



Taphonomic phenomenon of ancient hair from Glacial Beringia: perspectives for palaeoecological reconstructions

IRINA V. KIRILLOVA, JOHANNES VAN DER PLICHT, STANISLAV V. GUBIN, OKSANA G. ZANINA, OLGA F. CHERNOVA, ELENA G. LAPTEVA, SVETLANA S. TROFIMOVA, EUGENY V. ZINOVYEV, ANTON A. ZHAROV, ELENA O. FADEEVA, THIJS VAN KOLFSCHOTEN, FEDOR K. SHIDLOVSKIY AND ALEXEY A. KOTOV

BOREAS



Kirillova, I. V., van der Plicht, J., Gubin, S. V., Zanina, O. G., Chernova, O. F., Lapteva, E. G., Trofimova, S. S., Zinovyev, E. V., Zharov, A. A., Fadeeva, E. O., van Kolfschoten, T., Shidlovskiy, F. K. & Kotov, A. A.: Taphonomic phenomenon of ancient hair from Glacial Beringia: perspectives for palaeoecological reconstructions. *Boreas*. 10.1111/bor.12162. ISSN 0300-9483.

An accumulation of mammoth hair, discovered in the Bol'shaya Chukochya River valley (northeast Yakutia, Russia), was found to contain remains of terrestrial and aquatic organisms, including plants, insects, crustaceans, birds and mammals. Radiocarbon dating indicated that this post-mortem taphocoenosis represented multiple time periods. The mammoth hair was dated to older than 45 ka BP, the plants were dated to 12 750±50 a BP (which corresponds to a shift in the environmental conditions and landscapes during the formation of thermokarst in northeastern Russia) and the bird feathers were dated to 4115±40 a BP. A scenario of the formation of this fossil assemblage is proposed, covering the MIS 3-1 time range. The hair also yielded various Arctic branchiopod crustaceans, which inhabit shallow temporary water bodies and therefore are important for reconstruction of palaeoenvironments. The cladoceran subgenus *Daphnia* (*Ctenodaphnia*), currently absent from the Asian part of Beringia, is reported from this region for the first time. The study demonstrates that the discovered permafrost-preserved hair is a unique repository of Ice Age organisms.

Irina V. Kirillova and Fedor K. Shidlovskiy, National Alliance of Shidlovskiy 'Ice Age' Ice Age Museum, Mira Prt. 119, Moscow 129223, Russia; Johannes van der Plicht, Center for Isotope Research, Groningen University, Nijenborgh 4,9747 AG Groningen, the Netherlands; Johannes van der Plicht and Thijs van Kolfschoten Faculty of Archaeology, Leiden University, Einsteinweg 2, 2333 CC Leiden, the Netherlands; Stanislav V. Gubin and Oksana G. Zanina, Institute of Physicochemical and Biological Problems of Soil Science, Institutskaya Str. 2, Pushino, Moscow Region, 142290 Russia; Olga F. Chernova, Anton A. Zharov, Elena O. Fadeeva and Alexey A. Kotov (corresponding author: alexey-a-kotov@yandex.ru), A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences Leninskiy Prt. 33, Moscow, 119071 Russia; Elena G. Lapteva, Svetlana S. Trofimova and Eugeny V. Zinovyev, Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Vos'mogo Marta Str. 202, Yekaterinburg, 620144 Russia; received 26th July 2015, accepted 29th November 2015.

Permafrost is a natural and unique cryoconservant, which preserves abundant remains of ancient organisms. These include remains of mammals of the Mammoth Fauna (Tchershki 1891; Zalenskii 1903; Popov 1948; Flerov 1977; Vereshchagin & Mikhelson 1981; Guthrie 1990; Tomskaya 2000; Rozanov 2001; Boeskovrov *et al.* 2011; Kosintsev *et al.* 2012; Spasskaya *et al.* 2012; Kirillova *et al.* 2013), plants (Tomskaya 1981, 2000; Yurtsev 1981; Ukraintseva 1993; Lopatina & Zanina 2006; Yashina *et al.* 2012), insects (Kiselev 1981; Berman 1990) and ancient microorganisms (Gilichinsky & Wagener 1995; Gilichinsky 2002). These remains enable reconstruction of past environments. In recent years, permafrost deposits have also been investigated for microfossils (Schirrmeister *et al.* 2002; Gubin *et al.* 2003; Sher *et al.* 2005; Zanina *et al.* 2011). However, fossil small crustaceans, a potentially valuable source of data for palaeoecological reconstructions, have only been reported sporadically and cursorily from permafrost. Our multidisciplinary study was triggered by the unexpected discovery of such crustaceans in a sample of permafrost-preserved mammoth (*Mammuthus* sp.) hair found near the Bol'shaya Chukochya River.

Large masses of hair shed by present-day tundra mammals, such as reindeer, are frequently found. The

heaps of hair shed by herds at river crossings can become preserved if high water carries them into shallow backwaters, where they get rapidly buried by fluvial or snow-melt sediments. The adsorbing properties of hair are well known and are used, for example, to remove oil from water. Loose materials are also known for their ability to trap small particles: moss polsters accumulate pollen (Cundill 1991) and some types of sediments naturally purify water from mineral and organic particles. The importance of ancient hair as a new source of information on organisms and environments of the past was pointed out for the first time by Kirillova *et al.* (2015).

Near the end of the 1990s, Ivan Khristenko from the village of Andryushkino found over 100 L of yellowish grey hair (Fig. 1) in a landslide of an alas terrace (a steep-sided depression resulting from thawing of permafrost) in the middle reaches of the Bol'shaya Chukochya River in the Kolyma Lowland (Republic of Sakha-Yakutia, eastern Russia). The permafrost base in that area is formed by Ice Complex deposits overlain by 'taberal' layers, the term used in Russian literature to denote mineral and organic matter derived from the thawed ice complex and deposited at the bottoms of thermokarst lakes. Their age corresponds to Marine Oxygen Isotope Stages (MIS) 2 and 3. At the level of

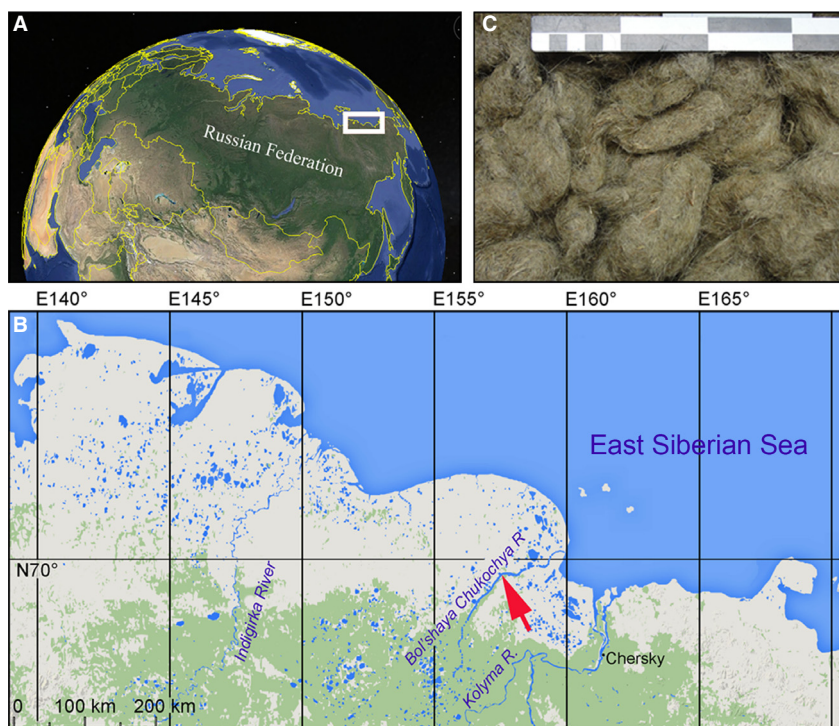


Fig. 1. The site in the middle reaches of the Bol'shaya Chukochya River where the mammoth hair was discovered. A. Northern hemisphere. B. Northern portion of eastern Siberia. C. The larger mats of mammoth hair.

the tabular layers, there are remains of a lacustrine terrace formed during regression of the thermokarst lake. These deposits descend to the Bol'shaya Chukochya river bed as an extensive landslide, which is dissected by the river. At the location where the hair was found, the bank is normally 1.5 m high; at times of low water this can increase to 1.8 m.

Preliminary laboratory inspection of the hair revealed it to contain abundant remains of organisms, including plants, invertebrates and vertebrates. The goals of our study were to identify these remains and to reconstruct the corresponding past environments and the process of burial.

Material and methods

We examined the yellowish-grey coarse mammoth hair, which was matted in clumps when found. The sample is preserved at the Ice Age Museum in Moscow (coll. no. F-2362/1). The trapped debris was extracted manually under a stereomicroscope. The total yield was 2 L, half of which comprised small hair fragments and the other half plants, invertebrate and vertebrate remains, and small (5–10 mm) grey clayey pellets. We examined 50 hairs and eight bird feathers from the inner part of the hair mats. Spores and pollen grains came from the middle parts of the four most dense small mats. The majority of samples mostly consisted of decomposed plant detritus; some samples additionally included up to 50% of mineral particles.

Plant remains were identified from different fractions. Particles smaller than 0.5 mm were used to search for phytoliths and pollen, whereas those larger than 0.5 mm were used to study macroscopic plant remains. Remains of aquatic invertebrates were also recovered. Radiocarbon dates were obtained for hair samples, large plant remains and several bird feathers.

Optical microscopy

The thicknesses of the hairs and their medullae (when preserved) were measured under a Keyence Biorevo BZ-9000 microscope (Japan) at 70, 140 and 360 \times magnifications. Taxonomic identification was performed using the database compiled by Chernova & Tselikova (2004), Chernova *et al.* (2009, 2014) and Chernova & Kirillova (2013).

