Table 1. Radiocarbon dates of palaeoenvironmental proxy records from the middle Kolyma study area (2013-2019 investigations)

Site/section	Unit	Dated material	Context (*in situ*)	Age (^{14}C y BP)	Age (cal. a BC) 68.2/92.1%	Laboratory code	Year (sample)
Zyryanka 3	II	Wood *Salix* sp.	Colluvial	320±30	1515–1590 1484–1644AD	Poz127443	2019
Irelyakh-Siene 1	III	Mushroom *Fomes fomentarius*	Lacustrine	9240±50	8550–8422 8576–8309	Poz-92444	2014
Irelyakh-Siene 2	IV	Shell *Radix auricularia*	Lacustrine	10 000±50	9553–9390 9761–9319	Poz-91685	2014
Irelyakh-Siene 1	IV	Bone/skull *Mammuthus primigenius*	Alluvial	18 330±100	20 409–20 120 20 476–19 965	Poz106029	2018
Zyryanka 1	III	Tusk (flaked) *Mammuthus primigenius*	Colluvial	19 270±120	21 444–21 086 21 606–20 942	Poz-91848	2014
Irelyakh-Siene 2	VI	Tusk (flake) *Mammuthus primigenius*	Alluvial	21 420±140	23 946–23 722 24 026–23 571	Poz-130745	2015
Irelyakh-Siene 1	IV	Bone (perfor.) *Coelodonta antiquitatis*	Alluvial	21 960±150	24 387–24 052 24 601–23 944	Poz-91849	2014
Irelyakh-Siene 1	IV	Tusk (flaked) *Mammuthus primigenius*	Alluvial	23 100±220	25 637–25 278 25 805–25 050	Poz-83288	2014
Irelyakh-Siene 2	VII	Bone (flaked) *Mammuthus primigenius*	Alluvial	44 000±2000	47 034–42 676 50 657–41 976	Poz-130744	2015
Zyryanka 1	III	Tusk (perfor.) *Mammuthus primigenius*	Alluvial	44 000±2000	47 123–43 926 >limit–42 943	Poz-93289	2014
Zyryanka 1	III	Bone *Mammuthus primigenius*	Alluvial	44 200±1900	47 211–44 166 >limit–43 205	Poz106845	2018
Zyryanka 1	III	Bone *Mammuthus primigenius*	Alluvial	44 400±2000	47 397–4 4367 >limit–43 263	Poz106028	2018
Zyryanka 1	V	Bone (flaked) *Mammuthus primigenius*	Alluvial	45 700±2500	>limit–45 454 >limit–43 716	Poz119806	2019
Zyryanka 3	IV	Coprolite *Mammuthus primigenius*	Colluvial	50 000±4000	56 431–44 040 69 225–42 776	Poz-120576	2019
Zyryanka 3	V	Wood *Larix* sp.	Alluvial	>50 000	52 097–50 506 >limit–50 449	Poz-127444	2019

wild garlic (*Allium*) and fireweed (*Chamerion*) show the broad floral diversity at the site. The appearance of spruce (*Picea obovata*) and pine (*Pinus silvestris*) shows points to the settings of moderate atmospheric humidity at the expense of the typical xerophytic steppe elements.

A markedly different (Early Holocene) setting is evident in the upper part of the laminated clayey silt formation (Irelyakh-Siene 1, stratum III at approx. –3 m; IS 3) showing a sub-arctic environment supporting a dense riverine taiga forest (mainly of white birch, alder and some willow) amid a mosaic of northern parklands with isolated conifer groves (*Juniperus* and *Pinus cembra*). The arboreal taxa dominate over those of grasses. The higher pollen percentages of *Galium*, *Chrysosplenium* and Polypodiaceae along with (together with) Poaceae suggest semi-humid conditions with bogs and marshlands or a shallow pond (thermokarst lake) setting.

A landscape similar to the present day based on the digested vegetation composition and plant species requirements is inferred from the mid-Last Glacial (MIS 3) rhinoceros coprolite sample RC 4 (Irelyakh-Siene 2/Unit VI). The recorded palynomorphs and macro-fossil plant residues (twigs) are mainly of white birch and alder with some contribution of other arboreal taxa (larch, pine and dwarf willow). The pollen spectrum of grasses, sedges and ferns, dominated by Poaceae (*Poa* t., *Festuca* t.), Cyperaceae and Polypodiaceae, respectively, points to the selective animal diet diversity within a mosaic boggy parkland habitat with isolated trees and an undergrowth thicket at the better drained locations. No common coprophilous fungi or mushrooms were detected in the analysed faecal sample.

The most representative interstadial botanical macrofossils originate from Zyryanka (summer 2019) from the cryolithic sedimentary facies (Units III–IV) (Fig. 4). The perfectly preserved plant residues from the central and basal parts of the MIS 3 colluvia include several taxa of mosses, lichens (*Cladonia portentosa*, *C. rangiferina*) and grasses, leaves of cranberry (*Vaccinium oxycossus*), cowberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum nigrum* L.), wild rose (*Rosa* sp.), willow (*Salix* sp.), and larch (*Larix* sp.) needles and cones among other arboreal species (indet.) (Fig. 7A, B). The frozen patches of the fossil plants included green-coloured remains some of which contained preserved chlorophyll. Moreover, preserved wood (trunks, branches) of *Larix* sp., *Salix* sp. and *Betula* sp. (Fig. 7D) is stratigraphically distributed in

several distinct levels with isolated wood fragments incorporated in the Pleistocene permafrost grounds (3–10 m below the present surface). This unit is overlain by a buried Holocene forest horizon at –1 m (Fig. 4). The recorded arboreal and non-arboreal plant species composition (Table 2) points to semi-humid continental conditions with biotically rich swampy northern boreal (taiga) forest communities. The identified plant taxa largely mirror the modern natural setting of the site.

The macro-fossil plant spectra correspond with the fossil pollen records as well as the digested plant residues in herbivores' coprolites from the mid-Last Glacial sites in the middle Kolyma as well as the lower Indigirka and Yana basins, all dominated by grasses and bushes. The reconstruction of past landscapes based on the megafauna excrements is, indeed, biased by the dietary choices of the particular animals involved. The Zyryanka fossil coprolite plant composition (Fig. 7C) matches the Late Pleistocene megafauna faecal residues from the NE Russian Arctic (Kirillova *et al.* 2016), uniformly showing a relatively rich vegetation and high diversity of grasses and herbs with dominance of xeric species.

