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‘Semi-dwarf’ woolly mammoths from the East Siberian Sea coast, continental Russia

IRINA V. KIRILLOVA, OLGA K. BORISOVA, OLGA F. CHERNOVA, THIJS VAN KOLFSCHOTEN, JEROEN H. J. L. VAN DER LUBBE, ANDREY V. PANIN, PATRICIA PEČNEROVÁ, JOHANNES VAN DER PLICHT, FEDOR K. SHIDLOVSKIY, VADIM V. TITOV AND OKSANA G. ZANINA

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A pioneer comprehensive study of several diminutive last-generation woolly mammoth teeth (M3) found on the coast of the East Siberian Sea between the mouths of the Alazeya and Malaya Kuropatoh'ya rivers was conducted. Two teeth belonged to one individual. These teeth have a similar lamellar frequency and enamel thickness as teeth of *Mammuthus primigenius* Blumenbach. The molar crowns from the lower Alazeya region are similar in size to those of the small Late Pleistocene–Holocene mammoths from Wrangel Island. However, the number of plates (17–19, excluding talons) is much lower than that in the teeth of typical Late Pleistocene *M. primigenius* (23–25). The age data of the examined teeth are beyond the limits of the ^{14}C dating method (>45 000 years BP). Nevertheless, palaeobotanical data allow correlation of the enclosing sediments with the warm Kazantsevo Interglacial (Eemian, MIS 5e) and reconstruction of the average annual temperature, which was warmer than present-day temperatures. These conditions are confirmed by the $\delta^{18}\text{O}$ isotopes from the structurally bound carbonate in tooth enamel. The ancient landscape was wetter and more forested than modern landscapes. The diminution of M3 size and loss of posterior plates were a result of the overall decrease in body size, likely in response to landscape change and narrowing of resource space. Mammoths from the lower Alazeya region demonstrate a stage of significant size reduction, although the dwarfing was not finalized. Their teeth are the oldest amongst the small teeth found in west Beringia.

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The Eurasian Pleistocene mammalian fauna was characterized by the occurrence of large-sized species, the so-called megafauna, which included the woolly mammoth *Mammuthus primigenius*, the straight-tusked elephant *Palaeoloxodon antiquus*, the woolly rhinoceros *Coelodonta antiquitatis*, the Siberian unicorn *Elasmotherium sibiricum*, the bison *Bison priscus*, etc. However, fossil records show that not all Pleistocene elephants possessed ‘mega’ stature. Ancient elephant/mammoth populations from isolated islands indicate a substantial decrease in size, which led to the occurrence of dwarf forms. An example of this was the pygmy *Mammuthus exilis* (Stock & Furlong, 1928), a descendant of the Colombian mammoth that lived in North America, from the Channel Islands near the coast of southern California (Agenbroad *et al.* 1999; Agenbroad 2009; Bryson *et al.* 2010). Remains of a dwarfed mammoth referred to as *M. lamarmorai* (Major 1883), considered the descendant of the steppe *M. trogontherii* (Pohlig

1885), were found on the Mediterranean island of Sardinia (Palombo *et al.* 2012). On Crete, the remains of a very small mammoth referred to as *M. creticus* (Bate 1905), a derivative of *M. meridionalis* (Herridge & Lister 2012), were collected. This species was even smaller than the Sardinian *M. lamarmorai*. In all these cases, the animals lived in insular isolation, where limited expansion of habitat combined with the absence of large carnivores facilitated substantial size reduction and resulted in viable populations of dwarfed elephants/mammoths. As exemplified by other species such as *Palaeoloxodon* and *Stegodon* dwarfs from the islands of Sunda Archipelago (Sulawesi, Flores, Timor, Sumba and Java), the landscape and remote location of the isolated territory were not the only decisive factors in the reduction of these elephants’ body size. Other factors such as interspecific competition are also assumed to be important (Crockford 2008; van der Geer *et al.* 2016). It was noted that the degree of elephant dwarfism varied

from island to island and was independent of the islands' sizes (Palombo 2009; van der Geer *et al.* 2016). It was noted that decrease in body size of elephants from the eastern Mediterranean islands occurred when a population was isolated by at least 6–10 km and there was an absence of genetic contact with the mainland ancestors (Sen 2017; Athanassiou *et al.* 2019). Small (but not dwarfed) woolly mammoth teeth found on Wrangel Island (East Siberian/Chukchi Seas) and the Pribilof Islands (Alaska) date to the Holocene (Garutt *et al.* 1993; Averianov *et al.* 1995; Tikhonov *et al.* 2003). Taimyr Peninsula, Yakutia, Great Britain, Ireland and the North Sea also yielded relatively small Late Pleistocene mammoths (Garutt 1964; van Essen 1986; Averianov *et al.* 1995; Boeskorov & Mol 2004; Maschenko *et al.* 2006; den Ouden, *et al.* 2012; Lister & Grün 2015) and these remains have been known for a long time (van Brandt 1832; Adams 1877–1881; Zalen-sky 1902; Soergel 1912; Vangengeim 1961). However, there are no true dwarves amongst them. Investigations of the fossil records from the Russian Plain confirmed the presence of both large- and small-sized mammoths within the cultural layers of some Late Palaeolithic sites (Gromov 1929).