For macrofossil analysis, we treated plant remains using the standard method of Nikitin (1969). For pollen analysis, the samples were prepared according to Faegri & Iversen (1989). At least 500 pollen grains were counted in every sample. The percentages of arboreal (AP) and non-arboreal (NAP) pollen and also of spores were estimated based on the total pollen sum that includes sum of tree, shrub and herb pollen.

Phytoliths were extracted from samples by the wet oxidation method (Piperno 1988), using 10% HCl and 30% H₂O₂, followed by drying in a furnace at 350 °C. The material obtained was examined in glycerol under a Carl Zeiss Axiostar Plus microscope at 200–400 \times

magnifications. Microfossils were studied under Olympus BX 51 and Carl Zeiss Axiostar Plus microscopes at 100, 400 and 1000 \times magnifications.

Aquatic invertebrate remains were identified using a stereoscopic Leica MZ75 microscope at various magnifications.

Scanning electron microscopy

We used JSM 840A (Jeol, Japan), Vega 3 (TESCAN, Czech Republic) and MV 2300 (Camscan, Cambridge, UK) microscopes. The specimens for SEM were prepared according to the standard method, which was essentially the same for hair, feathers and remains of microscopic crustaceans (ephippia and chitin fragments). They were dehydrated in graded alcohols, dried and coated with gold using an Edwards S-150A sputter coater. For the hairs and feathers, the surface and cross and longitudinal sections of hair shafts and feather barbs were examined. Microfossils were examined in high and low vacuum using back-scattered electron and secondary electron detectors.

Radiocarbon dating

The samples were analysed at the Groningen accelerator mass spectrometer (AMS) facility, which is based on a 2.5 MV accelerator and measures ^{14}C concentration in graphite (van der Plicht *et al.* 2000). Prior to measurement, the sample objects (mammoth hairs, fragments of barley *Hordeum* and feathers of representatives of genus *Anser*) were chemically pretreated in order to isolate the datable fraction and remove contaminants (Mook & Streurman 1983). The routine treatment consists of the following steps: (i) with acid (HCl) in order to remove soil carbonate and possibly infiltrated humic acids; (ii) with alkali (NaOH) to remove e.g. soil humates; and (iii) with acid (HCl) to remove any CO_2 absorbed during step (ii). This treatment is referred to as the 'AAA' treatment. The feather sample appeared to be very delicate and could only receive single acid (A) treatment. All other samples received the full standard AAA treatment.

The samples were then combusted and turned into CO_2 by an elemental analyser (EA), coupled on-line with a stable isotope mass spectrometer (MS). The EA was also used for purifying the CO_2 . In addition, the EA/MS system enabled precise measurement of the $\delta^{13}\text{C}$ values. The CO_2 was reduced to graphite by reacting under excess H_2 gas (Aerts-Bijma *et al.* 2001). This graphite was pressed into target holders, which were placed in the ion source of the AMS.

The results are reported as conventional ^{14}C years BP, calculated based on the conventional ^{14}C half-life and corrected for isotopic fractionation (Mook & van der Plicht 1999). The ^{14}C ages were calibrated into cal-

endar ages (referred to as 'cal. a BP', i.e. calendar years relative to 1950) using the recommended calibration curve IntCal13 (Reimer *et al.* 2013).

Results

Hair

Most of the hair was matted into mats ranging in size from 3 to 10 cm. Smaller, dense clumps of hair, <1 cm in diameter, were present in smaller numbers. These had probably formed during the animal's life. Individual reddish guard hairs up to 30 cm long stood out from the main substance of the mats. The mats mostly comprised mammoth hairs.

The colour and thickness of the hairs corresponded to those of the woolly mammoth and woolly rhinoceros. The hair fragments (from 4.5 to 14.1 cm long) formed several categories, which differed in their colour, structure and thickness of the shaft, and development of the medulla (Fig. 2). The overhairs were light or dark brown, cylindrical or slightly flattened and curved, $\sim 203\ \mu\text{m}$ in diameter. Their fragmental medulla occupied 5–21% of the shaft width or was absent. Guard hairs I (113–136 μm thick) and II (80–90 μm) were light yellow or white, with a longitudinal groove and fragmental medulla (20–50%). The underhairs (34–45 μm) were white, strongly curved (4–5 waves per 5.6–6.1 cm fragment) and lacked a medulla. The cuticle of the overhairs and guards had a circular pattern, with individual scales encircling the shaft completely. The maximum scale height was 30 μm on the overhairs and 40 μm on the guards. Most of the large hairs examined were identified as belonging to the woolly mammoth based on the architectonics and extent of development of their medulla and the cuticle pattern. In this species, the hair medulla is degenerative, in the shape of a narrow, uneven (sometimes resembling beads), continuous or fragmentary cord along the shaft axis, occupying 5 to 15% of the shaft width (Fig. 2D). However the medulla of some hairs was the same as in the woolly rhinoceros, i.e. well developed (occupying up to 50% of the shaft width) and resembling a longitudinal series of cylindrical discs (Fig. 2G). In addition, the hair mats yielded one hair of the ancient bison *Bison* sp., which is recognizable by the well-developed medulla (Fig. 2B, C, E, F).

Feathers

The feathers found in the hair mats belonged to the Anseriformes and Galliformes (Fig. 3). Four feathers shared the following diagnostic characteristics.

- The cuticular ornament is formed of longitudinal extended pentagonal–hexagonal spindle-shaped scales, and the smooth ornamentation of its surface

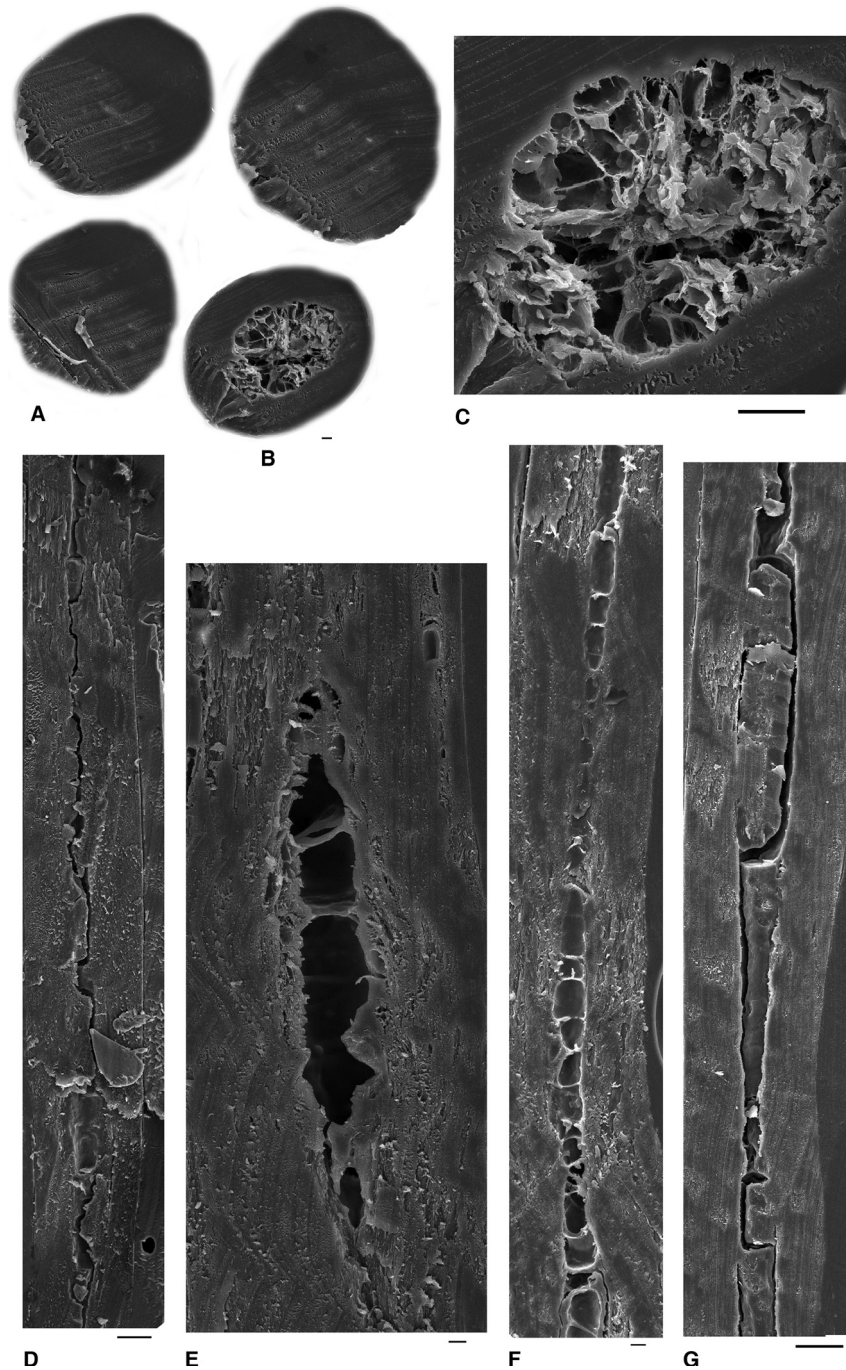


Fig. 2. Microstructure of fossil hairs found at the Bol'shaya Chukochya River. A. Cross-section of a hair shaft of woolly mammoth. B. The same, ancient bison. C. Medulla of an ancient bison hair. D. Longitudinal section of a woolly mammoth hair. E, F. The same, ancient bison. G. The same, woolly rhino. SEM photographs. Scale bars: A, B, D, E = 10 μm ; C, F, G = 50 μm .

- is composed of thick, tightly closed and interlacing fibres extending along the long scale axis. The scales are connected by thickened cords.
- The barbule internode smoothly continues into a rather narrow node with two or three needle-like prongs, as is characteristic for the genera *Cygnus*, *Anser* and *Cygnopsis*.
- Wide three-edged nodes, longitudinal ribs and a triangular slit in the apical part of the internode, gradual replacement of wide nodes towards the barb apex by relatively narrow nodes with small prongs, and then by narrow nodes with two long needle-like prongs. These features are all characteristic of the genus *Anas*.

