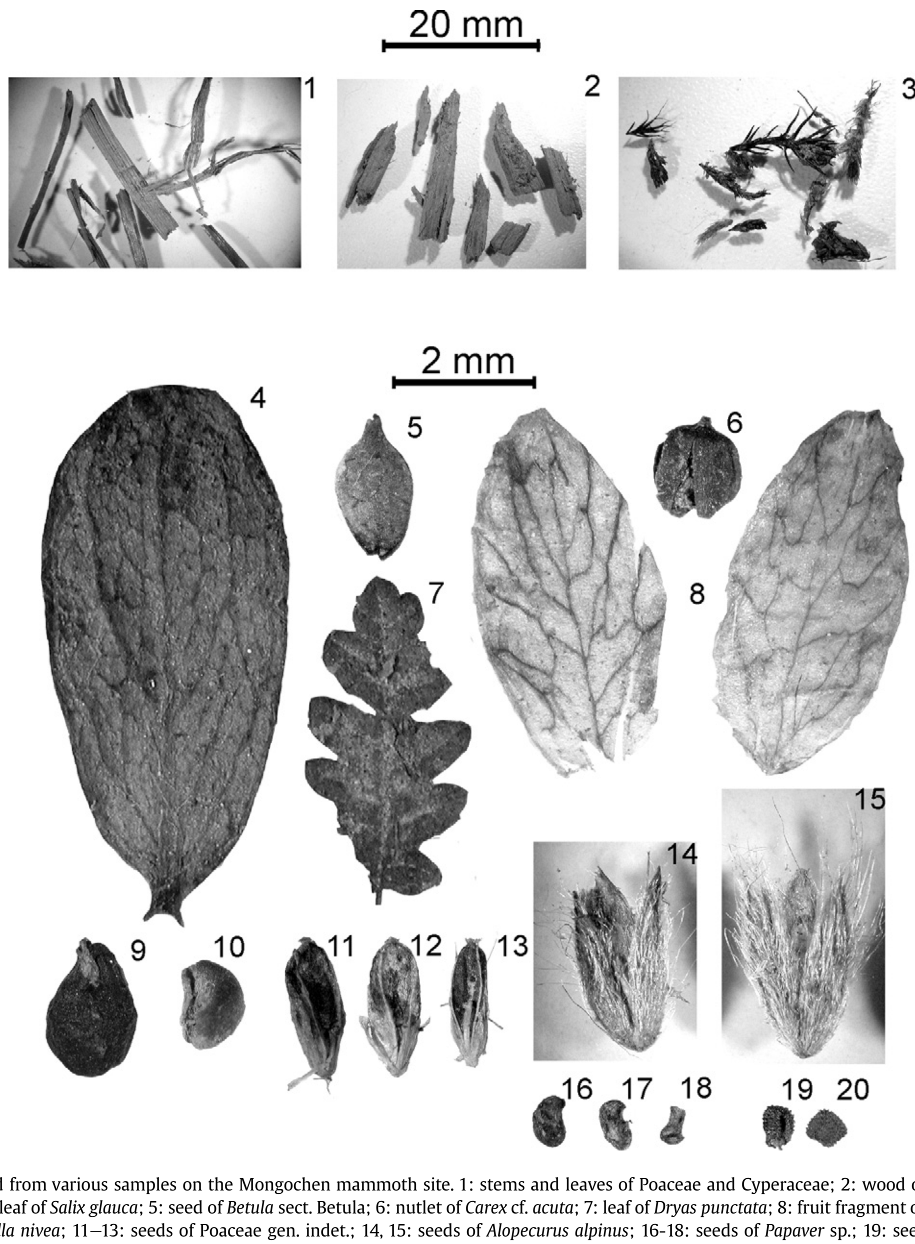

Fig. 5. Macrofossils recovered from various samples on the Mongochen mammoth site. 1: stems and leaves of Poaceae and Cyperaceae; 2: wood of *Larix sibirica*; 3: unidentified stem fragments of Bryales; 4: leaf of *Salix glauca*; 5: seed of *Betula* sect. Betula; 6: nutlet of *Carex* cf. *acuta*; 7: leaf of *Dryas punctata*; 8: fruit fragment of *Draba* sp.; 9: bulbil of *Bistorta vivipara*; 10: nutlet of *Potentilla nivea*; 11–13: seeds of Poaceae gen. indet.; 14, 15: seeds of *Alopecurus alpinus*; 16-18: seeds of *Papaver* sp.; 19: seeds of *Cerastium* sp.

Table 2
Percentage of pollen and spores in the intestinal contents and inner skull sediments of the Mongochen mammoth.

Groups of pollen and spores	Samples from the colon content				Sample from the inner skull sediments	
	1		2			
	Psc.	%	Psc.	%	Psc.	%
AP (trees and shrubs)						
Larix	2	0.3	3	0.4	5	0.9
Picea	15	2.0	5	0.7	21	3.9
Pinus	31	4.2	19	2.8	77	14.2
Betula pubescens type	5	0.7	2	0.3	34	6.3
Alnus fruticosa type	1	0.1	1	0.1	11	2.0
Betula nana type	12	1.6	2	0.3	95	17.5
Salix					4	0.7
Σ AP	66	9.0	32	4.7	247	45.6
NAP (herbs)						
Poaceae gen. indet.	561	76.1	543	79.6	106	19.6
Cyperaceae gen. indet.	57	7.7	54	7.9	36	6.6
Artemisia sp.	24	3.3	27	4.0	29	5.4
Rosaceae gen. indet.	5	0.7	6	0.9	18	3.3
Chenopodiaceae gen. indet.	1	0.1	2	0.3	16	3.0
Ericaceae gen. indet.	1	0.1	1	0.1	11	2.0
Asteraceae/ Asteroideae gen. indet.	1	0.1	1	0.1	10	1.8
Asteraceae /Cichorieae gen. indet.	3	0.4	1	0.1	1	0.2
Brassicaceae gen. indet.	1	0.1	1	0.1	5	0.9
Caryophyllaceae gen. indet.	1	0.1	5	0.7	7	1.3
Minuartia sp.			2	0.3		
Apiaceae gen. indet.	2	0.3			3	0.6
Saxifragaceae gen. indet.			2	0.3	6	1.1
Polygonum sp.	3	0.4			7	1.3
Polemonium sp.	1	0.1				
Fabaceae gen. indet.					3	0.6
Onagraceae gen. indet.					1	0.2
Ranunculaceae gen. indet.					8	1.5
Valeriana capitata					2	0.4
Herbetum mixtum	10	1.4	5	0.7	26	4.8
Σ NAP	671	91.0	645	95.3	295	54.4
Pollen sum	737	100	682	100	542	100
Spores						
Polypodiophyta					17	3.1
Lycopodium sp.	2	0.3	5	0.7	25	4.6
Selaginella selaginoides type					2	0.4
Bryales gen. indet.	45	6.2	24	3.5	87	16.1
Sphagnum sp.	7	1.0			40	7.4
Ascospores of coprophilous fungi (*Sordaria* type)	4	0.6				
Tardigrada (*Macrobiotus hufelandi* type)	1	0.1				
Reworked pollen				118	21.8	