The phylogeographical study by Palkopoulou *et al.* (2013) included three woolly mammoth specimens identified by Andrey Sher as 'dwarf' (= very small)-sized (L. Dalén, pers. comm. 2018). One of these specimens (GenBank: KC427955) was found on the New Siberian Islands and was dated to >55.6 ka, while the other two mammoths (GenBank: KC427976 and KC427977) were found in Vologda Oblast in western Russia and were dated to ~30 ka. According to DNA analyses, the three Siberian mammoths were not closely related as the New Siberian mammoth belonged to mt Clade II and the western Russian mammoths belonged to mt Clade I. Moreover, across the 741 base pairs of the analysed sequence, the New Siberian mammoth's mtDNA represents the most common Clade II haplotype (Palkopoulou *et al.* 2013), and is shared with other mammoths not identified as dwarf-sized mammoths. The available genetic evidence does not seem to indicate that Siberian mammoths with reduced body size differ in their mitochondrial phylogeny.

In 2012, several woolly mammoth teeth were discovered on the East Siberian Sea coast between the Alazeya and Malaya Kuropatoch'ya River mouths (approximately between latitude 70°51'N, longitude 153°41'E and 70°15'N, 155°36'E) located in the Kolyma Lowland north of the Arctic Circle (Fig. 1). Some of the extremely small upper third molars with a low number of plates attracted special interest. The results of a comprehensive study of these materials are presented in this paper. As this find of a 'semi-dwarf' mammoth with specific teeth characteristic of the continental Russian territory is the first, our goal was to study the environment in which it occurred, the

reasons for the size reduction, and its position amongst Late Pleistocene woolly mammoths.

Material and methods

We examined a collection of 24 complete upper M3 teeth of woolly mammoth (hereafter referred to as 'mam-moths from the Alazeya region') including a pair of isolated teeth with the collection numbers F-3326 (right) and F-3327 (left) from a single individual (Fig. 2), hereafter referred to as the 'Alazeya mammoth'. The roots of these molars were filled with sediment. In addition, the collection includes several mammoth teeth of various sizes, including other small specimens F-3889 and F-1959. All the remains are well preserved; they contain traces of vivianite and are often 'painted with iron compounds'. The materials are stored in the National Alliance of Shidlovskiy 'Ice Age', Moscow, Russia.

The morphological and morphometric data of the teeth were recorded following the procedure described by Dubrovo (1960) and Foronova & Zudin (1999). Incomplete enamel plates located at the anterior and posterior sides of the crowns, not at the tooth roots, were named 'talons' or 'platelets'. Authors support using the term 'talon' based on the above-mentioned methods. Upper molars are indicated by the capital letter 'M'; lower ones are indicated by the lowercase letter 'm'.

Light and scanning electron microscopy in microwear, pollen, spore, and biogenic fraction analyses

Seven enamel samples taken from different parts of the M3 masticatory surface of F-3326 were prepared according to the standard technique (rubbing with 70° alcohol and securing on a stage with plasticine). The photographs were taken with a light microscope (Keyence Digital Microscope VHX-1000, 'Keyence Corporation', Japan) using 5–50× lenses (Fig. 3A). The samples were studied using a scanning electron microscope (SEM; JSM-840A, JEOL, Japan) with an Edwards Sfl50A device (Edwards High Vacuum International, UK). The classification of the 'microwear' pattern was performed according to the method described by Semprebon *et al.* (2016).

For the pollen analyses, two sediment samples collected from the main posterior root (sample 1) of the tooth F-3327 and from the space between the small roots (sample 2) were used. Pollen and spores were extracted from the sediment following the Grichuk (1940) method of using a heavy liquid (CdI solution) with a density of 2.2 g cm⁻³ and were studied using a light microscope with a magnification of 400×. In the two samples, 300 and 500 grains were counted respectively, and both samples were scanned to detect rare forms.

The biogenic fraction (phytoliths, plant detritus, diatoms, amoebas, sponges, etc.) from the same samples

Fig. 1. The region where the 'semi-dwarf' woolly mammoth teeth were found on the map of Eurasia (indicated by a white arrow on the top inset and a black box on the bottom inset) and northeast Russia. The inset shows the region between the mouths of the Alazeya and B. Chukochya rivers with similar relief structure. 1 = Alazeya River; 2 = Malaya Kuropatoh'ya River; 3 = Bolshaya Kuropatoh'ya River; 4 = Bolshaya Chukoch'ya River. [Colour figure can be viewed at www.boreas.dk]

was sieved at 0.5 and 0.25 mm. The coarse fraction (>0.25 mm) was analysed after dry-ashing at 350°C . The finer fraction (<0.25 mm) was macerated in distilled water. The low-density biogenic fraction was separated using a heavy liquid (KI+CdI with a density of 2.2 g cm^{-3}). Microfossils were studied in a glycerol solution using a light microscope with magnifications of 200 and $400\times$. The standard procedure of including 10 rows, each 24 mm in length, resulted in the discovery of 83 particles. Thereafter, the dry biogenic fraction was studied using a scanning electron microscope (Tescan VEGA 3 LSU with BSE detector for high vacuum).