The retrieved ancient vegetation records from the middle Kolyma area corroborate the previous palaeobotany/palynology studies in Yakutia including the Kolyma Lowlands (e.g. Andreev *et al.* 2002; Bezusko *et al.* 2008). The Late Pleistocene (MIS 3–2) vegetation transformations of tundra-steppe/forest-tundra/the northern boreal forest, also documented in other parts of the Russian sub-Arctic and Arctic (Lozhkin 1976; Ukraintseva 1979; Blinnikov *et al.* 2011; Ashastina *et al.* 2018), point to the favourable conditions during MIS 3 in spite of switching warm and cold climate shifts registered in the northern and eastern regions of Siberia (the Taymyr Lowlands, the Laptev Sea coast and the Lake Baikal area) (Andreev *et al.* 2003; Swann *et al.* 2005; Mueller *et al.* 2009). The Kolyma Lowlands were most likely more forested than the easternmost territories of arctic Siberia (Chukotka) during the warm Last Glacial intervals. The locally specific early interstadial vegetation patterns largely correspond to those characterizing the area today.

Palaeontological records

The palaeontological investigations recorded amounts of well-preserved Pleistocene fauna remains of broad species diversity, some including soft tissue (Cheprasov *et al.* 2014). Except for minor occurrences, nine main palaeontological localities were found (Fig. 1C). A partial re-deposition of some osteological assemblages does not create constraints to the overall picture of the extinct animal species' composition and the megafauna community structure (Table 3, Fig. 9). The spectrum of the uncovered fossil records from the intact Pleistocene cryolithic contexts contributes to the reconstruction of the large mammals' evolutionary lineages, mainly of mammoth, rhinoceros and horse, and the palaeontological site taphonomies. The concentration of the fossil fauna records associated with the early cultural bone-made items make the Verkhnekolymskiy District of the Kolyma River area one of the richest palaeontological and the most promising archaeological regions in NE Siberia.

The Irelyakh-Siene locality. – At Irelyakh-Siene, numerous mammoth fauna fossils were recorded from the Pleistocene permafrost formations along the right bank of the Kolyma River for about 3 km downstream from the Irelyakh-Siene River mouth emptying into the Kolyma River (Fig. 2B–D). The varying fossilization degree of the skeletal remains points to non-uniform

Table 2. Fossiliferous geo-contexts and palaeoenvironmental proxies of the investigated sites (MIS 3–2 stratigraphical units).

	Site	Geo-context/Unit	Vegetation (botanical macro-fossils)
1	Irelyakh Siene 2	Lacustrine/V	*Sphagnum*, *Cladonia rangiferina*, *Salix* sp. *Larix sibirica*, *Betula nana*, *Betula pendula*, *Juniperus* sp.
2	Zyryanka	Colluvium	*Cladonia portentosa*, *C. rangiferina*, *Vaccinium oxycossos*, *Vaccinium vitis-idaea*, *Empetrum nigrum* L., *Ledum palustre*, *Salix* sp. *Larix sibirica*, *Betula* sp.
3	Presnyy Stream		*Empetrum nigrum*L., *Salix sibirica*, *Larix sibirica*, *Betula nana*, *Betula pendula*
	Site	Geo-context/Unit	Fossil fauna (osteology and soft tissue remains)
1	Irelyakh Siene 1	Alluvium/IV	*Mammuthus intermedius*, *Mammuthus trogontherii chosaricus*, *Mammuthus primigenius fraasi*, *Mammuthus primigenius primigenius*, *Mammuthus* sp., *Coelodonta antiquitatis*, *Equus* sp.
	Irelyakh Siene 2	Alluvium/VI–VII	*Cervus elaphus*, *Ovibos* sp., *Bison* sp., *Rangifer tarandus*, *Lepus* sp., *Ursus arctos*, *Panthera leo spelaea*, *Canis lupus*, *Dicrostonyx* sp., *Aves*(indet.). *Mammuthus primigenius* (hair), *Bison*sp. (leg, hair), *Spermophilus* sp.; Coprolites: *Mammuthus* sp., *Coelodonta antiquitatis*, *Bison* sp.
2	Zyryanka	Colluvium/III	*Mammuthus trogontherii*, *Mammuthus trogontherii chosaricus*, *Mammuthus primigenius fraasi*, *Equus* sp., *Coelodonta antiquitatis*, *Bison* sp., *Rangifer tarandus*, *Alces* sp., *Panthera leo spelaea*, *Canis lupus*, *Gulo gulo*; Coprolites: *Mammuthus* sp., *Alces alces*, *Rangifer tarandus*
3	Presnyy Stream Mayachnyy Creek	Alluvium	*Mammuthus primigenius*(foot, hair) *Mammuthus primigenius, Rangifer tarandus, Bison* sp., *Equus* sp., *Coelodonta antiquitatis*, *Panthera spelaea*, *Canis lupus, Gulo gulo*, *Vulpes vulpes*

Table 3. Quantitative representation of the fossil fauna species (total numbers and percentages) from the investigated sites Irelyakh-Siene and Zyryanka (MIS 3–2 stratigraphical units; 2018–2019 investigations).

	Irelyakh-Siene		Zyryanka	
Mammuthus trogontherii	–	–	2	2.5
M.trogontherii chosaricus	2	0.3	–	–
M.primigenius fraasi	3	0.5	2	2.5
M.primigenius primigenius	175	29.3	41	51.9
Coelodonta antiquitatis	84	14.1	–	–
Bison sp.	253	42.3	18	33.8
Equus sp.	27	4.5	3	3.8
Ovibos sp.	1	0.2	–	–
Rangifer tarandus	34	5.7	2	2.5
Alces sp.	–	–	1	1.3
Cervus elaphus	7	1.2	–	–
Panthera spelaea	1	0.2	2	2.5
Ursus arctos	1	0.2	–	–
Canis lupus	4	0.7	7	8.9
Gulo gulo	–	–	1	1.3
Dicrostonyx sp.	1	0.2	–	–
Citellus sp.	1	0.2	–	–
Lepus sp.	1	0.2	–	–
Aves undiff.	1	0.2	–	–
Total (specimens)	596	100%	79	100%

taphonomic histories and various chronologies of the osteological collections. This is best evidenced by the specific evolutionary lineages of the uncovered megafauna, especially of the proboscideans (Figs 6E, F, 7E, 8B). The large species were determined according to Foronova & Zudin (1986) and Foronova (2001) (Table 2). Among these, some extraordinary findings were recorded, such as the complete skull with the lower jaw (with M^3 sin. and M^3 dex.) of a mammoth (*Mammuthus primigenius fraasi*) from Irelyakh-Siene 1 (Fig. 8A) with ^{14}C age 18 330±100 a BP (Table 1). One of the mammoth tusks displays growth anomalies probably due a decease, with similar deformations also observed in other specimens previously reported from Yakutia at the Bolshoy Lyakhov Site and the Boiler Island found by V.V. Artamonov in 1916 (both specimens are stored in the Yakut State Museum of History and Culture of Northern Peoples in Yakutsk; Vereshchagin 1960; Vereshchagin & Tikhonov 1986; Boeskorov 2010; Cheprasov *et al.* 2015).