viviparum, *Papaver* sp.). Fragments of wood and a branch end identified to *Larix sibirica* were also found along with a few moss remains (Table 1, Fig. 5). The plant remains in this sample could originate either from the including soil or from the animal gut contents.

4.5. Palaeobotanical proxies from the colon content

Two pollen spectra were obtained from the colon contents of the Mongochen mammoth, which do not differ in dominance and quantitative relationships between the major pollen groups (Table 2, Fig. 6). In both spectra, non-arboreal pollen predominated, among which there is a large quantity of *Artemisia* pollen, Poaceae and Cyperaceae pollen. There are only a few arboreal pollen and Bryales spores.

The assemblage of detrital biomorphs is dominated by connective tissue of moss and epidermis remains of monocotyledons (Tables 3 and 4). Among siliceous biomorphs, phytoliths of meadow grasses and mosses are dominant. Additionally, we found various phytoliths of sedges and herbs and some isolated conifer phytoliths. There are phytoliths of plants that grow in fairly dry conditions.

Three groups of plants have been identified among the recovered macroremains, namely mosses, trees and grasses; their dry weight ratio is 20:2:1 (Table 1, Fig. 5). The moss remains were identified as *Drepanocladus* sp., *Calliergon* sp., *Hydrohypnum* sp., *Distichium* sp., *Bryum* sp. Most of species of those genera prefer wet habitats. Mosses are of small nutritious value. Herbivores practically do not eat them, except for reindeer, caribou and musk ox feeding on mosses when no other forage is available (Thieret, 1956; Bardunov, 1984). Moss got into the mammoth's stomach more or less casually along with grass when grazing; as the moss matter is hardly digestible, its remains tended to accumulate in the hindguts. A number of specialists who studied contents of gastrointestinal tract the mammoths and other herbivores of the mammoth complex are of the same opinion (Solonevich et al., 1977; Ukraintseva, 1982; Tomskaya, 2000). It is quite possible that the mosses present in abundance in the ground cover were taken occasionally when the animal was feeding on fodder grass. The most often found in the mammoth gastrointestinal tract are mosses of genera *Dicranum*, *Mnium*, *Hypnum*, *Polytrichum*, *Drepanocladus*, *Calliergon* (Thieret, 1956; Ukraintseva, 1982; Bardunov, 1984).

Arboreal plants are represented by *Larix sibirica* wood fragments, the largest being about 1 cm^3 in volume. The presence of lignified larch wood in the contents of large intestines of the Mongochen mammoth confirms the current opinion that mammoths ate branches and bark of trees (Solonevich et al., 1977; Ukraintseva, 1982). It is interesting that the *Larix* macroremains were recovered also from the gut contents of the Fishhook Mammoth (20,620 ± 70 BP) found about 200 km north of the present-day tree limit on the Taymyr Peninsula (Mol et al., 2006). As well, the intestines of the Mongochen mammoth contain seeds of *Betula* sect. Betula. Another find, a fragment of *Alnus fruticosa* scale, suggests the shrub alder could grow within the Mongochen mammoth grazing area. It is quite possible that alder was a constituent of the animal diet, as the nutritive value of some shrubs is higher than that of herbs and grasses (Tomskaya, 2000).

Herbs are represented by small fragments of Poaceae and Cyperaceae stems and leaves. There are also seeds of some herbs such as Caryophyllaceae (*Minuartia* sp.), *Ranunculus* sp., *Potentilla* sp. Most plant remains belong to mesophytic and hydrophytic plants typical of various tundra plant assemblages (Table 1). The grass and herb remains are rather scarce, as soft and succulent tissues of those plants are easily digestible.