Grain-size analysis

The same two sediment samples from tooth F-3327 that were used for the pollen, spores, and biogenic fraction analyses were used for the grain-size analysis. The analysis was performed using a laser diffractometer, a Malvern Mastersizer 3000 granulometer. The weight of the samples was 50–70 g. The samples were soaked for 24 h in 20% HCl at room temperature instead of the standard 10% HCl (Vorobiova 2006) to remove fine bone

fragments that had contaminated the sediment while scraping it from the teeth. After rinsing the HCl remnants, the samples were soaked for 1 h in a 4% solution of sodium pyrophosphate to disintegrate the soil aggregates (Konert & Vandenberghe 1997). After sedimentation and the removal of excess liquid, the samples were mixed into a homogeneous suspension; an average sample of 1–3 mL was transferred to the cuvette of the laser analyser using a pipette. The material in the cuvette was subjected to ultrasonic treatment for 100 s for additional disintegration. After this, the measurements were repeated 10 times, and the results of the repeated measurements were averaged.

DNA analysis

Tooth powder obtained from the dentine of the specimen F-3326 using a manual Dremel drill was used for DNA analysis. DNA was extracted from the tooth powder using a silica-based method (Yang *et al.* 1998) with modifications (Ersmark *et al.* 2015). A barcoded, double-stranded Illumina library was prepared following Meyer & Kircher (2010). This included a uracil-DNA-

Fig. 2. Small upper teeth of the last generation (M3) of *Mammuthus primigenius* from the Eastern Siberian Sea coast: specimens F-3327 (left) and F-3326 (right). A. Lingual view of both teeth. B. Occlusal view of both teeth. C. Right tooth, buccal view, with plate numbers (on a white background). D. Anterior view of both teeth. E. Left tooth, posterior view. F. Right tooth, view from the rooted surface. Collection of the National Alliance of Shidlovskiy 'Ice Age', Moscow. Scale bar: 20 cm. [Colour figure can be viewed at www.boreas.dk]

glycosylase treatment to remove uracils (Pečnerová *et al.* 2017a). The library was pooled in equimolar concentrations with 35 other samples, and the pool was sequenced on one Illumina HiSeq2500 lane at the Science for Life Laboratory in Stockholm.

The sequencing yielded 1 838 666 read pairs that were trimmed and merged in SeqPrep 1.1 (<https://github.com/jstjohn/SeqPrep>), using a slightly modified script as described by Pečnerová *et al.* (2017b). The sequencing reads were mapped to a reference consisting of the African savannah elephant *Loxodonta africana* Blumenbach 1797 nuclear genome (LoxAfr4; Broad Institute, USA) and the woolly mammoth mitochondrial genome (Krause; GenBank accession: DQ188829) using BWA 0.7.8 (Li & Durbin 2010). The BWA aln algorithm was used with several modifications to the default settings,

including deactivated seeding ($-l$ 16500), allowing more substitutions ($-n$ 0.01), and up to two gaps ($-o$ 2). Using SAM tools 0.1.19 (Li *et al.* 2009), the alignment was converted to BAM format, sorted, indexed and deduplicated (using the single-end read parameter).

Radiocarbon dating

Specimens F-3326 and F-3889 were ^{14}C -dated by AMS in Groningen (the Netherlands). Collagen was extracted from the dentine following a modified Longin procedure (Mook & Streurman 1983). The collagen was combusted into CO_2 , which was transferred into graphite for ^{14}C analysis (van der Plicht *et al.* 2000). The combustion system used was an elemental analyser coupled to a isotope ratio mass spectrometer (IRMS).

The ^{14}C date was reported in radiocarbon years (BP), which by convention includes a correction for isotopic fractionation based on $\delta^{13}\text{C}$ and the use of the conventional half-life (Mook & van der Plicht 1999). The ^{14}C date was calibrated into calendar age (reported in cal. a BP, which is calendar years relative to AD 1950) using the calibration curve IntCal13 (Reimer *et al.* 2013) and the OxCAL program (Bronk Ramsey 2009).

Stable isotopes in the enamel

A strip of enamel (7.2 cm in length) was taken from the buccal side of the plate of the mammoth tooth F-3327 and vertically subsampled at 36 intervals (~2 mm per sample interval) to produce an incremental carbon and oxygen isotopic growth record (from MT-1 to

MT-36). After the removal of the adhering dentine and cementum, the enamel pieces were ground using a pestle and mortar. For the stable isotope analyses, tooth enamel was targeted as it is less susceptible to diagenetic alteration compared with other apatite minerals (Thomas & Carlson 2004). Because of the permafrost conditions, the collagen was (partly) preserved, inhibiting the recrystallization of the apatite crystals, whereas the precipitation of secondary carbonate was expected to be minimal on the outer tooth surface. When sufficient material was available, a subsample was treated with 2.5% NaOCl and 1 M acetic-Ca acetate buffer, which is routinely applied to reduce the interference of contingent organic matter and exogenous carbonate, respectively, on isotope analysis (Bocherens *et al.* 1996).

Fig. 3. Photomicrographs (A, B) and electronic images (C, D) of the M3 of the Alazeya *Mammuthus primigenius*, specimen F-3326. A. General view of the masticatory surface, the sampling topography for the SEM (samples 1–7, arrows). B. Relief details (*en* = enamel; *de* = dentine; *ce* = cement). C. Narrow, straight strokes and wider scratches on the enamel of probe 4. D. Small pits on the enamel of sample 2. Scale bars: A = 1 cm, B = 0.1 cm, C and D = 10 μm .