The amounts and the taxonomic diversity of the fossil remains found at all three sites (Irelyakh-Siene 1–3) following the 2014–2019 investigations allowed for a closer quantitative assessment of the Pleistocene fauna composition (Table 3). The palaeontological material (Irelyakh-Siene 1) from Unit III differs from that of Unit IV by a darker chocolate-brown to black mineral colouring due to manganese- and iron-precipitation from seasonal permafrost thaw-enriched groundwater percolation. The megafauna bones and mammoth ivory display both human-induced tool marks as well as gnaw marks by large carnivores (lion, bear) implying the coexistence of early people and the Pleistocene animals.

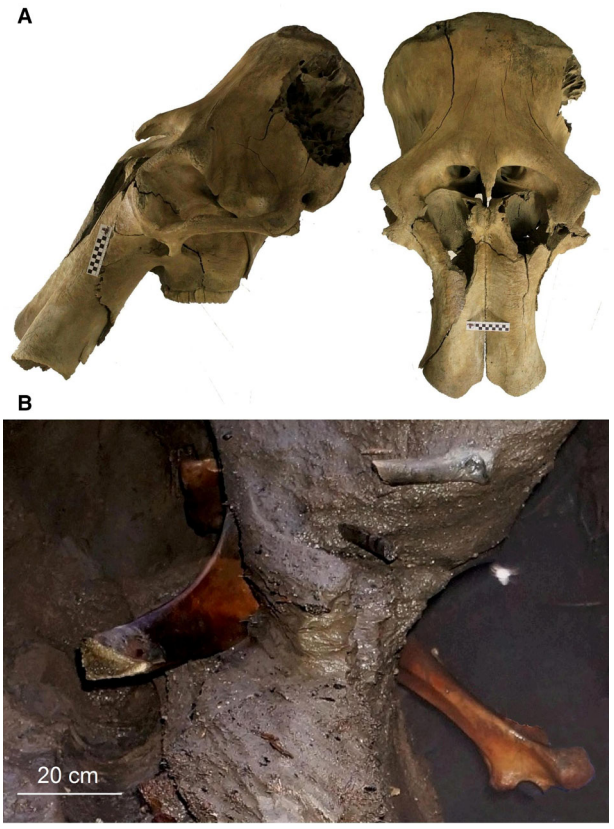

Fig. 8. Irelyakh-Siene. A. Complete skull of an early form of the woolly mammoth (*Mammuthus primigenius fraasi*) with preserved molars (M3 sin. & dex.), ^{14}C age 18 330±100 BP, found in the MIS 2 alluvial deposits (Site 1, Unit IV) and pointing to the survival of this species in NE Siberia into the late Last Glacial stadial. B. Adult mammoth ulna attached in the articulated position to a fragmented pelvis frozen *in situ* (*sensu lato*) in the basal mid-Last Glacial interstadial formation (Site 2, Unit VII).

The most complete fossil remains with an excellent state of preservation were removed *in situ*(*sensu lato*) from the cryolithic grounds (Fig. 8B). Some of these findings retain the original content of hydroxyapatite in the bone tissue which has been currently closely studied at the chronologically analogous MIS 3 sites in the Yana basin.

Small fauna is represented by bone fragments of hare, rodents, birds, and some invertebrates. Freshwater molluscs of the family Lymnaeidae – *Radix auricularia* (Linnaeus, 1758) and terrestrial molluscs of the Bradybaenidae/Succineidae family – *Novi succinea* (an endemic Siberian gastropod) (Kantor *et al.* 2009), found in the silty clay lacustrine deposits of the Irelyakh-Siene 2 section (Unit Va) (Fig. 6A), characterize the stagnant or slowly flowing water settings with densely vegetated banks of low-elevation Early Holocene landscapes.

The Zyryanka locality. – The palaeontological material at Zyryanka was collected in several alluvial and colluvial cryolithic stratigraphical levels (Fig. 4), with mammoth and bison being the most representative species (Fig. 7E,

F) (Table 3) (Cover page). Based on the morphological measurements of molars, the presence of *Mammuthus trogontherii* (*M. trogontherii trogontherii* = *trogontherii* elephant), *Mammuthus intermedius*(*M. trogontherii chosaricus*), *Mammuthus chosaricus* and *Mammuthus primigenius fraasi* (an early form of mammoth) were determined, suggesting different ages of the buried Pleistocene faunal assemblages recorded in the basal alluvial formation (Unit V). Apart from mammoth, other large ungulates such as *Equus* sp., *Bison* sp., *Rangifer tarandus*, *Alces* sp. together with *Coelodonta antiquitatis* were identified. Some of the uncovered and chronologically earlier bones display a geochemical alteration with precipitation of vivianite and manganese minerals during low-oxygen conditions while being enclosed in the ancient permafrost grounds (Fig. 7E).

The numbers of the palaeontological remains do not exceed the amounts collected at the Irelyakh Siene sites. The species compositions between the two localities also differ, with the Zyryanka palaeo-fauna assemblage dominated by >50% by woolly mammoth followed by bison (23%) (Cover page) and a significant representation of Carnivora (wolf, cave lion and wolverine; 13% in total), which are close to absent at Irelyakh Siene. In contrast, at the Irelyakh Siene locality, bison (42%), mammoth (29%) and woolly rhinoceros (14%) (Fig. 6D) are the most encountered Pleistocene megafauna species (Fig. 9). In addition to the large fauna, small and fragmentary fossil mammal bones (indet.), and patches of pale yellow bison hair of 7–8 cm in length and 200–300 g in weight (under investigation) were retrieved by sediment washing.