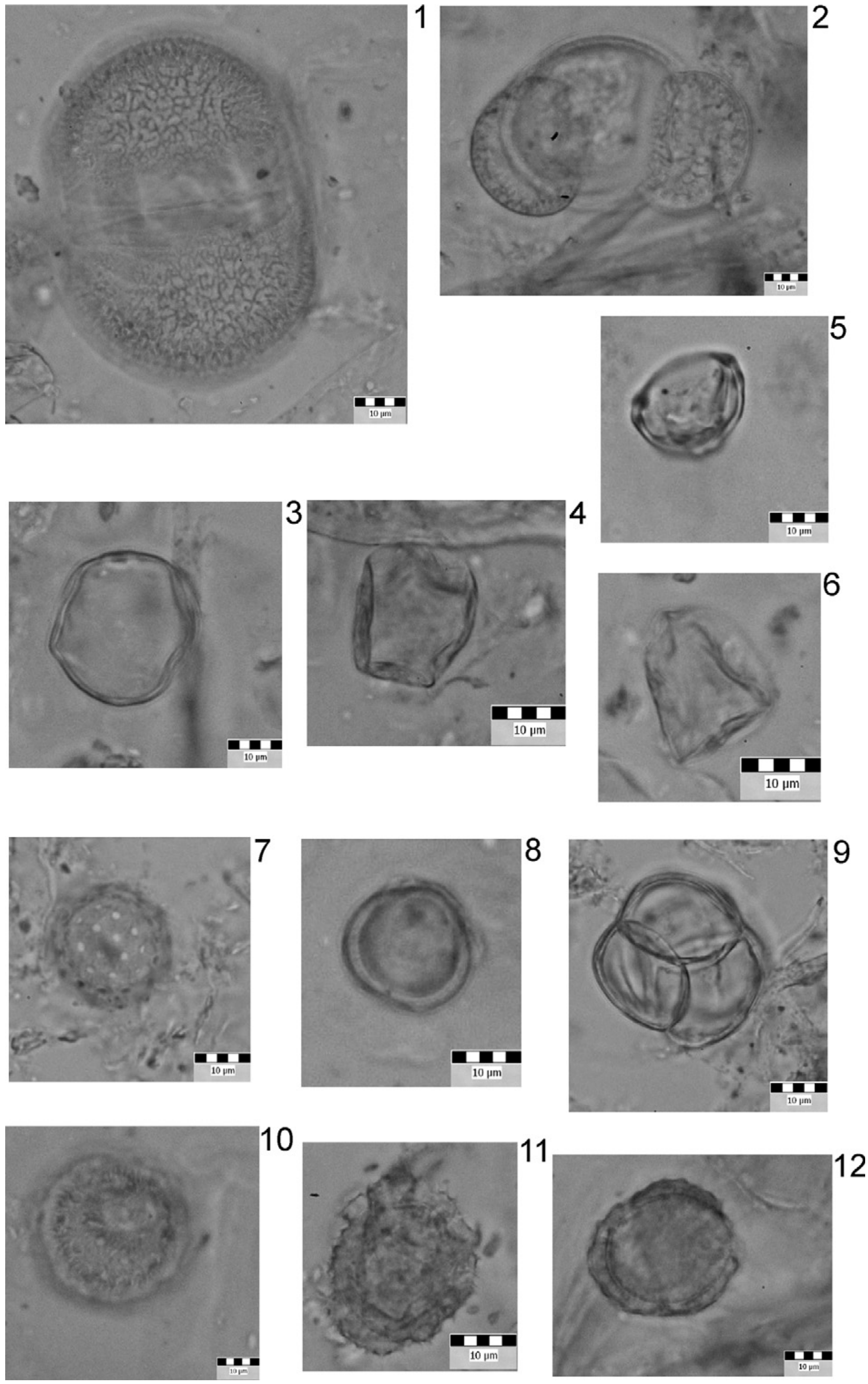

Fig. 6. Pollen of various samples from the Mongochen mammoth site. 1: *Picea*; 2: *Pinus sylvestris* type; 3: Poaceae; 4, 6: Cyperaceae; 5: *Betula nana* type; 7: Chenopodiaceae; 8: *Artemisia*; 9: Ericales; 10: *Polemonium boreale* type; 11: Asteraceae Liguliflorae; 12: Asteraceae Tubuliflorae.

The season of the Mongochen mammoth death may be inferred from a specific proportion of pollen and macroremains. The presence of a sedge seed indicates the mid-summer, when those plants are seeding. Grass and sedge pollen are most abundant at that time, both in anthers of the plants themselves and on the soil surface. The lack of grass seed fragments also suggests the middle of the summer period, when seeds either have not developed yet, or were at the stage of milky ripeness, so that their soft tissues have been readily digested in the gastrointestinal tract.

It seems from the above that the Mongochen mammoth diet included herbs and grasses, as well as shoots of larch and shrubs. That is attested to by abundant pollen and occasional macroremains of grasses, sedges and herbs; by the presence of larch (both pollen and macroremains) and coniferous phytoliths; and by scarce pollen of *Betula nana* type, and pollen and scales of *Alnus fruticosa* type. Mosses may be considered as an accidental constituent of the mammoth's diet. The species composition and abundance of moss remains suggest a wide occurrence of bogs on the Gydan Peninsula

Table 3
Results of the biomorphic and phytolith analysis of various samples from the Mongochen mammoth site.

Group biomorphs	Sample of the mammoth colon contents	Sediments								
		Turf	Gray silts					Bluish-gray silts		
		Depth, cm								
		5–10	10–20	20–30	30–40	40–50	50–60	60–75	75–85	90–95
Phytoliths (psc.):	137	281	167	60	184	50	169	62	121	360
Conifers	Single	Single	±		±	±		±		±
Dicotyledonous plants	++	+++	++	++	++	++	++	++	++	+
Forest grasses	+	Single			±		+		++	±
Meadow grasses	+++	±	+	++		Single	++	Single	±	
Sedge	++		+	+	+	+				+
Mosses	+++	+++	+	++	Single	±	++	±	+++	++
Sponge spicules (psc.)		181	60	65	131	19	55	16	93	103
Diatoms (psc.)		51	44	50	70	27	50		50	48
Other biomorphs		++	+	+++	+++	+++		++	+	
Fungi	++									
Detritus	++++		+++		+++	+		+		
Cuticular casts (psc.)	30	16	34	17	9	20	26	6	29	21
Soil fauna (psc.)			N		12	N	3	1		

Symbols: ++++, >50%; +++, 50–20%; ++, 20–10%; +, 10–5%; ±, 1–5%; single, <1%, N, *Nematoda*.

at the time the Mongochen mammoth lived and died there. Judging from the data obtained, its death happened in mid-summer.

The diet of the Mongochen mammoth is similar to that of the Yukagir mammoth, which also lived during the LGM period (van Geel et al., 2008). Pollen and macrofossils of Poaceae, Cyperaceae and herbs dominate both complexes (Table 5). However, there was no arboreal pollen found in the gastrointestinal tract of the Yukagir mammoth. Furthermore, there were no remains of *Salix* found in the Mongochen mammoth complex, though *Salix* pollen and macroremains occurred in the Yukagir mammoth record. Also, the amount of moss macrofossils in the Yukagir mammoth record is lower than in the Mongochen mammoth. According to results from van Geel et al. (2008), the composition of the dung of the Yukagir mammoth indicates that this animal lived in cold, treeless vegetation in a mosaic of perennial wet areas within a largely arid steppe-tundra.