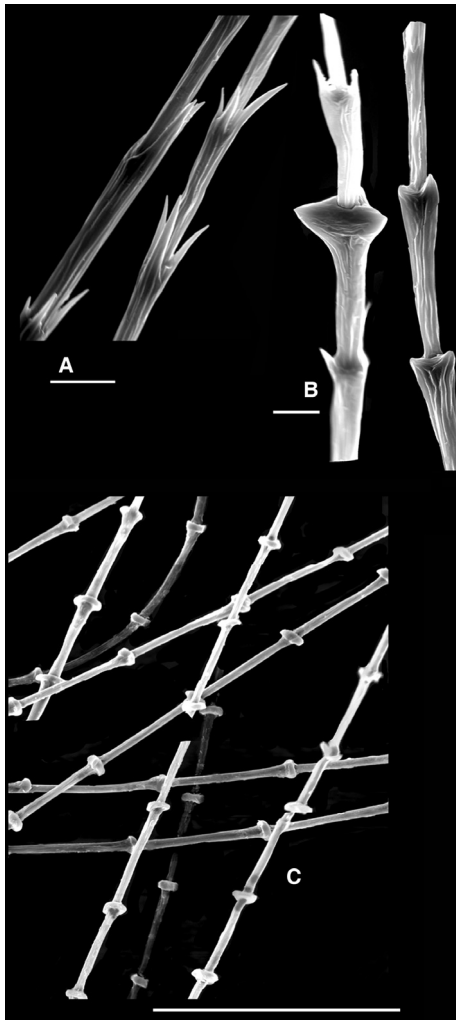


Fig. 3. Barbulus nodes of the down feathers of representatives of Anseriformes (A, B) and Galliformes (C). Scale bars: A, B = 10 µm; C = 100 µm.

- In tested feathers, the pigmentation is absent in the hamuli and cilia, but it is present at node-internode of feather barbulus. First feature is common for *Cygnus cygnus*, *C. olor*, *Anser fabalis*, *Anser albifrons* and *Cygnopsis cygnoides*; second feature is typical of some species of the genus *Anas*, in particular *Anas querquedula*. Therefore, we attributed the tested feathers to Anseriformes.

The other four feathers shared the following characteristics: (i) the ring nodes (tori) on the down barbules correspond to the morphology of *Lagopus lagopus* and *L. mutus*. *Perdix perdix* lacks such nodes and has slightly widened nodes with four small conical prongs; and (ii) mosaic pigmentation of the internodes and nodes is more pronounced in the down barbules, and the pigment is accumulated in the medial part of the node, as in *L. lagopus* and *L. mutus*. In *P. perdix* mosaic pigmentation is only

present in the internodes. These feathers were attributed to Galliformes.

Palaeobotanical studies

The number and morphological diversity of discovered phytoliths were low. These were mostly large forms (about 100 µm size): massive trichomes, elongated structures, with varying margins (wavy, scalloped, serrated and smooth) and plates. The material consisted mostly of tissues and phytoliths of Poaceae (Fig. 4), which were well preserved, showing distinct cell structure and stomatal complexes. We identified *Poa* sp., *Calamagrostis* sp. and *Bromus* sp. Tissue remains of *Hordeum* sp., which grows today on flood-plains and alas meadows in Yakutia, were also recorded. Remains of *Carex* sp. and *Eriophorum* sp. (Cyperaceae) were less common, and those of moss (*Aulacomnium* sp.) and undershrubs (probably willow, blueberry and *Arctous*) were rare.

Remains of woody plants were not observed. Mycelia of microscopic keratinophilic fungi and chains of four to eight cells of the colonial algae *Scenedesmus* sp., which inhabits stagnant freshwater ponds, were abundant. Diatoms were not found.

The palynological spectra (2000 pollen grains) were dominated by Poaceae (Table 1). A small percentage of pollen (1–9%) belonged to the family Caryophyllaceae. Pollen grains of wormwood (*Artemisia* sp.), forbs, Chenopodiaceae, trees (*Pinus* subg. *Diploxylon*, *Betula* sect. *Albae*) and shrubs (*Salix* sp., *Betula* sect. *Nanae*, *Alnus fruticosa* (Rupr.)), and the spores of bog mosses (*Sphagnum* sp.) and coprophilous fungi of the family Sordariaceae (*Podospora*-type and *Sordaria*-type) occurred sporadically.

The macroremains of plants (Table 2) were mostly represented by grasses, dominated by the wild barley *Hordeum brevisubulatum* (Trin.) Link, which also dominates in the modern alas meadows of the Kolyma Region. The chamomile *Tripleurospermum hookeri* Sch. Bip., Chenopodiaceae, the knotweed *Polygonum* sp. and the cinquefoil *Potentilla anserina* L. are indicators of disturbed meadow sites and shore slopes. Aquatic vegetation was represented by shallow-water species, the pondweed *Potamogeton* sp. and the buttercup *Batrachium* sp. The sedge *Carex* sp. and the buckbean *Menyanthes trifoliata* L. are characteristic of wetlands. Shrubs appear to have been widespread in the flood-plain (alder *Alnus fruticosa*) and watersheds (dwarf willows of the genus *Salix*).

Insects

Table 3 shows the taxonomic composition of insect remains retrieved from the hair mats (Fig. 5). Most of the insects belonged to the Coleoptera and some to Hymenoptera. The assemblage was dominated (36.6%

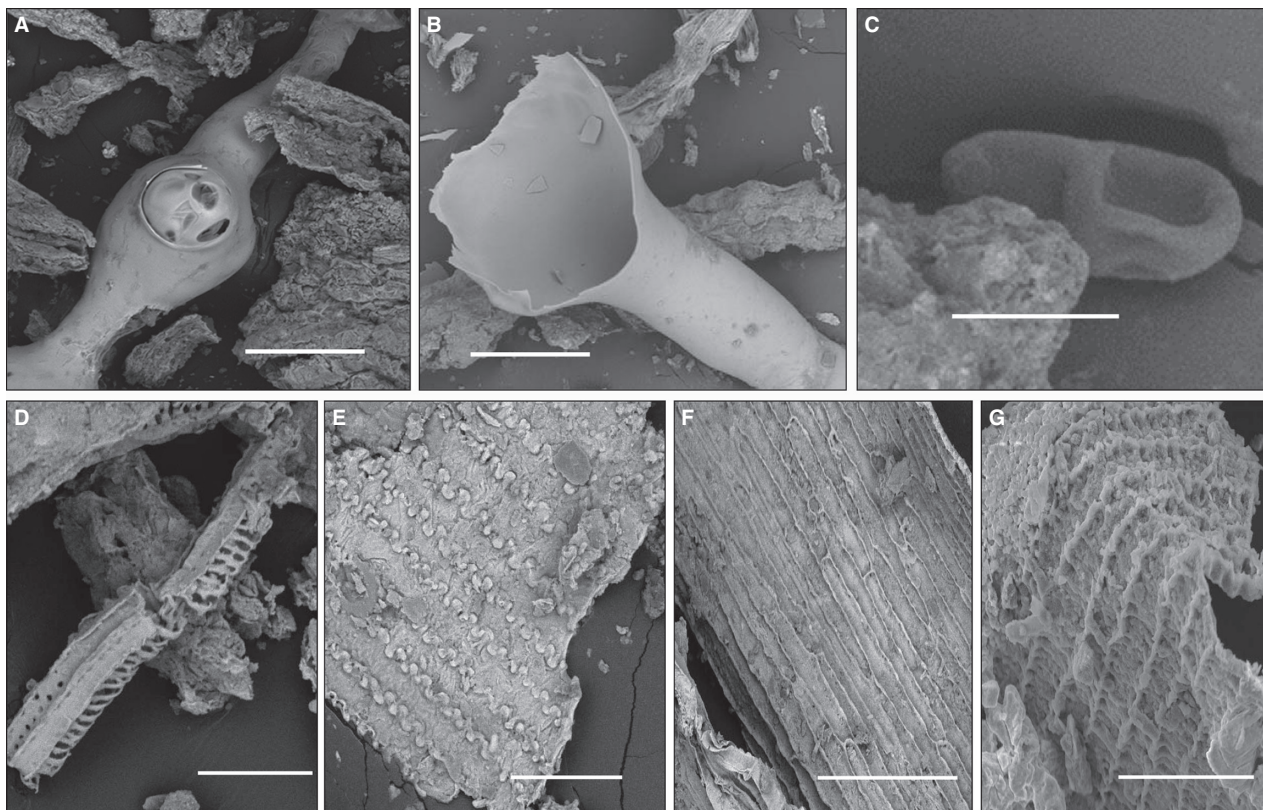


Fig. 4. Phytoliths, plant tissues and fungi found in large hair mats from the Bol'shaya Chukochya River. A, B. Remains of keratinophilic fungi. C. Fungal spore. D. Vascular tissue. E, F, G. Grass tissues. Scale bars: A, B = 100 μm ; C = 10 μm ; D = 20 μm ; E, F, G = 50 μm .

Table 1. Pollen and spore spectra from the small dense hair mats.