For stable carbon and oxygen isotope measurements, ~0.3 mg of powdered enamel was placed in Exetainer vials, which were flushed with pure helium gas. At an elevated temperature of 45 °C, CO₂ was liberated by adding 100% anhydrous phosphoric acid (H₃PO₄). It was analysed using a Thermo Finnigan GasBench II connected to a Thermo Finnigan Delta Plus isotope ratio mass spectrometer (IRMS) at the Earth Science Stable Isotope Laboratory (Vrije Universiteit (VU), Amsterdam). Ten aliquots of the international calcite isotope standard IAEA-603 produced an average $\delta^{13}\text{C}$ value of 2.48‰ and an average $\delta^{18}\text{O}$ value of -2.44‰, both with a standard deviation of 0.07‰. This result agrees with the internationally accepted $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of 2.46 and -2.37‰, respectively. The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of structurally bound carbonate are reported in ‰ to V-PDB. For comparison, phosphate $\delta^{18}\text{O}$ values obtained from modern elephants by Ayliffe *et al.* (1992) and mammoths by Genoni *et al.* (1998) were converted to equivalent structural carbonate $\delta^{18}\text{O}$ values using the regression from the study by Martin *et al.* (2011): $\delta^{18}\text{O}_{\text{structural carbonate}} (\text{V-SMOW}) = \delta^{18}\text{O}_{\text{phosphate}} (\text{V-SMOW}) \times 1.037 [\pm 0.026] + 8.57 [\pm 0.504]$. Subsequently, the $\delta^{18}\text{O}_{\text{sc}}$ values in V-SMOW, including those from the study by Fox *et al.* (2007) were expressed on the V-PDB scale using:

$$\delta^{18}\text{O}(\text{V-PDB}) = (\delta^{18}\text{O}(\text{V-SMOW}) - 30.86) / 1.03086$$

The $\delta^{18}\text{O}$ values of drinking water with their progressive uncertainties were reconstructed using the regression from the study by Ayliffe *et al.* (1992), which was based on modern elephants: $\delta^{18}\text{O}_{\text{drinking water}} (\text{V-SMOW}) = (\delta^{18}\text{O}_{\text{phosphate}} (\text{V-SMOW}) - 23.3 [\pm 0.7]) / 0.94 [\pm 0.1]$ before the $\delta^{18}\text{O}_{\text{structural carbonate}} (\text{V-PDB})$

were converted into equivalent $\delta^{18}\text{O}_{\text{phosphate}} (\text{V-SMOW})$ values using the aforementioned equations.

Results

Generation and completeness of the teeth couple F-3326 and F-3327

There are no pressure marks on the posterior surface of either specimen, which indicates that we are dealing with M3 specimens. The anterior part of the tooth is wider than the posterior. The posterior root is large, has a pointed posterior edge and is orientated along the axis of the tooth. Both the main and additional large anterior roots are well developed. The posterior part of the tooth crown is not significantly damaged; the anterior part is polished by wear from the M2 (i.e. the adjacent molar). The outer part of the main anterior root, which is the base of the anterior plate, is preserved. Consequently, it is clear that the molar is complete, and no original plates are missing in either M3 specimen.

The tooth crown consists of 17 plates and worn anterior and incompletely formed posterior talons (= platelets). Thirteen plates and the anterior talon are partly worn. The dental formula is $\overset{t}{1} 16t$ (t = the talon, 16 fully developed plates, incomplete wear of the first true plate, and the anterior talon was erased). There are three plates and a talon under the main root. The enamel is relatively thin (1.4 mm on average) and slightly plicated (Table 1). The height of the crown at the 12th slightly worn plate is 95.0 mm at the right side of the tooth and 92.0 mm at the left side. There is a small additional enamel column 11.0×1.8 mm in the section at the lingual side of the right tooth between the 6th and 7th plates. A minor displacement of the plates' lingual halves with respect to the buccal halves is observed. This feature should not be interpreted as pathology; it is often found in proboscidean M3s. Incipient wear marks on the occlusal surface of the trinomial plate are of the intermediate type, consisting

Table 1. Measurements of small upper M3 of *Mammuthus primigenius* from East Siberian Sea coast region; collection of the National Alliance of Shidlovskiy 'Ice Age', Moscow. * = the number of plate, where the height was measured is given in superscript; ** = by Garutt *et al.* (1993); Averianov *et al.* (1995); number of plates with talons/talonids; *** = holotype of *M. primigenius vrangeliensis*; – = not preserved; t = talon/talonid.

Teeth, collection no.	F-3326, dex	F-3327, sin	F-3889, sin	F-1959, sin	Middle and large size mammoth's teeth		<i>M. p. vrangeliensis</i> **
					n	min-(Med)-max	
Measurements (mm)							
Tooth formula	t17t	t17t	t19t	t17t	–	–	
Number of plates (without talonids)	17	17	19	17	15	22-(24.2)-27	21-(23.7)-25
Length of a crown	>179	182	>186	197.7	7	214-(267.7)-308	204-(226.7)-240
Width of plates	72.60	73.00	75.8	76	18	73.5-(90.4)-108	63-(72.7)-88
Height*	95 ¹²	92 ¹²	113 ¹⁶	91 ¹⁶	15	125.5-(164.6)-331	114-(136)-159
Lamellar frequency	9.44	9.30	9.44	8.9	18	7.8-(10.0)-11.8	9.5-(11)-13.0
Length of single plate	11.06	10.87	10.49	11.49	18	8.5-(10.4)-13.9	9.2***
Enamel thickness	1.36	1.42	1.74	1.5	18	1.25-(1.44)-1.92	1.0-(1.1)-1.3
Index length to width of crown	–	2.49	–	2.60	7	2.58-(2.98)-3.54	–
Wear stage	4	4	4	4	–	–	

of two round medial and two oval lateral parts. The cover cement adjacent to the chewing surface is slightly polished by food abrasion.