The seeds and pollen assemblages of the studied intestinal content of the Mongochen mammoth are similar to those retrieved from the gastrointestinal tracts of the Lyuba baby mammoth and the Yuribey mammoth (Table 5). Differences between the three records are attributed to different habitat conditions. The Lyuba baby mammoth and the Yuribey mammoth lived in warmer periods during the Middle Weichselian and the Early Holocene, when tree species were more widespread in the West Siberian Arctic (Sokolov, 1982; Strukova et al., 2010). The Mongochen mammoth died during the LGM, when small populations of boreal trees and shrubs may have existed in small refuges. The considerable quantity of moss, tree and wetland plant remains in the gastrointestinal tracts of Northwest Siberian mammoths suggests climate conditions in this area were less continental than in northeastern Siberia during the Middle Weichselian, the LGM and the Early Holocene.

Table 4
Different phytolith morphotypes in samples.

Sediments		Turf	Gray silts					Bluish-gray silts			Sample of the mammoth colon contents
Depth, cm		5–10	10–20	20–30	30–40	40–50	50–60	60–75	75–85	90–95	
Phytoliths (psc.)		281	167	60	184	50	169	62	121	360	137
Globular (3D)	Orbicular (2D)	+++	+	+	−	±	+	±	+++	++	++
	Oblong (2D)	++	++	−	+++	+	+	−	+++	+++	sin.
	Rondels elongate	±	++	±	+	−	++	−	+++	+++	sin.
Morphotypes Tabular (3D)	Plates smooth	±	±	±	±	++	±	−	±	±	+
	Plates saddle	+	±	−	−	+	sin.	−	++	−	±
	Plates rectangle	sin.	±	++	±	±	±	−	−	−	−
Trapeziform	Oval (2D)	±	±	−	±	±	±	+	±	+	+
	Trilobate (2D)	sin.	−	−	−	−	−	−	−	−	sin.
	Polylobate regular	−	−	−	−	−	−	−	−	−	+
Bilobate (2D)	Dumbbell	−	sin.	−	−	−	±	−	−	±	+
	Cross	−	sin.	−	−	−	−	−	−	−	−
Cylindric (3D)	Smooth long cells	+++	+++	+++	+++	+++	+++	++++	+++	++	+++
	Long cells with wavy margin	−	±	−	±	−	±	−	−	sin.	+
	Long cells	±	±	−	±	±	sin.	±	sin.	sin.	±
Cubic (3D) square (2d)		sin.	±	−	±	±	−	±	−	±	sin.
Trichom prickle		±	±	++	±	sin.	+++	sin.	±	±	++
Other types		++	+++	-	+	++	±	±	±	++	+
Morphotypes		11	14	6	9	9	12	5	9	11	13

Symbols: «++++», >50%; «+++», 50–20%; «++», 20–10%; «+», 10–5%; «±», 1–5%; «sin.», <1% (singular); «−», absent.

Table 5
Palaeobotanical finds in the intestinal contents of some Siberian mammoths.

Taxon	Geography	West Siberia			East Siberia
		Yamal Peninsula	Gydan Peninsula		Yakutia
		Lyuba baby mammoth	Mongochen mammoth	Yuribey mammoth	Yukagir mammoth
	Age (^{14}C BP)	41,700 (+700, −550)	18,370 ± 350	10,000 ± 70	18,510 ± 80
Bryophyta gen. indet.		m, p	m, p	m, p	m
Polypodiaceae gen. indet.		p			
Equisetaceae					
Equisetum sp.				p	
Lycopodiaceae					
Lycopodium sp.			p	p	
Selaginellaceae					
Selaginella pleistocenica				m	
Pinaceae					
Larix gmelinii				m, p	
Larix sibirica			m, p		
Larix sp.				m, p	
Picea obovata				p	
Picea sp.		p	p	p	
Pinus sibirica		p	p	p	
Pinus sylvestris		p	p		
Poaceae					
cf. *Agrostis* sp.					m
Arctophila fulva				p	
Hordeum sp.					m
Festuca sp.		m		m	
Gliceria sp.					m
Poa cf. *arctica*					m
Poa sp.				p	
Poaceae gen. indet.		p	m, p	m, p	m, p
Cyperaceae					
Carex cf. *acuta*			m		
Carex aquatilis			m		
Carex concolor				m	
Carex dioica					m
Carex hepburnii					m
Carex rostrata			m		
Carex sp.		m	m	m, p	m, p
Eriophorum cf. *brachyantherum*				m	
Eriophorum polystachion				m, p	
Eriophorum scheuchzeri				m	
Eriophorum vaginatum				m	
Eriophorum sp.				m, p	
Kobresia simpliciuscula				m	
cf. *Kobresia* sp.					m
Cyperaceae gen. indet.		p	p	m, p	p
Juncaceae					
Juncus castaneus				m	
Juncus sp.					m
Luzula sp.				m	
Liliaceae gen. indet.					p
Orchidaceae					
Epipactis sp.					p
Salicaceae					
Salix cf. *arctica*					m
Salix glauca				m, p	
Salix polaris				m	
Salix pulchra				m	
Salix sp.				m, p	m, p
Betulaceae					
Alnus (*Duschekia*) *fruticosa*			m, p	p	
Alnus incana		p			
Alnus hirsute				p	
Betula fruticosa				p	
Betula exilis				p	
Betula nana				m, p	
Betula sect. Betula(Albae)		p	m, p	p	
Betula sect. Nanae		p	p		
Betula sp.				m, p	

Table 5 (*continued*)