Taxon	Samples								Total	
	1		2		3		4		N	%
	N	%	N	%	N	%	N	%		
<i>Alnus fruticosa</i>	1	0.2							1	0.1
<i>Artemisia</i>	6	1.2	10	2	7	1.4	3	0.6	26	1.3
Asterioideae	3	0.6	6	1.2	2	0.4	3	0.6	14	0.7
<i>Betula</i> sect. <i>Albae</i>			2	0.4			1	0.2	3	0.2
<i>Betula</i> sect. <i>Nanae</i>	3	0.6							3	0.2
Caryophyllaceae	7	1.4	20	4	45	9	16	3.2	88	4.4
Chenopodiaceae			1	0.2					1	0.1
Cichorioideae	4	0.8	4	0.8	1	0.2	2	0.4	11	0.6
Cyperaceae	2	0.4			2	0.4	3	0.6	7	0.4
<i>Pinus</i> subg. <i>Diploxylon</i>	2	0.4			1	0.2			3	0.2
Poaceae	472	94.4	457	91.4	442	88.4	470	94	1841	92.1
Rosaceae							1	0.2	1	0.1
<i>Salix</i>							1	0.2	1	0.1
Pollen sum	500	100	500	100	500	100	500	100	2000	100
<i>Sphagnum</i>	1	0.2							1	0.1
Sordariaceae	1	0.2	15	3	11	2.2	6	1.2	33	2.5

of the total number of fragments) by pill beetles of the genus *Morychus*, usually identified as *M. viridis* Kuzm. et Kor. This species was a key element of the so-called tundra-steppe Pleistocene communities of northeastern Siberia (Berman 1990; Sher *et al.* 2005). Another,

subdominant (19.4%) member of the assemblage was the ground beetle *Poecilus nearcticus* (Lindr.). Arctic species were represented by the ground beetles *Amara alpina* (Payk.) and *Pterostichus costatus* (Men.) and the leaf beetle *Chrysolina cavigera* (Sahlb.). An interesting

Table 2. Plant macro-remains from large hair mats.

Taxon	Remains
<i>Alnus fruticosa</i> (Rupr.) Pouzar.	1 scale
Betulaceae gen. indet.	1 nutlet
<i>Salix</i> sp.	2 leaf fragments, 3 fragments of seed capsules
<i>Alopecurus</i> sp.	1 spikelet
<i>Deschampsia</i> sp.	1 spikelet
<i>Hordeum brevisubulatum</i> (Trin.) Link	220 spikelets
<i>Festuca</i> sp.	2 spikelets
Poaceae gen. indet.	66 caryopsis
<i>Carex</i> sp.	70 nutlets, 2 utricles
<i>Polygonum</i> sp.	217 nutlets
<i>Atriplex</i> sp. sp.	56 seeds
<i>Chenopodium</i> cf. <i>prostratum</i> Bunge	6 seeds
Chenopodiaceae gen. indet.	835 seeds
Caryophyllaceae gen. indet.	7 seeds
Brassicaceae gen. indet.	1 seed
<i>Rubus</i> sp.	4 seeds
<i>Potentilla anserina</i> L.	1 fruit
<i>Potentilla</i> sp. sp.	20 fruits
<i>Batrachium</i> sp.	1 nutlet
<i>Ranunculus</i> sp.	150 nutlets
<i>Tripleurospermum hookeri</i> Sch. Bip.	7 achenes
<i>Taraxacum</i> sp.	1 achene
<i>Menyanthes trifoliata</i> L.	1 seed fragment
<i>Potamogeton vaginatus</i> Turcz.	3 endocarps
<i>Potamogeton</i> sp.	9 endocarps

Table 3. Insects remains from large hair mats.

Taxa	Number of fragments
Order Coleoptera	
Family Carabidae	
<i>Poecilus nearcticus</i> (Lindr.)	18
<i>Pterostichus costatus</i> Men.	1
<i>Pterostichus</i> (<i>Cryobius</i>) sp.	1
<i>Pterostichus</i> (<i>Phonias</i>) sp.	1
<i>Amara alpina</i> Payk.	6
<i>Harpalus</i> sp.	1
Carabidae indet.	1
Family Dytiscidae	
<i>Hydroporus</i> sp.	2
Family Catopidae	
<i>Catops</i> sp.	1
Family Scarabaeidae	
<i>Aphodius</i> sp.	1
Family Byrrhidae	
<i>Morychus viridis</i> Kuzm. et Kor.	34
Family Chrysomelidae	
<i>Chrysolina cavigera</i> (Sahlb.)	1
Family Curculionidae	
<i>Hypera</i> sp.	10
<i>Stephanocleonus</i> sp.	1
<i>Sitona borealis</i> Kor.	10
Order Hymenoptera	
Hymenoptera indet.	4
Total	93

record is a ground beetle of the subgenus *Pterostichus* (*Phonias*). Species of this subgenus, such as *Pterostichus diligens* (Sturm) and *P. strenuus* (Panz.), are presently associated with the boreal zone. The remains

of small diving beetles from the genus *Hydroporus* are indicators of ponds or saturated soil.

Of the fossil ecological groups defined by Sher *et al.* (2005), we recorded members of the 'dry tundra' (*Poecilus nearcticus*, *Amara alpina*, *Hypera* sp. and others) and 'sedge heath' (*Morychus viridis*) communities. The herbivorous species were associated with grassy (*Sitona borealis* Kor., *Hypera* sp., *Stephanocleonus* sp.) and shrub (*Chrysolina cavigera*) vegetation. In particular, the weevil *S. borealis* is associated with sweetvetch (*Hedysarum* sp.) and *Ch. cavigera* with willows.

Some of these species (such as *Poecilus nearcticus*) presently inhabit eastern Siberia and northwestern North America (Kryzhanovskij *et al.* 1995). The ground beetle *Amara alpina* is Palaearctic, *Pterostichus costatus* occurs from the Yamal Peninsula in the west to Beringia and Alaska in the east (Kryzhanovskij *et al.* 1995) and *Sitona borealis* occurs from the Krasnoyarsk Region to the Chukchi Peninsula and Magadan Region (Korotyaev 1980).

Crustaceans

The mats of hair contained numerous remains of branchiopod crustaceans of the orders Anostraca, Notostraca and Anomopoda. The delicate bodies of these animals were not preserved, but distal portions of their mandibles, resting eggs, ephippia and filtering setae were found (Figs 6, 7). The distal portions of mandibles with molar surfaces that have numerous diagonal ridges probably belong to a single species of fairy shrimp (order Anostraca; Fig. 6F), and those with strong spines belong to a representative of tadpole shrimps (Notostraca; Fig. 6D, E). We also found branchiopod resting eggs of at least of four different types, belonging to some representatives of Anostraca and, maybe, Conchostraca (Fig. 6A).

Numerous ephippia of Daphniidae Straus (Cladocera: Anomopoda) of several different morphological types were found, most of them excellently preserved: (i) ephippia with two eggs, the axes of which are perpendicular to the dorsal margin, belong to the *Daphnia* (*Daphnia*) *longispina* s. lat. species group (Fig. 7A–C); (ii) ephippia with two eggs, the axes of which are almost parallel to the dorsal margin, most probably belong to the *Daphnia* (*Ctenodaphnia*) *atkinsoni* species group (Fig. 7D–F); (iii) a few ephippia with a single large egg, the axis of which is parallel to the dorsal margin, belong to another genus of the Daphniidae, *Simocephalus* (Fig. 7G, H).

We also found some series of branchiopod filtering setae (Fig. 6I), which may belong to *Daphnia*, *Simocephalus* or Anostraca. Despite the large size difference between anostracans and cladocerans, their filtering setae are similar in diameter, setule length and distance between setules (Fryer 1991).

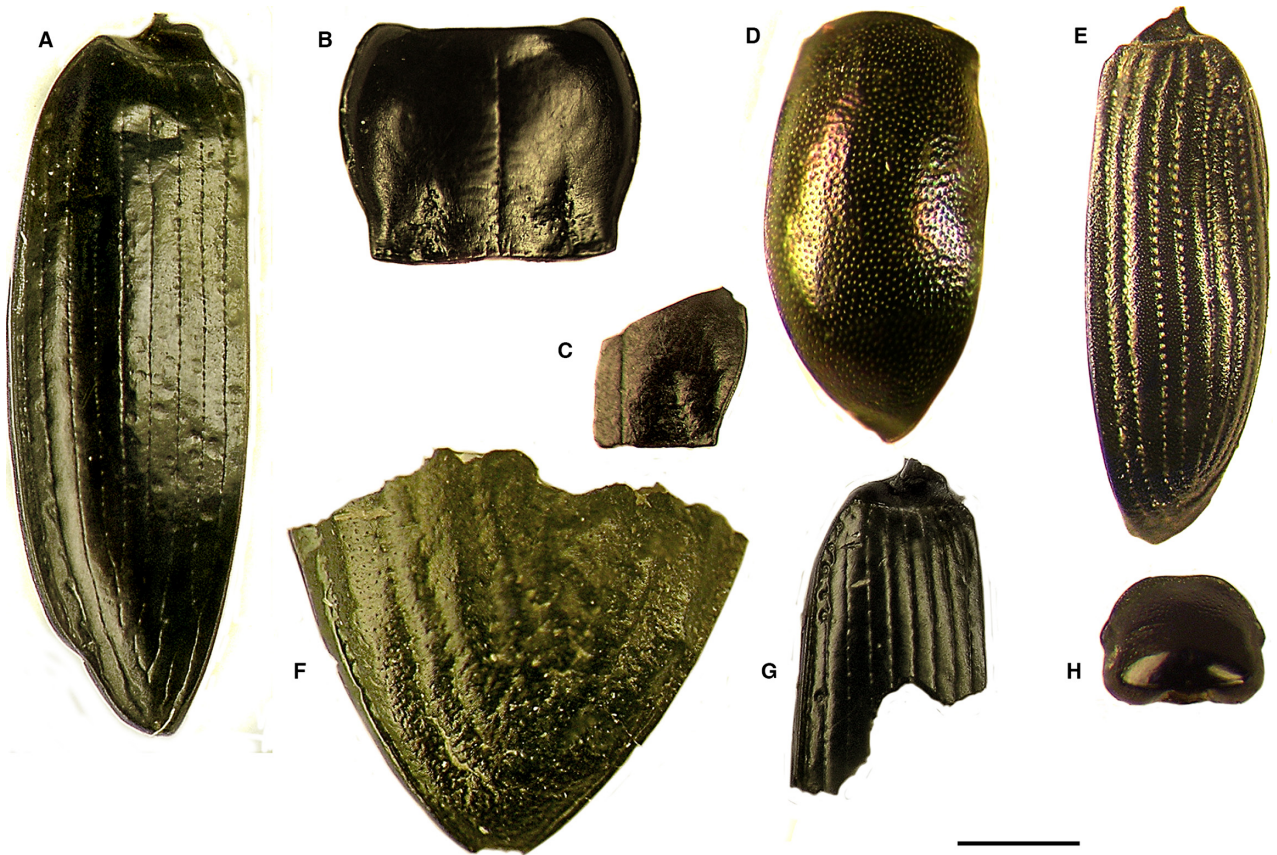


Fig. 5. Beetle remains found in the hair from the Bol'shaya Chukochya River. A. *Poecilus nearcticus*, left elytron. B. *Poecilus nearcticus*, pronotum. C. *Pterostichus (Cryobius)* sp., pronotum. D. *Morychus cf. viridis*, right elytron. E. *Sitona borealis*, right elytron. F. *Chrysolina cavigera* top of right elytron. G. *Pterostichus (Phonias)* sp., left elytron. H. *Aphodius* sp., head. Scale bar = 1 mm.