The Presnyy Stream site. – At the Presnyy Stream site (Fig. 1C), the taxonomically diverse Pleistocene fauna contextually relates to the main fossiliferous MIS 3 interstadial alluvia of coarse, dark yellowish sands with small pebbles exposed by erosion over ~50 m distance of active permafrost grounds. In addition to/apart from single animal bones, complete parts of the skeletons were found. This includes an articulated front right leg bone of an adult mammoth (*Mammuthus primigenius*) still attached by joints of a total length of 280 cm and a foot diameter of 38 cm recorded in 2013 (stored in the Mammoth Museum, Yakutsk).

A concentration of well-preserved and intact articulated thoracic mammoth vertebrae was retrieved from the fossiliferous grounds. This may indicate that the original location of the animal's carcass was in the close vicinity of the fossil find. An articulated mammoth femur and tibia found proximally to these mammoth remains suggest that the location of the dissected animal's body may have been (i) a Palaeolithic kill site, or (ii) the natural death site of the animal, which was subsequently exploited by people who dismembered and butchered the corpse. Palaeontological remains

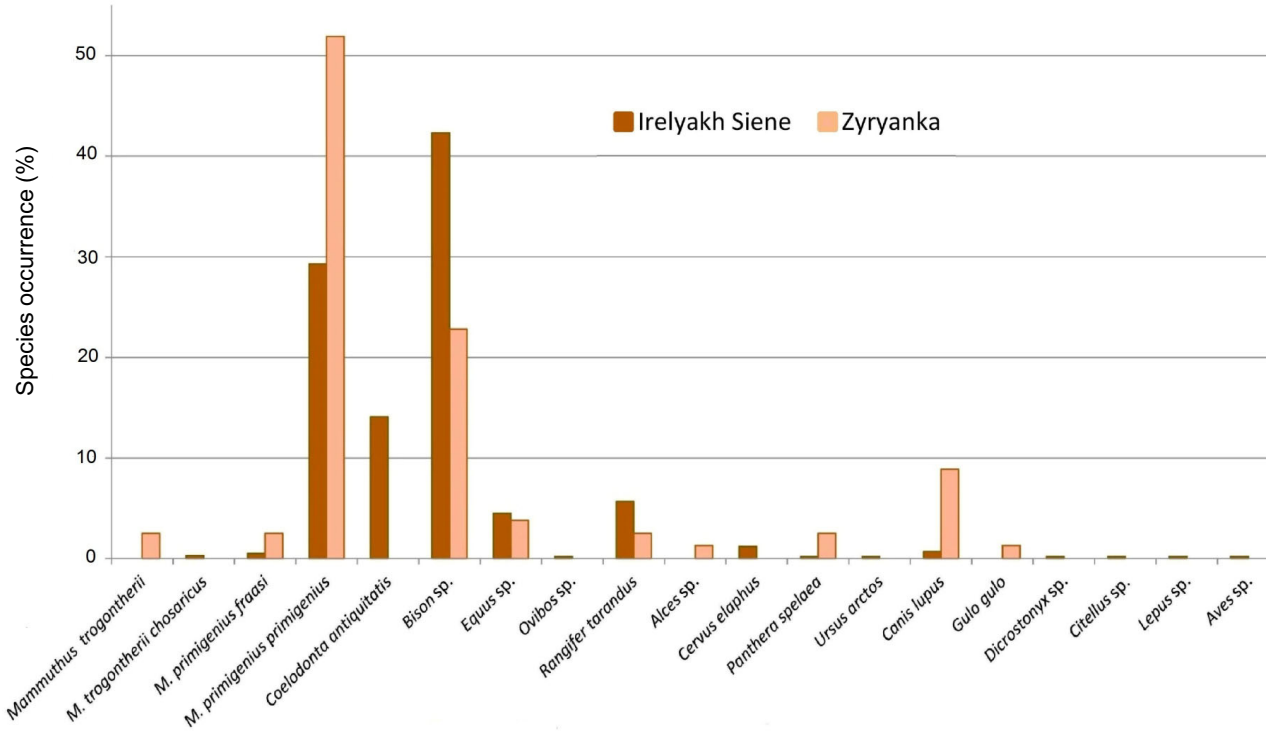

Fig. 9. The recorded Pleistocene fauna species composition for each of the investigated sites (see Table 3).

suggesting early human actions – potential megafauna butcher sites – are also observed at the Irelyakh-Siene sites.

The Popovka, Ozhogina and Omulevka River sites. – The rest of the surveyed and investigated sites in the Verkhnekolymsk area (Fig. 1C) were less productive in terms of faunal records as compared to the main Irelyakh-Siene and Zyryanka localities. Numerous fossil remains were found on the left bank of the middle Kolyma and its tributaries – the Popovka, Ozhogina and Omulevka rivers (mostly *Mammuthus primigenius*,*Coelodonta antiquitatis*,*Bison* sp., *Equus* sp.). In the Mayachnyy Creek, being the northern-most investigated site (Fig. 1C), frequent carnivore remains (*Panthera spelaea*, *Canis lupus*,*Gulo gulo* and *Vulpes vulpes*) were recorded in addition to large ungulate fauna fossils (*M. primigenius*, *Rangifer tarandus*, *Bison* sp., *Equus* sp., *C. antiquitatis*) (Table 2).

In summary, the assembled Pleistocene mammal collections from the permafrost formations of the middle and upper Kolyma Basin document a very productive (sub-)arctic tundra-steppe periglacial environment established at different stages during the Last Ice Age.

Archaeological evidence

The Late Pleistocene sections produced some early and most interesting cultural records in direct associations with the megafauna embedded in the cryolithic formations. The cultural findings provide the first indications of an (pre-LGM) occupation of the middle Kolyma area. The bone- and stone-made-artefact-bearing geo-contexts occur in stratigraphical positions in the main fossiliferous MIS 3 units. Some documented places with the Palaeolithic inventories lay within the cryogenically uplifted topographic elevations 'kochkas' located in close proximity to the main palaeo-river channels. The ^{14}C ages (>40 ka BP) on the enclosing/incorporating geological strata, and the associated tooled bone and ivory objects imply the presence of pre-modern people in the Kolyma Basin during the mid-Last Glacial interval, and document a diversity of largely prey- and osteological raw-material-processing activities.