Taxon	Geography	West Siberia			East Siberia
		Yamal Peninsula	Gydan Peninsula		Yakutia
		Lyuba baby mammoth	Mongochen mammoth	Yuribey mammoth	Yukagir mammoth
	Age (^{14}C BP)	41,700 (+700, −550)	18,370 ± 350	10,000 ± 70	18,510 ± 80
Polygonaceae					
Bistorta maior				p	
Bistorta vivipara			m, p		
Persicaria maculata					p
Polygonum sp.				m	
Rumex acetocella					m, p
Rumex arcticus				m	
Rumex sp.					m
Polygonaceae gen. indet.		p			
Chenopodiaceae gen. indet.		p	p	p	m, p
Caryophyllaceae					
Cerastium maximum				m	
Cerastium sp.			m		
Gastrolychnis involucrata				m	
Minuartia rubella				m	
Minuartia sp.			m, p		
Sagina intermedia					m
Caryophyllaceae gen. indet.		p	m, p	p	p
Ranunculaceae					
Caltha palustris					m
Ranunculus acris		m			
Ranunculus cf. *flammula*		m			
Ranunculus gmelinii				p	
Ranunculus hyperboreus			m		
Ranunculus cf. *nivalis*					m
Ranunculus cf. *pygmaeus*					m
Ranunculus sceleratus			m		
Ranunculus sp.			m	p	
Thalictrum cf. *alpinum*				p	
Ranunculaceae gen. indet.		p		p	p
Papaveraceae					
Papaver pulvinatum				p	
Papaver sect. Scapiflora					m
Papaver sp.			m	p	m, p
Brassicaceae					
Draba sp.			m, p	p	m
Brassicaceae gen. indet.			m, p		p
Crassulaceae					
Sedum telephium				m	
Saxifragaceae					
Saxifraga hirculus				m	
Saxifraga sp.			p	m, p	
Grossulariaceae					
Ribes sp.				m	
Rosaceae					
Comarum palustre				m, p	
Dryas punctata				m, p	
Dryas sp.			m, p	m	
Potentilla hyparctica					m
Potentilla nivea			m		
Potentilla stipularis				m	
Potentilla sp.					m, p
Rubus cf. *chamaemorus*				m, p	p
Sanguisorba officinalis					p
Rosaceae gen. indet.		p	p		p
Fabaceae					
Lotus sp.					p
Apiaceae gen. indet.		P		p	p
Ericaceae gen. indet.		p	p	m, p	p
Primulaceae					
cf. *Androsace*					p
Lysimachia sp.					m
Plumbaginaceae					
Armeria sp.					p

(*continued on next page*)

Table 5 (*continued*)

Taxon	Geography	West Siberia			East Siberia
		Yamal Peninsula	Gydan Peninsula		Yakutia
		Lyuba baby mammoth	Mongochen mammoth	Yuribey mammoth	Yukagir mammoth
	Age (^{14}C BP)	41,700 (+700, −550)	18,370 ± 350	10,000 ± 70	18,510 ± 80
Polemoniaceae					
Polemonium boreale		p			
Polemonium sp.				p	p
Lamiaceae gen. indet.				m	
Plantaginaceae					
Plantago sp.					p
Valerianaceae					
Valeriana capitata		p		p	
Valeriana sp.				p	
Asteraceae					
Achillea/Petasites					m
Artemisia furcata				p	
Artemisia tilesii				m	
Artemisia sp.		p	p	p	p
Nardosmia sp.				p	
Liguliflorae		p	p		p
Tubuliflorae		p	p		p
Asteraceae gen. indet.			m	p	

Symbols: p – pollen, m – macrofossils.

The paleobotanical data obtained by studying the Mongochen mammoth gut contents provided the basis for reconstructions of environments at the time of the animal's life and death. Predominance of the plant remains typical of the present-day tundra suggests the existence of diversified formations of the tundra-like vegetation in the northwest of the Gydan Peninsula. Flat interfluves were most probably occupied by sedge and grass communities forming a thick grassy turf. In lower places, there was wet tundra with sedge, grass and mosses in combination with moss and grass communities. Some shrubs (dwarf birch, willow and dwarf alder) and undersized larch (probably, of prostrate form) could occur in such places. In the herbaceous layer there were sedge and grass species, mountain avens (*Dryas*), and herbs, with some green mosses on the soil surface.

Reconstructions of plant communities that existed at the time of the Mongochen mammoth based on studies of his intestinal tract contents agree well with the reconstructions of the LGM vegetation in northern West Siberia performed by other authors. Thus, pollen assemblages recovered from peat sampled in the north of Gydan Peninsula and ^{14}C-dated to 21,900 ± 900 (GIN-2469) reflect tundra environments with patches of meadow vegetation (Vasil'chuk, 2002). In the north of the Yamal Peninsula 22 to 14 ka BP, there was a thick cover of tundra vegetation, with widely occurring peatlands (Vasil'chuk et al., 2000).

The paleocommunities reconstructed for the northern Gydan Peninsula differ noticeably from those of the LGM time at Taimyr. According to pollen analysis (Andreev et al., 2003), the northern Taimyr Peninsula was dominated by steppe-like vegetation, along with tundra-like communities with *Betula* sect. *Nanae*, *Salix* and Cyperaceae. Macroremains of plants are mostly those of steppe xerophytes and tundra cryophytes (Kienast et al., 2001). Besides, some *Larix* macrofossils dated to LGM were found on Taimyr north of the modern tree limit (Mol et al., 2006; Binney et al., 2009).

4.6. Pollen record from sediments infilling the inner skull

Non-arboreal pollen, such as Poaceae, Cyperaceae, *Artemisia* and forbs, dominated in the pollen spectrum obtained from the single sample taken from the inside of the skull (Table 2). Pollen of *Betula nana* type, *Alnus fruticosa* type and *Salix* occur. Arboreal pollen and moss spores abound in the sample. The composition of pollen and spores in the resulting pollen spectrum is comparable with the pollen spectrum from the bluish-gray silt sampled at a depth of 80–75 cm. The lithological characteristics (e.g. colour and grain size distribution) of the deposits from the inner skull are similar to those of the adjacent and subjacent deposits, what suggests a common source.