A few of the mandibles discovered had a complicated system of teeth in their distal portions. These most probably belong to representatives of Copepoda or Ostracoda (Fig. 6G, H).

Radiocarbon dating

The results of the ^{14}C measurements are shown in Table 4. All of the stable isotope ratios (expressed as $\delta^{13}\text{C}$ values) were within the normal range. The ^{14}C age of the mammoth hair was indistinguishable from the background age, reported as >45 ka BP (van der Plicht & Palstra in press).

Discussion

Taphonomy

A large accumulation of matted hair, including guard and down hairs, found at one location, suggests that the hair came from one individual and was not shed by several animals. There is no indication that it was transported over any significant distance. First of all, hair decomposes much faster than bone, and even a

brief exposure to the open air would have caused relatively rapid collagen loss and destruction of the hair. Moreover, transportation by river would have inevitably led to dispersal of this voluminous accumulation. The absence of other mammoth remains is probably due to erosion of the river bank: the cadaver was washed out and transported away, while some of its body hair remained frozen into the ground. In fact, hair frozen into permafrost can facilitate sliding of a cadaver down a slope.

The large, loose hair mats, abundant plant detritus and partly decomposed hairs indicate that the hair had been in subaerial or aquatic conditions for some time before it became trapped in permafrost. This makes the formation of matted hair clumps more likely, which then absorbed other organic remains. Importantly, the abundance of crustaceans indicates that the water was sufficiently warm for their development, which in sub-polar regions usually occurs in small water bodies rather than rivers.

The composition of the plant remains in the mammoth hair mats suggests the presence of high-quality forage, typical of alpine meadows. The latter were suitable for large herbivores of the mammoth fauna and

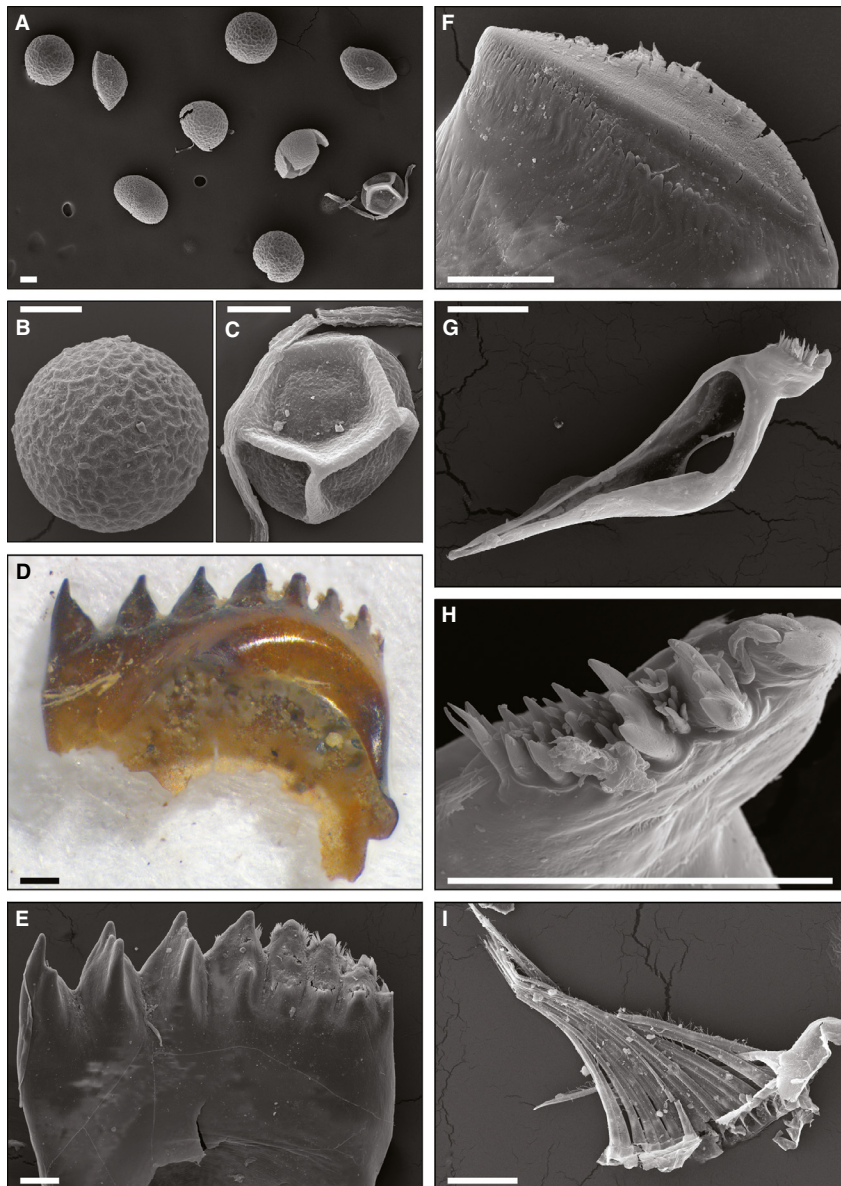


Fig. 6. Remains of large branchiopods found in the hair from the Bol'shaya Chukochya River. A. Resting eggs of the Anostraca (and Conchostraca?) of four different morphological types. B. Resting egg of the first type. C. Resting egg of the second type. D, E. Mandible of Notostraca, optical and SEM photo. F. Mandible of Anostraca, SEM photo. G, H. Mandible of Copepoda or Ostracoda. I. Filtering limbs of Branchiopoda. Scale bars = 100 μm .

remain so for the extant taxa. The occasional hairs of the woolly rhinoceros and bison found during this study probably represent animals visited that meadow.

The differences between the estimated ages of the trapped organisms and that of the hair itself suggest that the history of the taphocoenosis was rather complex. We propose the following scenario (Fig. 8):

Stage 1. – The small, very dense hair mats were most likely formed during the animal's life; they yielded pollen grains and spores from that epoch.

Upon the animal's death its body was buried in permafrost.

Stage 2. – During permafrost degradation 13–12 ka ago, the entire mammoth cadaver or only its hair thawed out and ended up in a littoral zone of shallow thermokarst lake. Action of wind-induced ripples led to the formation of large hair mats and entrapment of floating organic remains (i.e. the wild barley remains dated in Table 4), including small aquatic organisms. The meadow that formed around the thermokarst lake attracted herbivores.

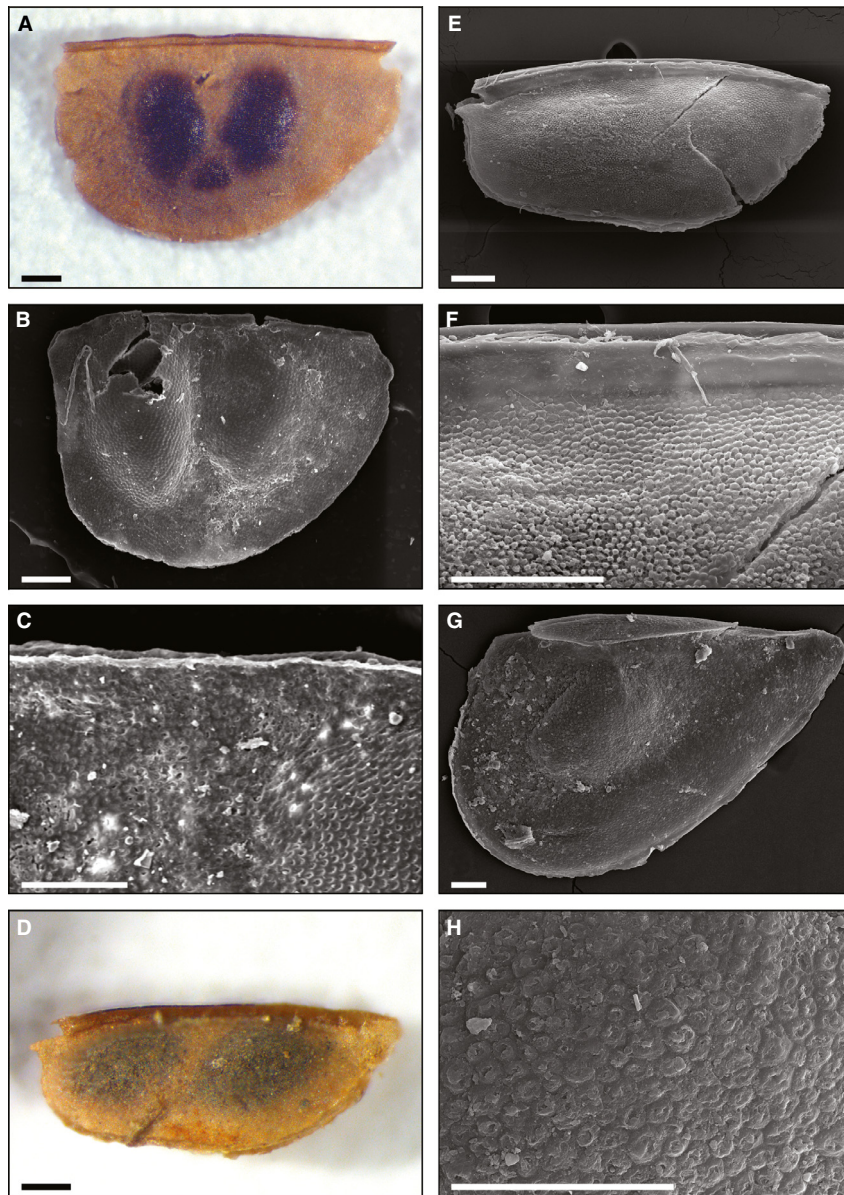


Fig. 7. Ephippia of Daphniidae found in the hair from the Bol'shaya Chukochya River. A. Ephippium of a representative of the *Daphnia* (*Daphnia*) *longispina* s. lat. species group, optical photo. B, C. The same, and its dorsal portion, SEM photo. D. Ephippium of a representative of the *Daphnia* (*Ctenodaphnia*) *atkinsoni* species group, optical photo. E, F. The same and its dorsal portion, SEM photo. G, H. Ephippium of *Simocephalus* sp., general view and surface sculpture. Scale bars = 100 μ m.