Bone processing. – In the studied palaeontological collections, a number of bones (~20%) reveal clear traces of ancient human treatment and use. The skeletal parts of the Pleistocene megafauna show anthropogenic manipulation in the form of cut-marks, carving as well as bone-shaft crushing, polishing and fracturing, presumably for marrow removal as well as for bone fragments. At Irelyakh-Siene, the cultural items made from organic materials were unearthed from the palaeo-channel deposits (Site 1, Unit IV; Site 2, Unit VI-VII; Fig. 3). Some bones display a pattern of a long-bone splitting and preparation of small compact segments with concave, crescent-shaped cut-outs best-exemplified on a mammoth humerus (Fig. 10A). Perforated large animal bones (mammoth, rhinoceros and bison) with openings (Fig. 10B) suggest their use as objects for a tent-cover fixing. Parallel finds from Late Palaeolithic sites in eastern Europe, the Urals and West Siberia were interpreted as dwelling accessories (Pidoplichko 1978; Soffer 1993; Sergin 2001; Borziac *et al.* 2007; Obada *et al.* 2010; Chlachula & Serikov 2011). A similar function may have been fulfilled by the crania of mammoth (Fig. 8A), rhino or bison.

The nature of the physical actions done to the Pleistocene fauna skeletal parts shows that these were

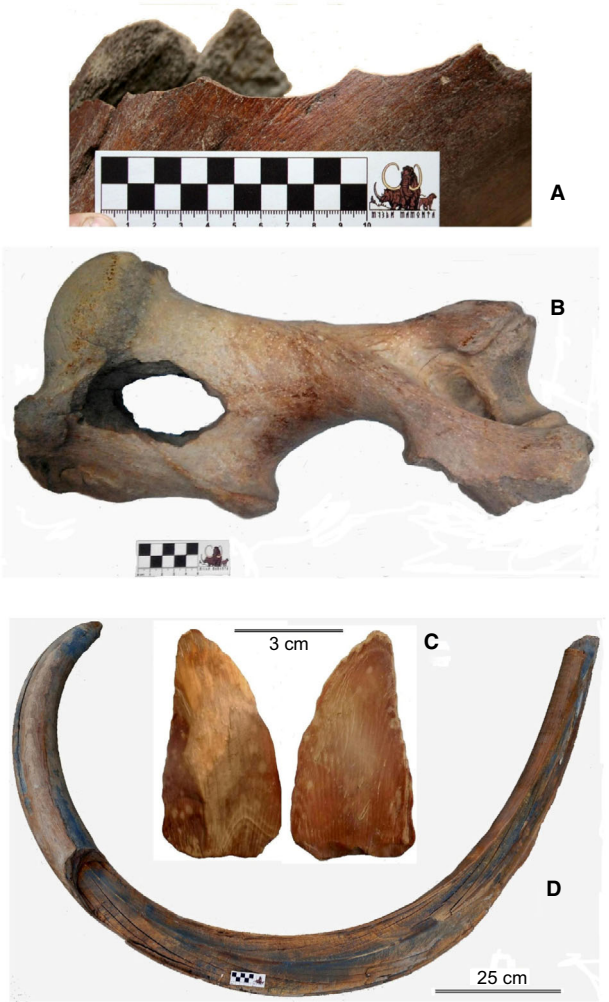

Fig. 10. Anthropogenically worked and used fossil fauna remains. A. Regular concave cuts at the distal end of a mammoth humerus (Irelyakh-Siene 1, Unit IV). B. Perforated rhinoceros humerus (Irelyakh-Siene 1, Unit IV upper part, ^{14}C age ~22 ka). C. A point made from a mammoth ivory flake with a lateral retouch (Irelyakh-Siene 1, Unit IV lower part). D. Anthropogenic splitting and flaking of a *Mammuthus primigenius* tusk from the late Last Glacial silty clayey colluvium (Zyryanka 1, Unit III, ^{14}C age ~19.3 ka).

treated by early people whilst still in a fresh bone/ivory state with an intact spongy structure. Tool marks on some of these remains from Irelyakh-Siene 1 indicate their modification by using flaked lithic instruments found at the site (see below). Specific smoothening tools ('gladilniki') with flat dorsal working faces were recorded at the same locality. One of these instruments made from a mammoth rib-bone fragment found *in situ* displays stone-flake cuts and simple ornamentation in the form of thin grooves and scratches. Various modified bone pieces and plaques cut from animal bones presume their decorative use.

Teeth processing. – In addition to bone processing, use of the Pleistocene megafauna teeth by the Kolyma Palaeolithic people is also documented. Within an erosion of a small tributary creek at the Presnyy Stream site (Fig. 1C), a mammoth tusk fragment with a clearly artificially/anthropogenically modified upper molar (M3 dextr.) was discovered. The frontal parts of the teeth roots (the first half of the lingual and buccal segments) display traces of oblique artificial cuts presumably made by the Palaeolithic people (Cheprasov *et al.* 2015). This and other finds of culturally manipulated osteological remains indicate early human practices, either utilitarian or religious.

Mammoth ivory processing. – The most interesting type of the osteological material processing recorded is that of mammoth ivory. Complete mammoth tusks and more often their fragmentary parts display patterned flaking and splitting for extraction of long and thin ivory flakes presumably used for spear point finishing. In addition to the mammoth tusk fragments, some uncovered specimens made from mammoth ribs can be interpreted as spearheads and dart points. Puncturing and polishing at distal ends of mammoth tusks suggest some specific use. Cuts and flaking on mammoth tusks are regularly encountered as well as detached and preshaped ivory pieces possibly employed as awls and polishing tools. Analogous finds are known from the Palaeolithic sites in the Yana–Indigirka and the Kolyma Lowlands (Kashin 2003; Nikolskiy & Pitulko 2013). A tusk fragment of a rectangular shape with a laterally retouched margin, rounded corners and traces of polishing possibly used as an arrowhead or a scraper (Fig. 10C) was found at the Irelyakh-Siene Site 1 (Unit IV) along with a longitudinally cleaved and distally retouched compact ivory piece (^{14}C-dated to 23 100±220 a BP; Cheprasov *et al.* 2015). A well-finished ivory spear point was uncovered at the Irelyakh-Siene Site 2 in the clayey deposits (Unit VI). Man-utilized mammoth tusks with cuts, drilling and splitting traces originate from the Zyryanka Site 1. The splinted large mammoth tusk (^{14}C age 19 270±120 a BP) from the colluvial Unit III (Fig. 10D) together with two anthropogenically worked (drilled and flaked) ivory segments (^{14}C age 44 000±2000 a BP) at the base of the formation show the broad time range of the mammoth ivory Palaeolithic utilization in the Kolyma region.