4.7. Section of deposits from the mammoth site

As has been described above, the sequence of sediments at the mammoth locality is as follows (Fig. 4): 1) turf – 0–5 cm; 2) gray silts – 5–60 cm; 3) bluish-gray silts – 60–105 cm. The mammoth carcass lied within the layer of perennially frozen bluish-gray silts at a depth of 70–100 cm. The numerical dating results have not been obtained as yet.

Results of pollen analysis of the sediments sampled at the mammoth site are given in the pollen diagram (Fig. 7). According to changes in the pollen and spore composition, the diagram is subdivided into 4 local pollen zones (PZ).

Pollen spectra recovered from the bluish-gray silts at a depth 100–60 cm (PZ-1) feature the presence of AP and NAP in almost equal amounts and a high percentage of spores. Poaceae, Cyperaceae and *Artemisia* pollen is found in abundance, herb pollen is highly diversified in composition. The AP group is dominated by pollen of *Pinus sylvestris* type and *Betula nana* type; *Larix*, *Picea*, *Pinus sibirica* type, *Betula pubescens* type, *Alnus fruticosa*, *Salix* pollen are also found. There are moss spores in abundance, as well as some spores of *Selaginella selaginoides* type and *Lycopodium clavatum* type.

Pollen assemblages attributed to PZ-2 (gray silts at a depth of 60 to 15 cm) show higher proportions of arboreal pollen (up to 60–75%) due to a higher Pinaceae content (*Picea* and *Pinus sylvestris* type). It is not inconceivable that a part of the Pinaceae pollen has been redeposited; it is not easy, however, to distinguish between the redeposited and *in situ* pollen grains because of good preservation of the former. That is typical for pollen spectra of the northern West Siberia (Vasil'chuk, 2002; Andreev et al., 2006). Proportion of Poaceae and Cyperaceae is diminished. Of spore-

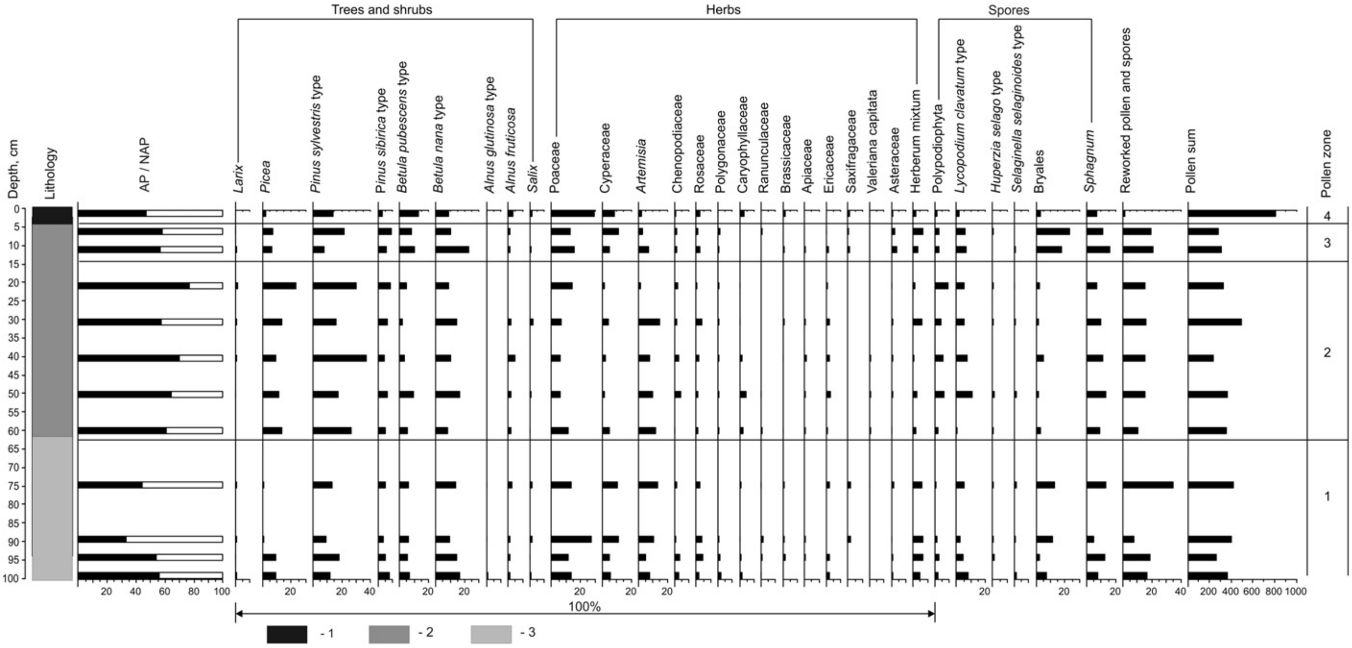

Fig. 7. Percentage pollen and spore diagram of samples from Mongochen mammoth site.

bearing plants, spores of *Sphagnum*, *Lycopodium clavatum* type and Polypodiophyta occur in abundance.

Pollen assemblages of PZ-3 (the uppermost part of gray silts, at 15 to 5 cm depth) are noted for a decrease in Pinaceae content along with rise in proportion of *Betula*, both tree and shrub forms. Mosses gain considerably in importance.

Pollen assemblage PZ-4 characterizes the modern vegetation of the mammoth site area. It contains AP and NAP pollen in almost equal proportions, while the content of higher cryptogam spores is rather low. Poaceae and Cyperaceae pollen is abundant. Some grains of *Artemisia* pollen are present, along with those of arctic herbs. The pollen assemblage of herbs and dwarf shrubs corresponds on the whole to the grass cover of the arctic tundra.