Stage 3. – Somehow (probably during next winter?) the mammoth hair again became part of the permafrost.

Stage 4. – The subsequent thawing occurred when the river cut through the terrace, eventually causing a landslide. This was probably the stage when the bird feathers got into the hair mats.

Stage 5. – The final stage was thawing due to erosion of the river bank.

Taphocoenosis from the mammoth hair

The abundance of Poaceae pollen and the presence of herb pollen grains in the palynological spectra from the small hair mats suggest the existence of plant communities with grasses and herbs at the time of their formation. Shrubs probably also grew not far from the locality. Such vegetation characterizes the first stage. The phytoliths from the large hair mats appear to have formed and accumulated in the taphocoenosis during the subsequent stage.

Table 4. Results of radiocarbon dating.

Sample	Laboratory code	Age (a BP)	Age (cal. a BP)	C (%)	$\delta^{13}\text{C}$ (‰)	Extracted	Treatment
F-2362/1	GrA-60510	>45 000	>48 000	49.1	-22.52	Mammoth fur	AAA
F-2362/2	GrA-60511	12 750±50	15 270–15 120	32.7	-26.87	Plants ¹	AAA
F-2362/3	GrA-60221	4115±40	4805–4535	44.4	-20.11	Feathers ²	A only

¹Macro-remains of the wild barley *Hordeum*.

²Representatives of the genus *Anser*.

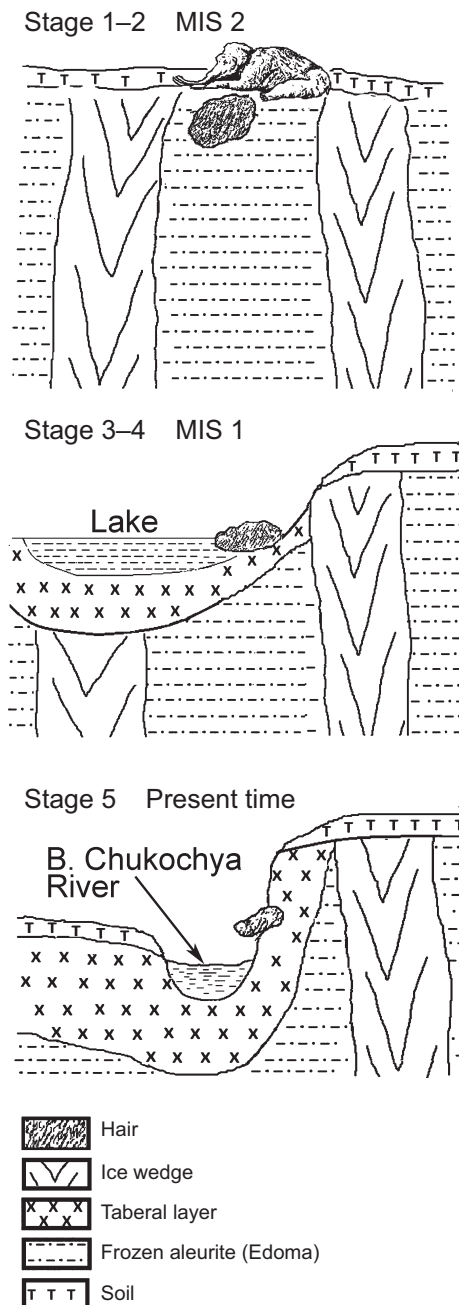


Fig. 8. Proposed scenario of the formation of the mammoth hair taphocoenosis found at the Bol'shaya Chukochya River.

The corresponding plant communities included shrubs, sedges and grasses, with some mosses, as is characteristic of the moist areas of the present-day boggy tundra. The macro-remains of the plant assemblage correspond to herb-grass meadows of the tundra zone, with *Alnus fruticosa* shrubs growing on the flood-plain and dwarf willows of the genus *Salix* growing on the watershed. Our pollen analysis led to similar conclusions on the herbaceous assemblages of that time, which were composed of grasses, sedges and forbs. Woodlands were not widespread: pollen grains of tree species are scarce and tree macro-remains were not observed in our material.

The entomological material from the mammoth hair mats is very similar to the taphocoenoses described from the Edoma Formation, located nearby (Kiselev 1981; sample 201), and other localities in northeastern Russia (Kiselev 1981; Kiselev & Nazarov 2009; Zanina *et al.* 2011). Its composition suggests open communities of the tundra type.

According to Berman (1992), *Morychus viridis* has a narrow ecological niche. Its larvae develop in the moss *Polytrichum piliformum*, but only when it grows together with xerophytic sedges (*Carex argunensis* and probably *C. rupestris*). The beetle occurs in habitats with little snow during the winter and cryoxerotic (cool and dry) to thermoxerotic (warm and dry) conditions during the summer. Remains of this species, which dominated in Pleistocene samples from northeastern Russia collected in a previous study (Sher *et al.* 2005), are traditionally associated with dry open habitats that sparsely vegetated with the xerophytic sedge *Carex argunensis* Turcz. ex Trev. (Berman 1990). However, several morphologically similar species of pill beetles occur in northeastern Siberia, differing primarily in the structure of the genitalia and microsculpture of the elytra (Tshernyshev & Pütz 1999; Tshernyshev *et al.* 2013). Pending a more detailed revision, the fragments extracted from the mammoth hair are provisionally assigned to *Morychus viridis*.

Therefore, the species found in the hair are typical of both modern and Pleistocene faunas of the area studied. They suggest that the fossil assemblage was formed in open communities of the tundra type with well-developed grassy vegetation and shrub willows.

Species associated with forest vegetation were not found.

The abundance of coprophilous fungi (Fig. 4) can be explained by the origin of the material. The depression around the thermokarst lake, where the hair ended up after thawing out of permafrost, appears to have been an attractive pasture for large herbivores. This would therefore have led to the accumulation of dung.

Prospects of using crustacean remains to reconstruct palaeoenvironments

An ephippium is a modified, strongly chitinized and characteristically sculptured dorsal shell portion of gamogenetic females from the cladoceran order Anomopoda (Kotov 2013). It is cast off together with resting eggs, which it encloses and protects (Green & Figuerola 2005; Kotov 2013). This stage of the cladoceran life cycle is especially resistant and therefore preserves well.

Study of ephippia buried in lake sediments is an important part of palaeolimnology. Identification of cladoceran ephippia to genus and, in some cases, even to species levels is possible (Frey 1964; Smirnov 2011; Frolova *et al.* 2014). Although precise identification of the *Daphnia* (*Ctenodaphnia*) ephippia to species level is very difficult, ephippium characters have been used to distinguish species within some species groups (Mergeay *et al.* 2005). Identification of species within the *Daphnia longispina* s. lat. species group is difficult even based on whole organisms (Benzie 2005).

Whereas cladoceran remains are commonly used for palaeoecological reconstructions, large branchiopods are used rarely (Bennike 1995). The mandibular surface has been studied in many species of recent Anostraca (Mura 1995, 1996), but the morphology of the mandibles from the mammoth hair examined here did not match any recent well-studied taxon. They probably belong to a less well-studied Arctic or boreal species, or perhaps even to an extinct species. The structure of mandibles varies greatly within the genera of Anostraca depending on the feeding type of the species (Mura 1995), but no keys for identification of genera and species based on the mandibles are currently available. Mandibles of the recent taxa occurring in northern Eurasia have never been studied in detail using SEM. Such a study is necessary before they can be used for palaeoecological reconstructions.

The recent Notostraca of northern Eurasia are represented by two genera, *Lepidurus* Leach and *Triops* Schrank, which together contain seven species (Brendonck *et al.* 2008). The mandibles from the Chukochya River mammoth hair probably belong to the genus *Lepidurus*, which has transverse ridges with sharper cusps and an unpaired median projection in the poste-

rior portion of the mandibular masticatory surface (Fryer 1988) in comparison to *Triops*, which has blunt cusps (Richter 2004).

Mandibles of branchiopods have not been used in palaeoecological studies, except for some records of notostracan mandibles (Bennike 1995) and 130-ka-old daphniid mandibles found together with ephippia in Antarctica (Cromer *et al.* 2006). Amongst recent Notostraca, the mandibular molar surfaces have been thoroughly studied in only three species (Fryer 1988; Richter 2004). Some data are available on anostracan (Mura 1996; Richter 2004) and cladoceran (Mergeay *et al.* 2005; Kotov 2013) mandibles.

During our study of the mammoth hair we for the first time discovered remains of Arctic branchiopods. These crustaceans provide new tools for reconstructing shallow (mostly temporary) aquatic environments of the past. However, a more precise identification of the mandibles from the mammoth hair will only be possible after additional studies of the recent taxa.