The cultural working and use of ivory by the Palaeolithic people across mid- and high-latitude Eurasia are quite common (Khlopatchev 2001;; Pitulko 2001; Amirkhanov *et al.* 2009; Khlopachev & Giria 2010; Pitulko *et al.* 2015). The earliest Siberian record from the Yenisei region (Ust'-Izhul site), OSL-dated to 125 ka, is attributed to local Neanderthals (Chlachula *et al.* 2003). Furthermore, the findings of the culturally modified woolly mammoth bones and ivory with the ^{14}C ages 22–19 ka (Table 1) indicate the presence of early humans in sub-arctic NE Siberia during the LGM and imply they had the technology and aptitude to cope with the extreme periglacial climates and environments.

Soft tissue processing. – In 2017, a dismembered and partly de-skinned bison back leg with flesh and the animal's hair was discovered at Irelyakh-Siene 1 frozen in a permafrost-sealed bed about 1 m under the present surface. The find is the first one of its kind in Siberia potentially documenting early prehistoric bison hunting and carcass processing (under investigation). Among the other Kolyma region discoveries of megafauna with preserved soft tissues and a post-mortem treatment evoking early human actions, there is a complete mummified woolly rhinoceros (*Coelodonta antiquitatis*) found *in situ* and radiocarbon dated to 39 140±390 cal. BP (Boeskorov *et al.* 2009). The animal's head was separated from the rest of the body of a calculated total weight ~900 kg (Boeskorov 2012). Other fossil fauna finds suggesting possible anthropogenic involvement are under study.

Lithic industry. – The Palaeolithic site at Irelyakh-Siene 2 delivered several stone artefacts from the basal mid-Last Glacial coarse sandy-gravel alluvial strata (Unit VII) associated with the fossil fauna remains. Isolated lithics were eroded from the Pleistocene geo-context onto the present river banks over a distance of ~70 m. The *in-situ*(*sensu lato*) stone implements with diagnostic anthropogenic stone-working and utilization attributes include three anvil-percussion-made chopping tools produced from massive quartzite cobbles, two scrapers made from longitudinally split, high-quality and fairly rare green chalcedony cobbles (Fig. 11), and a number of unmodified or partly laterally retouched flakes detached from 'serdolik' (a honey-coloured silica mineral) pebbles.

With respect to the archaeological character, this Pleistocene-age occupation represents the first location in the explored central Kolyma area that can be interpreted as a campsite that exhibits evidence of presumed hide processing (bone smoothening tools), and stone-tool production, primarily from local lithic raw material sources originating from the proximal alluvium and minor exotic imported high-quality min-

Fig. 11. Irelyakh-Siene 2. A green chalcedony scraper from the mid-Last Glacial deposits (Unit VII).

erals. Some discarded stone artefacts together with bone tools were also recorded in the nearby site Irelyakh-Siene 3, including several hammer-stones, a chopping tool shaped from light brownish-coloured sandstone with two sharp straight working edges, and a chalcedony micro-nucleus. The presence of the latter artefact indicates a more recent (MIS 2) age of this item and the site. At the most recently (2019) discovered site Irelyakh-Siene 4, several macro-lithic tools and micro-nuclei from 'serdolik' were found. Farther downstream of the Nikita Creek (over 300 m wide) delimiting the northern limits of the Irelyakh-Siene locality, no anthropogenically worked fossil bones, or stones, were found supporting the assumption of the presence of discrete Palaeolithic sites in the study sector along the right bank of the Kolyma main channel (Irelyakh-Siene 1–3).

Discussion

The MIS 3–2 environments of the Kolyma Lowlands

In spite of the rich Pleistocene fauna occurrences in Yakutia, there are just a few sites with well-documented and chronostratigraphically fixed fossil-bearing contexts. One of the most-referenced Late Pleistocene palaeontological loci is Duvannyy Yar in the lower reaches of Kolyma ~45 km downstream from the mouth of the Omolon River. The geological outcrop became the key reference section of the Kolyma yedoma formations (Baranova 1957; Biske 1957), incorporating the most representative Late Pleistocene fauna species of north Siberia (Lazarev 2008; Zimov *et al.* 2012; Macias-Fauria *et al.* 2020).

The palaeoenvironmental records from the middle Kolyma Basin and the analogous biotic data from the Yana Basin (Novgorodov *et al.* 2013; Ashastina *et al.* 2018) report on the woodland and parkland habitats during the first part of the interstadial ~50–38 ka ago and the landscape diversity. The unique or most complete finds palaeontological findings – such as the whole adult woolly mammoth carcass (*M. primigenius*) referred to as 'the Berezovsky Mammoth' found *c.* 1900 at the Berezovka River, the right tributary of Kolyma River (Zalenskiy 1903; Sukachev 1914; Fig. 1) – offer an unprecedented view on adaptation and diet as well as health status of that particular Ice Age animal supplemented by megafauna coprolites from the Pleistocene cryolithic contexts (Kirillova *et al.* 2016).

The reconstructed and rather dynamic fluctuating MIS 3 climates affected the palaeo-relief development with meandering channels shaping the ancient valleys, permafrost-degrading depressions and thermokarst lakes. The geomorphic processes are analogous to those currently acting in the NE Siberia sub-arctic riverine basins (Chlachula *et al.* 2016). The principal fossiliferous formations along the Kolyma riverbanks and the tributary streams represent buried and now exhumed mid-Last Glacial grounds sealing ancient woods of forest(-tundra) ecosystems, collapsed gleyed palaeosols, and the quantities of the mammoth fauna remains incorporated in the sediments. These deposits accumulated during the warmer interstadial climate oscillations under progressing permafrost thaw.

The retrieved palaeo-biota records point uniformly to a high bio-climatic diversity under conditions of an increased mean annual temperature (MAT) as well as humidity in NE Siberia during the earlier part (~55–38 ka) of the MIS 3 interstadial interval. The chronologically equivalent bio-stratigraphical archives from north Siberia point to the MAT being up to 0.5–2.0 °C higher than today with an annual precipitation rate increased by 25–100 mm with respect to modern values (Andreev *et al.* 2002), and warm summers relative to today (Kienast *et al.* 2005). A broad-leaved vegetation within the modern tundra zone, suggesting much warmer climate conditions than the present-day, was also documented on the Gyda Peninsula and the lower Tazov River Basin, NW Siberia, in chronologically corresponding fossil peat and organic detritus units ^{14}C dated to >48 000 a BP (Chlachula 2019). The corresponding moderate mid-Last Glacial climates in the lower Kolyma–Indigirka area are also evidenced by a series of buried black brunisolic and gleysolic palaeosols (cryosols) with patterned temporal stratigraphical occurrences around 43–42, 38–37, 33–31 and 28 ka (Gubin *et al.* 2008), and chronologically equivalent pedogenic units in the southern Siberian loess region (Chlachula 2003). Open tundra-larch forests with alder and dwarf birch, and herbaceous tundra grasslands were the principal Last Glacial (MIS 4–2) biotopes of the Kolyma Lowlands (Rybakova 1990).