As the northern limit of the modern ranges of *Pinus sylvestris*, *Betula pendula*, *Picea* sp., *Abies sibirica*, *Pinus sibirica* and *Larix sibirica* on the Gydan Peninsula is 2° latitude (220 km) south of the studied locality (Stanischeva, 1982; Kremenetsky et al., 1996), the high proportion of arboreal pollen in the recent pollen assemblage (sod) may result from input of pollen brought from the southern arctic or northern subarctic tundra by air. As dwarf shrubs (*Betula nana*) are absent from the northern arctic tundra communities either on flat interfluves or in valleys and other habitats (Aleksandrova, 1977), the high proportion of shrub pollen in the modern pollen assemblage may be considered as evidence for pollen transportation by air. The source of the pollen may be either nearby intrazonal plant formations, or distant plant formations (e.g. those of southern arctic or northern subarctic). On the whole, proportion of exotic airborne pollen is typically high in the recent pollen assemblage of northern West Siberia (Serova, 1982; Vasil'chuk, 2002, 2005). It is quite possible that the presence of arboreal pollen in lower-lying layers may be partly the result of long-distance transportation by air.

According to the result of biomorph analysis, the sediments contain sponge spicules and frustules of diatom algae in abundance (Table 3, Fig. 8), indicating that the silts were deposited during repeatedly occurring periods of hydromorphism. The biomorph assemblage recovered from the bluish-gray silts is dominated by phytoliths of mosses, grasses and bilobate herbs, with occasional phytoliths of sedges and conifers. In the biomorph assemblage from the gray silts, phytoliths of bilobate herbs, grasses and mosses are prevalent.

Most plant macrofossils from the section are attributable to mesophytes and hydrophytes characteristic of various tundra plant communities (Table 1). A complex of plant macrofossils recovered from bluish-gray silts includes numerous remains of Poaceae, *Papaver* sp., *Draba* spp. Some moss stems together with macroremains of larch and birch trees were found.

Gray silts yielded mostly macroremains of various herbs (*Minuartia* spp., *Papaver* sp., *Draba* spp., *Potentilla nivea*); grasses are less numerous, while mosses, dwarf birch (*Betula nana*) and undershrubs (*Dryas* sp.) occur only occasionally. Two fragments of *Rubus* cf. *idaeus* seed were found in a sample taken from a depth of 20–30 cm. Seeds found in a sod sample completely correspond to the present-day vegetation of the arctic tundra, with leaves of willow and mountain avens (*Dryas*), fruits and seeds of *Phleum* sp., *Luzula* sp., *Minuartia* spp., *Papaver* sp., *Draba* spp., *Saxifraga* sp., bulbs of *Bistorta viviparum*, as well as moss stems.

The integrated paleobotanical studies of sediments at the mammoth locality made it possible to reconstruct plant communities that existed at the time of sedimentation (Table 6). According to the paleobotanical data, tundra-like communities persisted in the region throughout the time of sediment accumulation. Dominant were communities consisting of mosses and herbs or mosses, grasses and dwarf shrubs, with prevalent sedges and grasses. Larch trees and shrubs occurred sporadically. *Artemisia* grew on disturbed grounds. It may be concluded, however, that the entire sequence was deposited under climatic conditions milder than the arctic climate of today. A more clement climate is suggested by the presence of macroremains and pollen of *Larix* and *Betula* sect. Betula. At present, the northern limit of both birch and larch ranges is 200 km south of the Mongochen mammoth locality. Another evidence of difference between the present and past environments is the presence of *Selaginella selaginoides* spores and macroremains in the deposits enclosing the mammoth carcass. This plant occurs south of the locality, in forest communities and in southern tundra; it is usually found in wet, well drained habitats (Krasnoborov, 1988; Heidel and Handley, 2006).