The almost complete absence of remains of adult and larval Copepoda (a highly diverse group whose representatives vary greatly in their lifestyles and ecological preferences) from freshwater sediments is a well-known fact (Frey 1964). In lacustrine sediments the remains of this group are almost entirely limited to resting eggs and faecal pellets (Knapp *et al.* 2001). The molar surfaces of copepod mandibles contain silica and are very hard (Michels *et al.* 2012), yet they have been found in sediments only once (Cromer *et al.* 2006). Our results suggest that copepod and/or ostracod mandibles can be found in Arctic basins and possibly can be used in palaeoreconstructions. However, identification of such mandibles will require morphological study of recent freshwater copepods and ostracods. To date, molar surfaces have been studied mostly in the marine (Sullivan *et al.* 1975; Michels & Schnack-Schiel 2005) or tropical freshwater copepod species (without using SEM; Suárez-Morales *et al.* 2003). The shells of Ostracoda have commonly been used in palaeoecological reconstructions (Holmes & Chivas 2002), but the mandibles of recent species are not sufficiently known to be identified in sediments.

Most palaeoecological studies to date have concerned large ancient water bodies, whereas small (often temporary) basins, where Notostraca, Anostraca and *Daphnia* (*Ctenodaphnia*) dwell, have received little attention. The aforementioned taxa may also occur in large basins, but only in the absence of fish. Populations of large branchiopods and ctenodaphnias are rapidly exterminated once a basin is colonized by fish (for exceptions, see Knecht *et al.* 2009). In tundra, the absence of fish means that a basin either appeared recently or freezes to the bottom in winter. Although the taphocoenosis of the mammoth hair studied here is allochronic, which somewhat complicates interpreta-

tion, it clearly accumulated when the hair was submerged in a shallow, possibly temporary, basin.

At present, species of *Daphnia* (*Ctenodaphnia*) are absent from the Chukochya River basin, as well as from the entire Asian part of Beringia. The closest area where a representative of this subgenus occurs is in the middle reaches of the Lena River near Yakutsk (*D. (C.) magna* s. lat.; Fig. 6). Other species occur much further to the south: the closest locality of *D. (C.) similis* s. lat. is in the Amur basin, and that of *D. (C.) cf. triquetra* Sars, 1903 (*atkinsoni* group) is in the Mongolian Altai (Flössner 1987). On the American side, ctenodaphnias are found in Yukon (*D. (C.) magna* s. lat. (Brooks 1957); *D. (C.) exilis* group) and are totally absent from Alaska. Therefore, ctenodaphnias were present in Beringia during the late Quaternary, but later became extinct in that region. Currently, the ranges of ctenodaphnias on both sides of the Bering Strait are isolated, but at the times when the Beringian bridge existed some groups (in particular *D. (C.) magna* s. lat.) had continuous Holarctic ranges.

Conclusions

The accumulation of permafrost-preserved mammoth hair from northeastern Russia turned out to be a valuable source of palaeoecological data. Some parts (small hair mats) retain information from the time when the animal was alive and from soon after its death. However, during subsequent periods of thawing and redeposition the sample may have been contaminated with organic objects from more recent times. We reconstructed several stages in the history of this taphocoenosis and its environments. The hair itself was dated by radiocarbon to older than 45 000 ¹⁴C a BP. During a period of warming at the MIS 2-1 boundary (c. 12 ka ago), the hair thawed out of the permafrost and became submerged in a shallow lake. At that time, shallow alar lakes were formed, which accumulated plant detritus and other organic remains and were surrounded by meadow vegetation. Subsequently, the mammoth hair was redeposited in a landslide of thawing lacustrine deposits. The most valuable specimens from the hair mats are the remains of small crustaceans, which have not previously been found at high latitudes. This mammoth hair has provided new data on the glacial biota and has significantly expanded the geographical and geological ranges of microscopic crustaceans of Beringia.

Acknowledgements. – The authors thank S. Widga, M. Castro and an anonymous reviewer for helpful comments, which significantly improved the manuscript and R. Rakitov for valuable criticism and editing of the text. The study of the hair, plant and insect remains was supported by the National Alliance of Shidlovskiy ‘Ice Age’ and the Russian Foundation for Basic Research (projects no. 15-04-08552a and no. 15-05-07686a). The study of the Cladocera was supported exclusively by the Russian Science Foundation (grant 14-14-00778).

References

- Aerts-Bijma, A. T., Van der Plicht, J. & Meijer, H. A. J. 2001: Automatic AMS sample combustion and CO₂ collection. *Radiocarbon* 43, 293–298.
- Bennike, O. 1995: Palaeoecology of two lake basins from Disko, West Greenland. *Journal of Quaternary Science* 10, 149–155.
- Benzie, J. A. H. 2005: The genus *Daphnia* (including *Daphniopsis*) (Anomopoda: Daphniidae). In Dumont, H. J. (eds.): *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World* 21, 376 pp. Kenobi Productions, Ghent and Backhuys Publishers, Leiden.
- Berman, D. I. 1990: Ecology of *Morychus viridis* (Coleoptera, Byrrhidae), a moss beetle from Pleistocene deposits in the north-eastern USSR. In Kotlyakov, V. M. & Sokolov, V. E. (eds.): *Arctic Research. Advances and Prospects: Proceedings of the Conference of Arctic*, 281–288. Nauka Press, Moscow (in Russian).
- Berman, D. I. 1992: Ecology of the pill beetle *Morychus viridis* (Coleoptera, Byrrhidae) and reconstruction of Pleistocene landscapes in northeastern USSR. *Readings in Memory of Aleksei Ivanovich Kurenkov* 1–2, 30–63 (in Russian).
- Boeskorov, G. G., Lazarev, P. A., Sher, A. V., Davydov, S. P., Bakulina, N. T., Shchelchkova, M. V., Binladen, J., Willerslev, E., Buigues, B. & Tikhonov, A. N. 2011: Woolly rhino discovery in the lower Kolyma River. *Quaternary Science Reviews* 30, 2262–2272.
- Brendonck, L., Rogers, D. C., Olesen, J., Weeks, S. & Hoeh, W. R. 2008: Global diversity of large branchiopods (Crustacea: Branchiopoda) in freshwater. *Hydrobiologia* 595, 167–176.
- Brooks, J. L. 1957: The systematics of North American *Daphnia*. *Memoirs of the Connecticut Academy of Arts and Sciences* 13, 1–180.
- Chernova, O. F. & Kirillova, I. V. 2013: Hair microstructure of the late quaternary bison from north-east Russia. *Proceedings of the Zoological Institute* 317, 202–216 (in Russian).
- Chernova, O. F. & Tselikova, T. N. 2004: *Atlas of Mammal Hair: Fine Structure of Guard Hairs and Spines under Scanning Electron Microscope*. 429 pp. KMK, Moscow (in Russian).
- Chernova, O. F., Perfilova, T. V., Fadeeva, E. O. & Tselikova, T. N. 2009: *Atlas of Bird Feather Microstructure*. 173 pp. Nauka Press, Moscow (in Russian).
- Chernova, O. F., Silaeva, O. L. & Perfilova, T. V. 2014: Diagnostic features of feathers of galliform birds. *Theory and Practice of Forensic Expertise* 1, 69–75 (in Russian).
- Cromer, L., Gibson, J. A. E., Swadling, K. M. & Hodgson, D. A. 2006: Evidence for a lacustrine faunal refuge in the Larsemann Hills, East Antarctic, during the Last Glacial Maximum. *Journal of Biogeography* 33, 1314–1323.
- Cundill, P. R. 1991: Comparisons of moss polster and pollen trap data: a pilot study. *Grana* 30, 301–308.
- Faegri, K. & Iversen, J. 1989: *Textbook of Pollen Analysis*. 328 pp. J. Wiley and Sons, Chichester.
- Flerov, K. K. 1977: Bisons of north-east Siberia. *Proceedings of the Zoological Institute* 73, 39–56.
- Flössner, D. 1987: A pedomorphic form type of *Daphnia triquetra* Sars, 1903 (Cladocera, Daphniidae) from Mongolia. *Hydrobiologia* 145, 47–49.
- Frey, D. G. 1964: Remains of animals in Quaternary lake and bog sediments and their interpretation. *Ergebnisse der Limnologie* 2, 1–114.
- Frolova, L., Nazarova, L., Pestryakova, L. & Herzschuh, U. 2014: Subfossil Cladocera from surface sediment in thermokarst lakes in northeastern Siberia, Russia, in relation to limnological and climatic variables. *Journal of Paleolimnology* 22, 107–119.
- Fryer, G. 1988: Studies on the functional morphology and biology of the Notostraca (Crustacea: Branchiopoda). *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 321, 27–124.
- Fryer, G. 1991: Functional morphology and the adaptive radiation of the Daphniidae (Branchiopoda: Anomopoda). *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 331, 1–99.