Warmer MIS 3 conditions in respect to the present ones are reported across the broad territory of east Siberia from the lower Lena area to NE Chukotka

(Laukhin *et al.* 1999; Schirrmeister *et al.* 2002; Bezusko *et al.* 2008). The Kolyma evidence supports an interpretation of productive biotopes in the Siberian sub-Arctic in spite of the assumed punctuated cooler climate fluctuations during some interstadial intervals, particularly in the intra-continental areas of western Beringia (Lozhkin & Anderson 2011). The fossil osteological material (bones, teeth and horns) buried in the ancient fine Kolyma River alluvia and bogs are occasionally covered by a greenish-blue vivianite mineral layer replacing the organic matter at the surface. Presence of this mineral indicates stable anaerobic conditions exemplified on the remains of *Mammuthus trogontherii* – the Siberian tundra-steppe antecedent of the Late Pleistocene woolly mammoth. These deposits likely developed in climatically moderate aquatic and palustrine settings. Apart from the rich palaeo-vegetation concentrations (wood, moss and peat), the disturbed/degraded mid-Last Glacial landscapes occasionally show signs of increased salinity (Fominykh 2013).

The climatically mild early interstadial MIS 3 environments corroborate the time-equivalent (~46–35 ka) coastal Arctic cryolithic records from western Beringia documenting mosaic mesic–xeric tundra-steppe meadows with high diversity of grasses and herbs having the present-day NE Yakutia relic steppe analogues (Kienast *et al.* 2005; Sher *et al.* 2005; Lozhkin *et al.* 2008; Lozhkin & Anderson 2011). The moderate mid-Last Glacial proxies from the investigated middle Kolyma sections markedly differ from the more recent stable isotope and pollen records from the yedoma complex in the lower reaches of the Kolyma River, indicating very harsh continental conditions with shrub- and herb-dominated frigid tundra towards the end of the interstadial, ~30–28 ka (Vasil'chuk & Vasil'chuk 2018). Continental aridity and low temperatures during MIS 2 are evidenced by massive sand accumulations across the Russian continental and arctic regions (Astakhov & Svendsen 2011; Velichko *et al.* 2011) that may correlate with the upper aeolian/colluviated facies of the Irelyakh-Siene and Zyryanka stratigraphical sequences (Units II; Figs 3, 4).

In terms of the investigated MIS 3 regional palaeohydrology regimes, the basal alluvial sedimentary bodies at the investigated localities with a coarsening-upwards grain-size distribution reflect laterally shifting channels with fluctuating flows of a slow (several m/s) to a higher-energy fluvial deposition. The interstratified cross-bedded coarse sands and fine gravel pockets characterize shallow tributary stream settings found in the sites' surroundings today. The overlying sandy silts and clay indicate standing water bodies (overbank or drying-up lacustrine pond deposits) adjacent to main river channels, closed water basins (ox-bow lakes), and marginal marshlands. The change in the local hydrology balance suggests gradual landscape transformations due to regional aridization and cooling during the second half of the interstadial. Marked short-term climate instability intervals contributed to colluviation of the amassed deposits prior to the onset of the late Last Glacial (MIS 2; Fig. 12). The progressing postglacial warming trends and increased surface water supplies generated active peat growth and formation of shallow, organic-rich thermokarst lakes culminating during the Early–Middle Holocene. Overall, the diversity of sedimentary facies points to the dynamically changing environments of the Last Ice Age (sub)arctic landscapes.

Palaeolithic occupation and adaptations of northeast Arctic Siberia

There is solid evidence of and a general consensus on the presence of the Middle Palaeolithic people in northern Eurasia at various stages of the Middle and Late Pleistocene (Chlachula 2011). The earliest definite human occupation of (central) Yakutia precedes the last interglacial with indications of potentially much older (Middle Pleistocene) sites (Mochanov & Fedoseeva

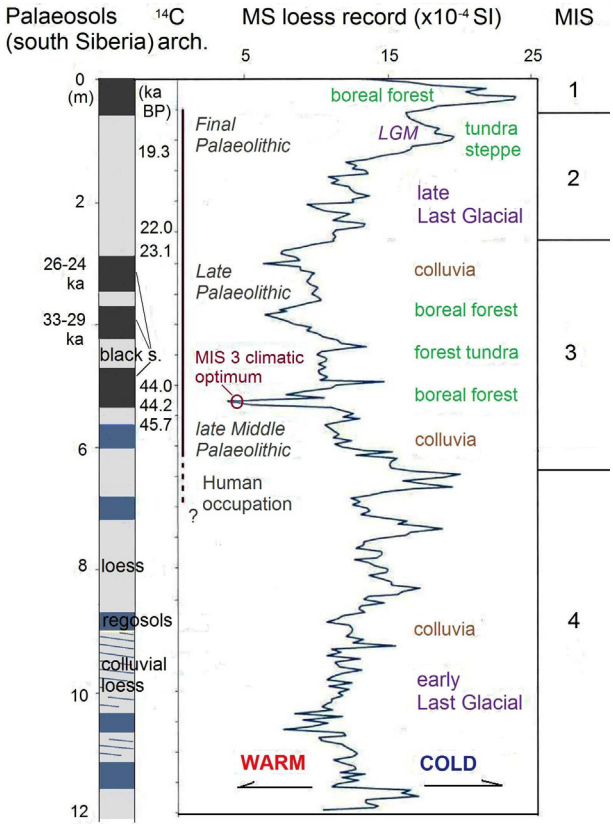

Fig. 12. Chronostratigraphical scheme of the Late Pleistocene to Holocene environmental history of the middle Kolyma area, the Last Glacial ecosystems and the stages of human occupation with the ^{14}C-dated archaeological finds. Correlation with the MIS 4–1 loess-palaeosol stratigraphy of southern Siberia and the palaeoclimate proxy record based on the high-resolution magnetic susceptibility variations of loessic sediments (Chlachula & Little 2011).