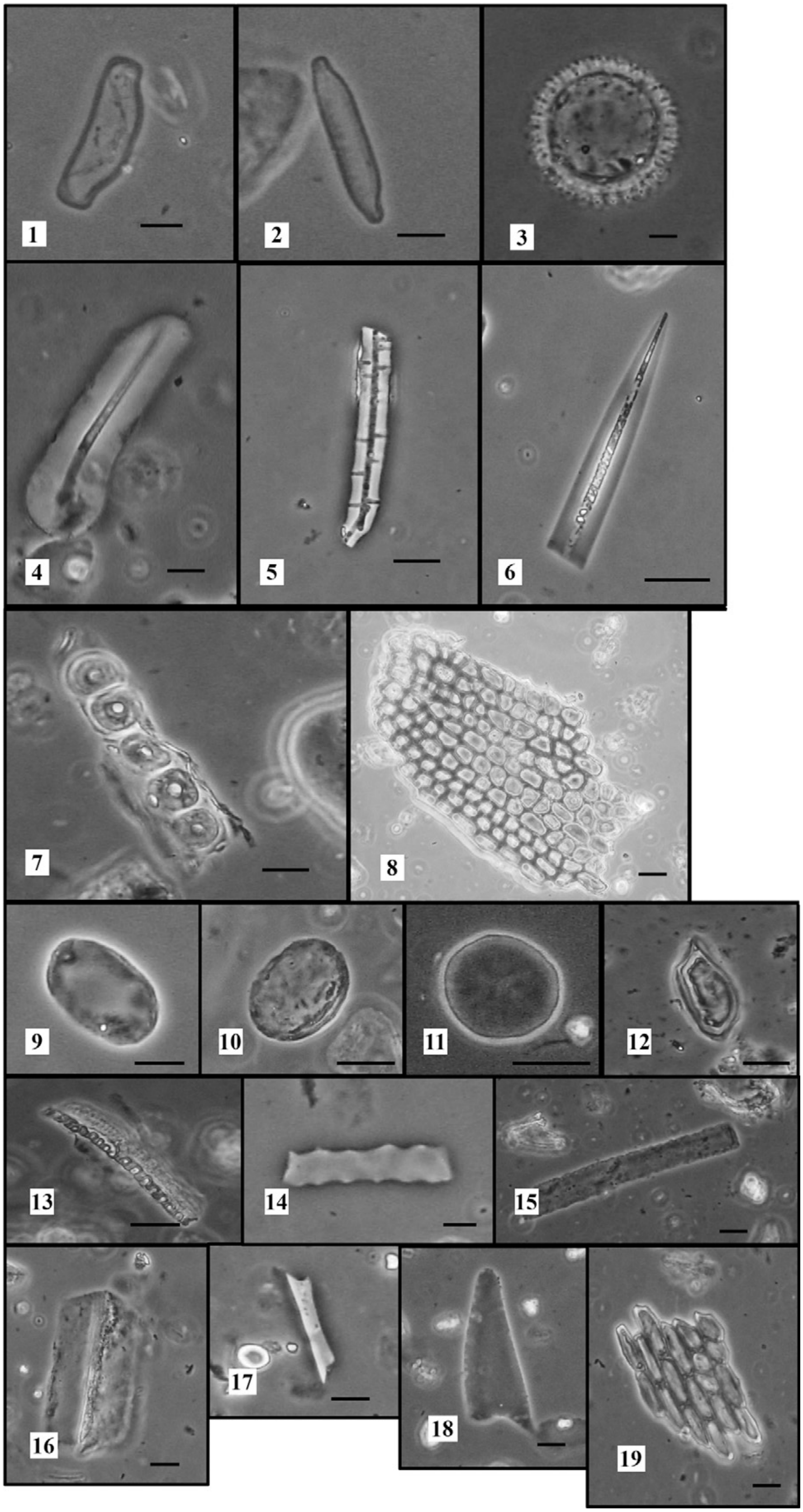

Fig. 8. Siliceous paleofossils, phytoliths and plant tissue from sediment of Mongochen mammoth site. 1–3: diatom algae; 4–6: sponge spicules; 7: tissue of *Carex sp.*; 8; moss tissue; phytoliths of moss: 9: oval smooth form; 10: granulate surface on oval form; 11: globular form; 12, 19: leaf cells of moss; 13: crenate, long cells with wavy margin; 14: prickle elongate form with prickle; 15: elongate form granulate surface; 16, 17: trapeziform phytolith; 18: trichome, prickle. Scale bar = 20 μm.

Table 6
Summarized results of paleobotanical studies at the Mongochen mammoth find.

Depth, cm	Sediments	Pollen analysis	Plant macrofossils analysis	Biomorphic and phytolith analysis	Reconstructed vegetation
0–5	Turf	PZ-4. AP and NAP are in practically equal quantities. Poaceae pollen is dominant, Cyperaceae and herb pollen are present. Arboreal pollen is brought from a distance.	*Dryas* sp. macrofossils are dominant. Some *Salix* and *Bistorta viviparum* are present. No remains of trees are found.	Bilobate herbs and moss phytoliths are dominant (20–50%).	Arctic tundra (with *Dryas* sp.)
5–60	Gray silts	PZ-3. Proportion of AP increased. Proportion of coniferous pollen lessened that of *Betula nana* type gained in importance. *Artemisia* became less abundant, and Poaceae pollen increased in number. Moss proportion increased considerably. PZ-2. Proportion of *Pinus sylvestris* type and *Picea* pollen has grown, while that of Cyperaceae fell; *Artemisia* underwent a rise. Spores of Lycopodium and *Sphagnum* mosses are present.	Poaceae macrofossils decreased in number. Seeds of *Papaver* sp., *Draba* spp. and *Minuartia* spp., *Potentilla nivea* are found in abundance. Tree macrofossils are absent, except for *Betula nana*. *Selaginella selaginoides* macrofossils are recorded.	There are numerous unidentifiable remains of plants (detritus) and mushroom fossils present. Bilobate herbs, grasses and moss phytoliths are rather numerous. Coniferous plant phytoliths are extremely scarce.	Tundra-like grass and herb communities with dwarf birch.
60–105	Bluish-gray silts	PZ-1. AP and NAP are found in practically equal number. Pollen assemblage is dominated by Poaceae, Cyperaceae and *Artemisia*. Pollen of *Betula nana* and *Pinus sylvestris* types are rather common, *Larix* occurs occasionally. *Selaginella selaginoides* spores are present.	Poaceae macrofossils are dominant. Seeds of *Papaver* sp., *Draba* spp. and *Minuartia* spp. are numerous. Macrofossils of *Larix sibirica*, *Betula* sect. Betula are found. *Selaginella selaginoides* remains are present.	Dominant are moss phytoliths (20–50%). Phytoliths of bilobate herbs are abundant (10–20%), some grass phytoliths are also present. Single phytoliths of coniferous trees are found. Mushroom remains are scarce.	Tundra-like herb and grass communities, probably with larch and birch.

5. Conclusion

As follows from the analysis of the Mongochen mammoth skeleton orientation, the animal fell into a frost fissure or in a narrow gully with its back downward and died in that position. This may account for the difference in age between the mammoth remains and the enclosing sediments, the former being younger than the latter.

In spite of small amount of herb and grass macroremains in the Mongochen mammoth intestines, its diet consisted basically of herbaceous plants, mostly grasses and sedges. The scarcity of their macroremains may be attributed to the fact that their skin and soft tissues are insufficiently resistant to attack of mechanical and biochemical agents in the gastrointestinal tract of the animal (Sukachev, 1914; Solonevich et al., 1977; Gorlova, 1982; Stanischeva, 1982; Ukraintseva, 1982; Savvinova, 2007; van Geel et al., 2007, and al.). As well, the mammoth diet included sprouts of larch and some shrubs. Abundant remains of moss in the intestine contents are indicative of widely spread wetlands on the Mongochen mammoth grazing area rather than the feeding habits of the animal. The specific assortment of micro-and macroremains in the gut contents suggests the mammoth died in the middle of the summer.

At the time of the Mongochen mammoth death and burial there were various tundra-like formations widespread in the northeast of the Gydan Peninsula, as suggested by the dominance (both in macro-and microremains) of plants characteristic of the modern tundra flora. Sedge and grass communities formed a thick turf on flat interfluves. Depressions were occupied with sedge-grass-moss tundra wetlands in combination with dwarf-shrub and moss communities. Some shrubs (such as dwarf arctic birch, willow, and *Alnaster*) as well as low larch trees could grow there. The layer of herbaceous plants and dwarf shrubs typically consisted of sedge and grass species, *Dryas punctata*, and herbs. In the ground layer of those formations were green mosses (*Drepanocladus* sp., *Calliergon* sp. and some others), most abundant in wetter places.

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