The dental formulas of the other complete M3 specimens F-3889 and F-1959 (Table 1) of small mammoth from the Alazeya region are $\overline{t}^2 17t$ and $\overline{t} 17t$, respectively. The number of plates in these teeth is also reduced.

Biological age of the Alazeya mammoth

Of the 17 plates, 13 are worn in the specimens F-3326 and F-3327. This wear stage corresponds to an age of 41–47 years (Laws 1966) or 42–46 years (Lee *et al.* 2011) for African elephants.

Morphological/morphometric analyses

The Alazeya small mammoth is comparable with the ‘dwarf’ *Mammuthus lamarmorai* from San Giovanni (Sardinia) in size, although it is distinctly larger than the *M. creticus* from Cape Malekas (Crete) and the *Mammuthus exilis* from the California Channel Islands (Fig. 4). However, *M. lamarmorai* has lower lamellar frequency and thicker enamel. The enamel thickness and lamellar frequency of the described M3s are similar to those of the Late Pleistocene Siberian *M. primigenius*. These values hardly vary from those of the ‘thin-enamel’ mammoths that lived during the Late Pleistocene Karginsky interstadial (MIS 3; Averianov

1994; Foronova 2007; Kirillova *et al.* 2012) and the *M. primigenius primigenius* neotype, whose calendar age is 11 500–12 000 years BP (Garutt 1989; Garutt *et al.* 1990) (Fig. 4). Specimens from the Alazeya region differ from the geologically younger small woolly mammoth from Wrangel Island (Garutt *et al.* 1993; Averianov *et al.* 1995; Table 1) by having slightly thicker enamel (Fig. 4B). Additionally, the crown size falls within the upper limits of the variability spectrum (for the width, Fig. 4B). However, the Alazeya mammoth’s molars are somewhat shorter (because of fewer plates). The crown sizes and single plate length of the Alazeya mammoth’s molars correspond closely to those of the Late Pleistocene woolly mammoth molars from Berelekh and fall within the lower limits of their variability, but they possess thinner enamel. When comparing specimens F-3326 and F-3327 with the teeth sample of the *M. primigenius* from the Alazeya region (Fig. 4), we can state that the crown width of the described teeth falls within the small array of points of other small teeth, which are considered additional material. They differ from the data of average- to large-sized individuals. In addition, the histogram (Fig. 5) displaying the number of plates in the M3 of the *M. primigenius* from the Alazeya region shows a distinct bi-modal distribution. The reduced number of plates is the primary distinguishing feature of the examined small teeth. This distinguishes them from other *M. primigenius* representatives.

Fig. 4. Comparison of some upper M3 teeth characteristics of the Alazeya mammoth, *Mammuthus primigenius* with several taxa of the genus *Mammuthus* from Eurasia. A. Ratio of crown width to lamellar frequency. B. Ratio of enamel thickness to lamellar frequency. The limits of the measurements are shown for *M. primigenius wrangeliensis*. [Colour figure can be viewed at www.boreas.dk]

Fig. 5. Frequency distribution of the number of plates (excluding talons) for the upper M3 teeth of *Mammuthus primigenius* from the lower Alazeya region (the Kolyma Lowland, Russia). * = the characteristics of the described teeth F-3327 and F-3326. [Colour figure can be viewed at www.boreas.dk]

Enamel microwear

Using an SEM, we revealed some microwear patterns on the occlusal surface of the right molar (F-3326). There are no pits and chips on the chewing surface, excluding one of the sides of sample 2, on which we discovered a group of six oval-shaped pits with uneven edges (Fig. 3D). The dimensions of the pits were $4.2 \pm 0.8 \times 5.8 \pm 1.9 \mu\text{m}$ ($n = 6$). Narrow strokes and wider scratches are visible on all seven samples (Fig. 3A). They range from rare to numerous, but do not form bundles, are randomly orientated, and are not curved (i.e. are always straight). Their widths vary from 0.7 to 12.4 μm ($n = 30$). The widest scratches are found in sample 4. The mean number ($n = 40$) of fine scratches (with a width between 0.7–10.0 μm) is 15.4 ± 6.8 (4–28). Regarding the coarse scratches (with a width >10 μm), there are only 1.6 ± 0.7 scratches (1–3) at 0.12 mm².

DNA-study results

Of the 1.84 million reads sequenced for this sample, only 1479 reads (0.11%) mapped to the elephant/mammoth reference, potentially representing the endogenous, i.e. authentic, mammoth DNA. After removing duplicates, the number decreased slightly to 1394 reads or 0.10% endogenous DNA. The low proportion of mammoth DNA in the tooth sample suggests that the endogenous DNA degraded due to suboptimal deposition conditions and/or exposure at the surface. Considering the low proportion of endogenous DNA, whole genome sequencing of this Alazeya mammoth sample would be ineffective, but further information could potentially be recovered using a target enrichment strategy.