- Gilichinsky, D. 2002: Permafrost as a microbial habitat. In Bitton, G. (ed.): *Encyclopedia of Environmental Microbiology*, 932–956. Wiley, New York.
- Gilichinsky, D. & Wagener, S. 1995: Microbial life in permafrost: a historical review. *Permafrost and Periglacial Processes* 6, 243–250.
- Green, A. J. & Figuerola, J. 2005: Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. *Diversity and Distributions* 11, 149–156.
- Gubin, S. V., Zanina, O. G., Maksimovich, S. V., Kuzmina, S. A. & Zazhigin, V. S. 2003: Reconstruction of ice complex sediment formation conditions, based of late Pleistocene rodent burrow studying. *The Earth Cryosphere* 7, 13–22 (in Russian).
- Guthrie, R. D. 1990: *Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe*. 323 pp. University of Chicago Press, Chicago.
- Holmes, J. & Chivas, A. (eds.) 2002: The Ostracoda: applications in Quaternary research. *Geophysical Monograph Series* 131, 1–538.
- Kirillova, I. V., Kotov, A. A., Trofimova, S. S., Zanina, O. G., Lapteva, E. G., Zinoviev, E. V., Chernova, O. F., Fadeeva, E. O., Zharov, A. A. & Shidlovskiy, F. K. 2015: Fossil fur as a new source of information on the Ice Age biota. *Doklady Biological Sciences* 460, 48–51.
- Kirillova, I. V., Zanina, O. G., Kosintsev, P. A., Kul'kova, M. A., Lapteva, E. G., Trofimova, S. S., Chernova, O. F. & Shidlovskiy, F. K. 2013: The first finding of a frozen Holocene bison (*Bison priscus* Bojanus, 1827) carcass in Chukotka. *Doklady Biological Sciences* 452, 296–299.
- Kiselev, S. V. 1981: *Late Caenozoic Coleoptera of Northeastern Siberia*. 116 pp. Nauka Press, Moscow (in Russian).
- Kiselev, S. V. & Nazarov, V. I. 2009: Late Caenozoic insects of northern Eurasia. *Paleontological Journal* 43, 723–850.
- Knapp, R., Garton, J. & Sarnelle, O. 2001: The use of egg shells to infer the historical presence of copepods in alpine lakes. *Journal of Paleolimnology* 25, 539–543.
- Knecht, R. J., Benner, J. S., Rogers, D. C. & Ridge, J. C. 2009: *Surculichnus bifurcauda* n. gen., n. isp., a trace fossil from Late Pleistocene glaciolacustrine varves of the Connecticut River Valley, USA, attributed to notostracan crustaceans based on neoichnological experimentation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 272, 232–239.
- Korotyaev, B. A. 1980: Materials on the weevil fauna (Coleoptera, Curculionidae) of the North-East of the USSR. In Medvedev, G. S. & Matis, E. G. (eds.): *Entomological Investigations of the North-East of the USSR*, 23–50. Far East Science Centre of the USSR Academy of Sciences, Vladivostok (in Russian).
- Kosintsev, P. A., Lapteva, E. G., Trofimova, S. S., Zanina, O. G., Tikhonov, A. N. & van der Plicht, J. 2012: Environmental reconstruction inferred from the intestinal contents of the Yamal baby mammoth Lyuba (*Mammuthus primigenius* Blumenbach, 1799). *Quaternary International* 255, 231–238.
- Kotov, A. A. 2013: *Morphology and Phylogeny of the Anomopoda (Crustacea: Cladocera)*. 638 pp. KMK Press, Moscow (in Russian).
- Kryzhanovskij, O. L., Belousov, I. A., Kabak, I. I., Kataev, B. M., Makarov, K. V. & Shilenkov, V. G. 1995: *A Checklist of the Ground Beetles of Russia and Adjacent Lands (Insecta, Coleoptera, Carabidae)*. 271 pp. Pensoft Publishers, Sofia.
- Lopatina, D. A. & Zanina, O. G. 2006: Paleobotanical analysis of materials from fossil gopher burrows and Upper Pleistocene host deposits, the Kolyma River lower reaches. *Stratigraphy and Geological Correlation* 14, 549–560.
- Mergeay, J., Verschuren, D. & De Meester, L. 2005: *Daphnia* species diversity in Kenya, and a key to the identification of their ephippia. *Hydrobiologia* 542, 261–274.
- Michels, J. & Schnack-Schiel, S. B. 2005: Feeding in dominant Antarctic copepods – does the morphology of the mandibular gnathobases relate to diet? *Marine Biology* 146, 483–495.
- Michels, J., Vogt, J. & Gorb, S. N. 2012: Tools for crushing diatoms – opal teeth in copepods feature a rubber-like bearing composed of resilin. *Scientific Reports* 2, 465, doi:10.1038/srep00465.
- Mook, W. G. & Streurman, H. J. 1983: Physical and chemical aspects of radiocarbon dating. *PACT Publications* 8, 31–55.
- Mook, W. G. & van der Plicht, J. 1999: Reporting ^{14}C activities and concentrations. *Radiocarbon* 41, 227–239.
- Mura, G. 1995: Morphological features of the mandible related to feeding habits of some Anostraca species. *Crustaceana* 68, 83–102.
- Mura, G. 1996: Pattern of mandibular morphology in Anostraca with some taxonomic remarks. *Crustaceana* 69, 129–154.
- Nikitin, V. P. 1969: *Paleocarpological Methods: Methodological Guidelines for the Study of Fossil Seeds and Fruits*. 82 pp. Tomsk University Press, Tomsk (in Russian).
- Piperno, D. R. 1988: *Phytolith Analysis: An Archaeological and Geological Perspective*. 280 pp. Academic Press, London.
- van der Plicht, J. & Palstra, S. W. L. in press: Radiocarbon and mammoth bones: what's in a date. *Quaternary International*. doi: 10.1016/j.quaint.2014.11.027.
- van der Plicht, J., Wijma, S., Aerts, A. T., Pertuisot, M. H. & Meijer, H. A. J. 2000: The Groningen AMS facility: status report. *Nuclear Instruments and Methods B* 172, 58–65.
- Popov, Y. N. 1948: Finds of fossil mammal cadavers in frozen layers of a Pleistocene of North Eastern Siberia. *Bulletin of the Commission on studying of the Quaternary Period* 13, 74–81 (in Russian).
- Reimer, P. J., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Bronk Ramsey, C., Buck, C. E., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Hafflidason, H., Hajdas, I., Hatté, C., Heaton, T. J., Hoffmann, D. L., Hogg, A. G., Hughen, K. A., Kaiser, K. F., Kromer, B., Manning, S. W., Niu, M., Reimer, R. W., Richards, D. A., Scott, E. M., Southon, J. R., Staff, R. A., Turney, C. S. M. & van der Plicht, J. 2013: IntCal13 and Marine13 Radiocarbon age calibration curves 0–50 000 years cal BP. *Radiocarbon* 55, 1869–1887.
- Richter, S. 2004: A comparison of the mandibular gnathal edges in branchiopod crustaceans: implications for the phylogenetic position of the Laevicaudata. *Zoomorphology* 123, 31–44.
- Rozanov, A. Y. (ed.) 2001: *Mammoth and Its Environment: 200 Years of Studying*. 362 pp. GEOS, Moscow (in Russian).
- Schirrmeister, L., Siegert, C., Kuznetsova, T., Kuzmina, S., Andreev, A. A., Kienast, F., Meyer, H. & Bobrov, A. 2002: Paleoenvironmental and paleoclimatic records from permafrost deposits in the Arctic region of northern Siberia. *Quaternary International* 89, 97–118.
- Sher, A. V., Kuzmina, S. A., Kuznetsova, T. V. & Sulerzhitsky, L. D. 2005: New insights into the Weichselian environment and climate of the Eastern-Siberian Arctic, derived from fossil insects, plants, and mammals. *Quaternary Science Reviews* 24, 533–569.
- Smirnov, N. N. 2011: Application fields of investigation of subfossil remains and living freshwater fauna. *Inland Water Biology* 4, 405–407.
- Spasskaya, N. N., Kuznetsova, T. V. & Sher, A. V. 2012: Morphometric study of the skull of a late Pleistocene mummy of the Bilibino horse from the western Chukchi Peninsula. *Paleontological Journal* 46, 92–103.
- Suárez-Morales, E., Gutiérrez-Aguirre, M. A. & Elías-Gutiérrez, M. 2003: Observations on the structure of the mandibular gnathobase in some American *Mesocyclops* (Copepoda: Cyclopidae). *Proceedings of the Biological Society of Washington* 116, 742–753.
- Sullivan, B. K., Miller, C. B., Peterson, W. T. & Soeldner, A. H. 1975: A scanning electron microscope study of the mandibular morphology of boreal copepods. *Marine Biology* 30, 175–182.
- Tchershki, I. D. 1891: A description of the post-Tertiary mammalian animals collected by the Novo-Siberian expedition in 1885–86. *Zapiski Imperatorskoi Akademii Nauk, St. Petersburg* 7, 1–706 (in Russian).
- Tomskaya, A. I. 1981: *Palynology of the Cenozoic of Yakutia*. 221 pp. Nauka Press, Novosibirsk (in Russian).
- Tomskaya, A. I. 2000: *The Food Supply of the Yakutia Mammoth in the Late Pleistocene*. 60 pp. Mammoth Museum, Yakutsk (in Russian).
- Tshernyshev, S. E. & Pütz, A. 1999: New data on the fauna of pill beetles (Coleoptera: Byrrhidae) of Russia. *Russian Entomological Journal* 8, 15–22.

- Tshernyshev, S. E., Tsepelev, K. A., Dudko, R. Y. U., Zinovyev, E. V. & Legalov, A. A. 2013: Pill beetles (Coleoptera, Byrrhidae) in Late Pleistocene deposits in the south of the West Siberia. *Euroasian Entomological Journal* 12, 109–119.
- Ukrainitseva, V. V. 1993: *Vegetation Cover and Environment of the 'Mammoth Epoch' in Siberia*. 309 pp. Mammoth Site of Hot Springs, Inc., Hot Springs.
- Vereshchagin, N. K. & Mikhelson, V. M. (eds.) 1981: *The Magadan Baby Mammoth*. 296 pp. Nauka Press, Leningrad (in Russian).
- Yashina, S., Gubin, S., Maksimovich, S., Yashina, A., Gakhova, E. & Gilichinsky, D. 2012: Regeneration of whole fertile plants from 30 000-y-old fruit tissue buried in Siberian permafrost. *Proceedings of the National Academy of Sciences of the United States of America* 109, 4008–4013.
- Yurtsev, B. A. 1981: *Relict Steppe Assemblages of Northeastern Asia (Problem of Reconstruction Cryoxerotic Landscapes of Beringia)*. 167 pp. Nauka Press, Novosibirsk (in Russian).
- Zalenskii, V. V. 1903: (ed.) Osteological and odontographic studies of the mammoth (*Elephas primigenius* Blum.), and elephants (*El. indicus* L. and *El. africanus* Blum.). *Scientific Results of the Expedition Equipped by the Imperial Academy of Sciences for Excavation of the Mammoth Found on the Berezovka River in 1901*. v. 1 114 pp. Imperatorsky University Press, St. Petersburg (in Russian).
- Zanina, O. G., Gubin, S. V., Kuzmina, S. A., Maximovich, S. V. & Lopatina, D. A. 2011: Late Pleistocene (MIS 3–2) palaeoenvironments as recorded by sediments, palaeosols, and ground-squirrel nests at Duvanny Yar, Kolyma lowland, north-east Siberia. *Quaternary Science Reviews* 30, 2107–2123.