2007; Mochanov 2010; Sharaborin 2015). The south–north-oriented Lena, Yana, Indigirka and Kolyma River valleys are seen as migration corridors of the Pleistocene megafauna as well as humans. The existence of the mammoth-fauna biome (Ukraintseva 2013) for the Palaeolithic spread was crucial. The extension of the occupation further north into the interior and coastal arctic regions was the logical continuation of the geographical dispersal of the early people and enhanced biological adaptations to the tundra-steppe and forest-tundra habitats.

The mid-Last Glacial interstadial (60/55–24 ka) is considered to be climatically the most suitable time interval for the Pleistocene inhabitation of the Siberian North (Laukhin & Firsoy 2008; Pitulko *et al.* 2016, 2017; Chlachula 2017; Velichko *et al.* 2017). The earliest investigated archaeological sites beyond the Arctic Circle (the Yana and Indigirka Basins), that are associated with the megafauna exploitation date well prior to the LGM (Chlachula *et al.* 2014; Pitulko *et al.* 2016; Dyakonov & Chlachula unpublished). The Irelyakh-Siene and Zyryanka sites provide the chronostratigraphical, geological and palaeo-environmental background for the Late Pleistocene geoarchaeology investigations of the Kolyma region. The early MIS 3 palaeo-environmental proxies associated with the initial interstadial peopling demonstrate biotically vital (sub-)arctic surroundings similar to the modern ones.

The species variety of the extinct Elephantidae together with other large ungulate species retrieved from the Pleistocene cryolithic formations illustrate the mosaic herb-rich grass steppe, tundra-steppe and forest-tundra ecosystems. The bone and ivory tools with the associated lithic implements from Irelyakh-Siene supported by the Zyryanka records point to a long-term presence of people in the Kolyma Basin during MIS 3, encompassing a time range of >20 000 years in view of the ^{14}C-dated cultural inventories (Fig. 12). The diagnostic anthropogenically worked osteological material with clear traces of artefact processing and functional use, and the associated stone industry, add to the present perceptions of the adjustment of early humans in the climatically most extreme regions of Siberia.

The evidence of the interstadial peopling of the middle Kolyma corroborates the archaeological records and the associated geo-contexts in the lower and middle Yana Basin at the Yana RHS and the Yunyugen sites, respectively (Pitulko *et al.* 2004; Novgorodov *et al.* 2013; Chlachula, unpublished). The large Pleistocene animals roaming across the broad open territories of western Beringia provided a rich food supply for the prehistoric people in view of the enormous amounts of fossil fauna bones, many of which show signs of human articulation and use. The functionally specific anthropogenic treatments of the fossil remains allow for better understanding of the adaptations of Palaeolithic people of north-east Siberia to the mid-Last Glacial (sub)arctic habitats and human survival strategies under the harsh conditions of the ensuing late Last Glacial stage (MIS 2; Hoffecker *et al.* 2020).

The climatic cooling approaching the LGM (22–18 ka) caused a retreat of taiga forest replaced by frigid periglacial tundra. The high-glacial arctic ecosystems allowed continued occupation by Palaeolithic hunters supported by the presence of large herbivores in spite of the severe environments and a very short growing season. The persistence of the early human settlement in the middle Kolyma area around the LGM is evidenced, by the longitudinally riven mammoth tusk from Zyryanka dated to 19 270±120 a BP (21 606–20 942 cal. a BC; Fig. 10D) among other finds from this locality (Table 1). Such anthropogenically treated megafauna remains indicate very effective biological and cultural adaptations considering the severely increased climate dryness and extreme low temperatures with just cold-resistant herbs, grasses and bryophytes (Poaceae, *Artemisia*, *Selaginella sibirica*) constituting the sparse vegetation cover in barren tundra.

The occupation of the eastern Russian Arctic well prior to the Last Glacial Maximum – as early as 45 000 years ago – has a direct bearing for the modelling of the dispersal of the Palaeolithic people across Pleistocene Beringia (West 1996). Under the moderate MIS 3 climates, and the territorial physiographic and palaeoecological situation (Hopkins *et al*. 1982; Harris 2019), there were no physical geomorphic and environmental barriers to prevent a spatial expansion of the humans eastwards into present-day Alaska within the close (<2000 km) geographical limits from the Kolyma area. The pre-Last Glacial (>24 000-year-old) archaeological records from caves in northern Yukon (Cinq-Mars 1979), and in western Alberta deeply buried (up to 50 m) below the Last Glacial tills and the related glacigenic deposits blanketing the western Canadian prairies and the Rocky Mountain foothills (Chlachula 1996a, 1996b, 2012) strongly support this interpretation. To what degree the supposed late Last Glacial moisture barrier in central Beringia (Elias & Crocker 2008; Anderson & Lozhkin 2015) affected the biotic transfers and the early American migrations remains open.

Conclusions

The Kolyma Lowlands, enclosing the eastern borders of the Siberian Mammoth Steppe, is along with the Yana and Indigirka Basins the principal region for comprehension of the timing and the natural conditions of the sequenced early prehistoric occupation of the NE Russian territories. The Pleistocene cryolithic formations provide the most valuable records on the past landscapes, the fossiliferous geological contexts and the buried cultural manifestations. The spread of the Palaeolithic hunter-gatherers beyond the Arctic Circle mirrors long-term sustainable conditions established with the

onset of the MIS 3/Karga interstadial seen as the main stage for the Late Pleistocene human colonization of the Siberian Arctic. The utilized bones and worked mammoth ivory show the inhabitation of the middle Kolyma by pre-modern (late Neanderthal?) people as early as ~47 ka ago. The archaeological inventories attest to a viable human adjustment to the mosaic boreal forest and forest-tundra habitats of meandering river valleys and thermokarst lake settings. The mid-Last Glacial temperature fluctuations spawned periodic frozen ground instability and massive colluviation evidenced by the site stratigraphies at the occupied locations. The climatic cooling approaching the late Last Glacial initiated the expansion of frigid periglacial tundra with the continuation of human settlement during the LGM. The final Pleistocene warming trends generated the formation of the present-day relief and the northern boreal ecosystems, and induced more semi-sedentary Mesolithic adaptation strategies. With respect to the intact tens of thousands of years old permafrost preserving unique palaeontological and organic archaeological records, the Quaternary investigations in the Kolyma region are of utmost scientific importance.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at http://www.boreas.dk.

Table S1. Irelyakh-Siene Site 1 (2014) stratigraphy (Fig. 3A).

Table S2. Irelyakh-Siene Site 2 (2015) stratigraphy (Fig. 3B).

Table S3. Zyryanka Site, Section 1 (2019) stratigraphy (Fig. 4B).