Particle size distribution of the filling sediments

Both sediment samples obtained from between the roots of the molar sample F-3327 possessed unimodal particle size distribution with the peak at 20–25 μm (Fig. 6). More than two-thirds of the material referred to the silt fraction (4–62 μm): 66% in sample 1 and 72% in sample 2. The fraction of clay (<4 microns) amounted to somewhat <25% in both samples. Sandy material was also found in small quantities (4.0 to 6.5%), although this material was mostly fine sand (62–250 μm). Coarse sand (500–1000 μm) constituted <3% of sample 1 and was almost absent in sample 2. Both samples were relatively well sorted.

Analysis of phytoliths and other micro-remains

A large amount of small plant detritus, represented by well-preserved moss tissue with fine cell structure and residual vascular tissue from the stems and roots of herbs, was discovered in the sediments from the roots of the mammoth molars. Epidermal tissue with stomata from grasses (Poaceae) and herbs (Dicotyledones) was iden-

Fig. 6. Grain-size composition of sediments from the roots of tooth F-3327.

Fig. 7. Spatial variation in the $\delta^{18}\text{O}_{\text{sc}}$ values (mean + 1 σ) of Late Pleistocene mammoths in northernmost Eurasia from the studies by Fox *et al.* (2007) and Genoni *et al.* (1998) in comparison with F-3327 (this study).

tified. A small amount of phytoliths was present. Other microfossils (freshwater sponge spicules, diatom frustules) were filled with sediment, suggesting their transport in an aquatic medium. The remnants of boggy and aquatic green mosses of the genera *Drepanocladus* and *Hylocomium* showed an increased amount of dissolved mineral substances in water. The shells of the amoebae genus *Diffugia* also indicated a waterlogged site with a large amount of dissolved mineral substances in the water.

Pollen analysis

In the pollen spectra, the arboreal (tree and shrub) pollen content was between 16 and 29% of the total terrestrial pollen and spores. The pollen of non-arboreal plants (grass, herbs and dwarf shrub) constituted 65–76%, while spores constituted 4–5% (Table S1). The larch (*Larix* sp.) pollen content reached 7%. Given the susceptibility of larch pollen to deterioration, this indicates a significant presence of *Larix* in the region's plant communities. A small amount of dwarf pine (*Pinus pumila*), birch tree (*Betula* sect. *Albae*), spruce (*Picea*), Scotch pine (*P. s/g Diploxylon*), and juniper (*Juniperus* sp.) pollen was found. The current geographical distribution of these trees and shrubs shows that they are most characteristic of the boreal (taiga) regions and penetrate the sub-arctic latitudes of Siberia only slightly (Areal of trees and shrubs of the USSR 1977). Thus, even though the pollen of anemophilous trees may have been at least partly transported to the site by wind, the arboreal pollen's composition indicates the regional spread of larch and birch forests with a diverse shrub layer. Pollen and spores identified in the sample were extremely diverse and included a variety of meadow, wetland and water-margin plants, species that are characteristic of a zone with forest (e.g. *Sanguisorba officinalis*, *Menyanthes trifoliata*,

Rubus chamaemorus and *Scheuchzeria palustris*; Arctic flora of the USSR 1980). Rare pollen grains of *Rumex* cf. *acetosella*, *Saxifraga* sp., and spores of *Riccia* and *Selaginella helvetica* found in the sediment indicate disturbed sandy soils and stony places. *S. helvetica* is a rare species presently found in Siberia only in the north Baikal and Shilka-Argun floristic regions (Krasnoborov 1988). Pollen of *Nuphar pumila*, *Nymphaea* sp. and *Myriophyllum verticillatum*, typical aquatic plants, were present in both samples. The present-day range of *N. pumila* in eastern Siberia is limited to the Vilyuisk-Upper Lena floristic region, while the present northeastern boundary of *Nymphaea* coincides approximately with that of spruce. Additionally, *Myriophyllum verticillatum* is a boreal species that extends to 58°N in the taiga zone of eastern Siberia (Arctic flora of the USSR 1980).

^{14}C dates

The ^{14}C dates for both samples F-3326 and F-3889 were older than 45 000 a BP (GrA-64660 and 64666, respectively). This was the ^{14}C background level (van der Plicht & Palstra 2016), which after calibration corresponded to 48 500 cal. a BP. Both samples yielded excellent collagen, both with an atomic C/N ratio of 3.1. The C and N contents were 41 and 16%, respectively.

Stable isotopes: diet and drinking water

On average, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the treated samples are 0.21 lower and 0.26‰ higher, respectively, than the untreated samples (Fig. S1). Although the treatment is used to remove organic matter and exogenous carbonate, it could potentially cause unexpected chemical effects and isotopic shifts even with modern material (Pellegrini & Snoeck 2016). Given the overall good preservation of apatite fossils under permafrost

Fig. 8. Reconstruction of the $\delta^{18}\text{O}$ value of drinking water of specimen F-3327 in comparison with modern monthly variations in precipitation $\delta^{18}\text{O}$ values and amounts along with air temperature as recorded at the nearby hydrometeorological station in the lower Kolyma River drainage (Chersky settlement, Russia, IAEA/WMO (2018)). The $\delta^{18}\text{O}$ values of the surface waters of streams, rivers, and the Kolyma headwaters from the Polaris Aquatic Survey Dataset (2012) and the study by Welp *et al.* (2005) are also plotted in the lower panel. The reconstructed range of the $\delta^{18}\text{O}$ value of drinking water for specimen F-3327 matches modern $\delta^{18}\text{O}$ values of surface water as well as late spring (May) and early autumn (September) rainfall. During winter, air temperature is below freezing point, while the amount of precipitation is low compared to the rest of the year.

conditions as noted in the northern Siberian mammoth studies (Genoni *et al.* 1998; Fox *et al.* 2007), it might be prudent to avoid chemical treatments in particular due to the absence of regional limestone occurrences. For F-3327, it is unclear if the isotope composition of the treated samples is more representative of the original isotope composition compared with the untreated samples. Therefore, the isotope compositions of both treated and untreated samples are considered. The $\delta^{13}\text{C}$ values of both the untreated and treated samples (Fig. S1) are well within the $\delta^{13}\text{C}$ apatite range for herbivores that primarily fed on C_3 plants (Cerling *et al.* 1997; Smith & DeSantis 2018). A C_3 plant diet for F-3327 is unsurprising given the virtual absence of C_4 vegetation at high latitudes (Still *et al.* 2003). On average, the untreated and treated samples have $\delta^{18}\text{O}$ values of -17.3‰ (± 0.4 , 1σ) and -17.1‰ (± 0.4 , 1σ), respectively. The untreated samples cover a slightly larger range (-18.6 to -16.2‰) compared to the treated samples (-17.8 to -16.3‰) (Fig. S1). The obtained $\delta^{18}\text{O}$ values are typical of other late Pleistocene mammoths from northern Siberia

(Fig. 7; Genoni *et al.* 1998; Fox *et al.* 2007). In modern elephants, the $\delta^{18}\text{O}$ values of apatite are linearly correlated with the $\delta^{18}\text{O}$ values of their drinking water, which is derived from local rainfall (Ayliffe *et al.* 1992). The calibration previously applied to deduce reliable $\delta^{18}\text{O}$ values for drinking water, and in turn, rainfall, from mammoth fossils (e.g. Tütken *et al.* 2007; Metcalfe *et al.* 2011) also allows for $\delta^{18}\text{O}$ estimations for F-3327. The reconstructed $\delta^{18}\text{O}$ drinking water values are close to the modern $\delta^{18}\text{O}$ values of rivers and streams during summer (June–August) in the lower Kolyma River drainage, east of the study area (Polaris Aquatic Survey Dataset 2012; Fig. 8). The $\delta^{18}\text{O}$ values of the headwaters of Kolyma River are slightly lower due to the meltwater, in particular from spring snow-melt, which has a $\delta^{18}\text{O}$ value of $26.2 \pm 5\text{‰}$ (Welp *et al.* 2005). In this region, the evaporation rates are relatively low and therefore have a negligible effect on the $\delta^{18}\text{O}$ values of surface waters (Welp *et al.* 2005). The isotope composition of the surface water is biased by local summer rainfall from late spring (May) to early autumn (September), as recorded at the nearby Chersky hydrometeorological station (IAEA/WMO 2018). The $\delta^{18}\text{O}$ precipitation is closely associated with the air temperatures, which are below freezing point during winter (IAEA/WMO 2018). Therefore, the $\delta^{18}\text{O}$ values of local ice wedges allow for the reconstruction of past winter temperatures (Vasil'chuk & Vasil'chuk 2018). Considering the substantial uncertainties in the aforementioned sample treatment and calibrations, the reconstructed $\delta^{18}\text{O}$ values of drinking water of specimen F-3327 occur in a range between -23.1 to -17.4‰ . Given the strong relationship between monthly air temperature and $\delta^{18}\text{O}$ precipitation variations (air temperature ($^{\circ}\text{C}$) = $2.57 \times \delta^{18}\text{O}_{\text{rainfall}}$ (V-SMOW) + 53.86 $r^2 = 0.94$), F-3327 experienced generally mild temperatures, probably reflecting overall warm interglacial conditions in combination with an eventual southward migration during winter. Although the incremental $\delta^{18}\text{O}$ record for F-3327 likely reflects a seasonal effect, whereby relatively high values can be linked to the summer months (Fig. 8), the resolution is too low to elucidate all the seasonal cycles recorded in the tooth.

Discussion

Evolutionary level of the *Alazeya* mammoth

The small teeth from the East Siberian Sea coast show particular characteristics that are, from an evolutionary point of view, similar to those of *M. primigenius* from deposits correlated with MIS 3 and MIS 2 (Urbanas 1980; Garutt 1989; Averianov 1994; Maschenko *et al.* 2003, 2006; Foronova 2007; Kirillova *et al.* 2012). The diagram showing the variability in the M3 parameters of Pleistocene elephants from eastern Siberia (Foronova & Zudin 1999; Fig. S2) also indicates the coincidence of the teeth's primary characteristics, with an 'adaptive peak'

in the late representatives of thin-enamel woolly mammoths. The characteristics of the *M. primigenius primigenius* neotype's teeth also fall within the same group.

Unfortunately, we have no comparative data of contemporaneous mammoths from NE Russia. Based on our results, we assume that the Alazeya mammoth's data fill this gap, characterizing a particular case of body size reduction in a regionally distinct group of woolly mammoths during this period.

Despite the long history of research, the systematics and evolution of woolly mammoths have not been completely clarified. According to some authors (Lister *et al.* 2005; Kahlke 2014; Lister & Sher 2015), the first *M. primigenius* appeared in northeast Asia as early as the late Middle Pleistocene, from where they spread throughout the Western Palaearctic. However, this concept assumes a rather broad interpretation of the composition of the *M. primigenius* species. In accordance with this point of view, the late Middle Pleistocene and the Late Pleistocene Eurasian descendants of *M. trogontherii* with an 'intermediate' morphology are referred to as woolly mammoths. Here, we follow an alternative point of view, assume a gradual evolution of this lineage of elephants within Eurasia, and distinguish several intermediate taxa of mammoths that appeared after *M. trogontherii* (*M. trogontherii chosaricus*, Dubrovo 1966; *M. intermedius*, Jourdan 1861) and before the appearance of the typical *M. primigenius* (Foronova & Zudin 1999; Labe & Guérin 2005). It is highly likely that the *M. primigenius* appeared at the very beginning of the Late Pleistocene (MIS 5a–d) in northeast Asia, earlier than it did in western Siberia and Europe.

The Alazeya region records indicate the existence of *M. primigenius* with progressive molar characteristics in NE Siberia during the early Late Pleistocene, whereas large, thick-enamel members of the genus *Mammuthus* (*M. trogontherii chosaricus* and *M. intermedius*) still existed in Europe and southern western Siberia (Labe & Guérin 2005; Foronova 2014; Titov & Golovachev 2017). The described teeth show characteristics that indicate we are dealing with *M. primigenius* specimens, a species that was widespread in Eurasia during the Late Pleistocene (Maglio 1973; Foronova & Zudin 1999).

Lithological data, geological age, climate, and environmental conditions

The composition of the sediment from the molar roots is similar to that of the Yedoma Complex (loess-like deposits with high ice content, typical of the eastern lowland Arctic regions of NE Russia), with a large silt fraction (more than 2/3). For comparison, in the outcrop of Oyogos Yar to the west of the Alazeya region, the main fraction (approximately 70%) of the Yedoma deposits is medium-coarse silt (25–56 microns) (Wetterich *et al.* 2016). The amount of clay particles in these sediments is no more than 10%, and sand particles constitute 20%.

The deposits in the Duvanny Yar section on the lower Kolyma River are similar to the Oyogos Yar deposits, and are considered aeolian sediments or 'cold loess' (Murton *et al.* 2015). In other cases, the Yedoma was considered an overbank alluvial facies because of the presence of sand lenses and characteristic stratification (Arkhangelov *et al.* 1979; Wetterich *et al.* 2016).

However, sediment from the Alazeya mammoth's teeth differs from the Yedoma deposits; the clay fraction (up to 25%) is much higher, and the sand fraction is lower (approximately 5%). This finding suggests deposition in a stagnant water body. The sand, silt and clay ratio is very similar to silty sediments at the base of the Duvanny Yar section, interpreted as taberal sediments thawed in the former lake-bottom talik (Murton *et al.* 2015). Such sediments at the base of the Yedoma Ice Complex are often dated to the last interglacial period (Kaplina 1987; Ilyashuk *et al.* 2006), which is regionally defined as the Kazantsevo Interglacial (an analogue of the Eemian, MIS 5e), 125 000–90 000 years ago. In addition, the silty composition is characteristic of deposits in some sections of the Olyor Formation (Arkhangelov 1977).

The composition of the host sediments indicates the sedimentary environment of a shallow lake, overbank flood-plain, or sluggishly flowing current.

A comparison of the lithological composition of the stratigraphical units exposed above the river channels in the region between Indigirka and Kolyma with the grain-size distribution of sediments from the Alazeya mammoth's tooth allowed us to select two possible sources of the sediment from the mammoth molars. These were stratigraphical units that were also palaeobotanically investigated, i.e. the lacustrine and taberal deposits of the Kazantsevo Interglacial (Eemian, MIS 5e) underlying the Yedoma Suite, and the Olyor deposits during the late Early–early Middle Pleistocene age. The latter may be excluded because of the evolutionary stage of the woolly mammoth molars.

The present-day vegetation of the arctic tundra in this region consists of low brush, grass and brush, and moss combined with grass-hypnum associations (Treshnikov 1985). Shrub birch (*Betula exilis*), dwarf willow tundra, shrub alder (*Alnus fruticosa*), and larch (*Larix gmelinii*) open forests occupy the area south of 70°N (Treshnikov 1985). The mammoth molar spore-pollen data presented above suggest deposition during a period with regional vegetation consisting of taiga (larch and birch) forests with a layer of shrub alder, shrub birch, and willow, with some dwarf pine, juniper, and rhododendron. Wet meadows with rich herbage, grass, and moss mires were widespread in the region. The formation of sediment probably occurred in the coastal part of the lake basin, as evidenced by the pollen of aquatic plants and algae. Based on the pollen composition, the boundaries of the ranges of spruce and pine were much closer to the area of research than at present. This suggests that the climate was interglacial. As the modern geographical ranges of

plants are largely limited by climatic conditions, one can estimate the lowest summer temperatures allowing for the existence of all the species of plants determined in the composition of a fossil flora by their pollen or spores. In this respect, the most thermophilic plant species are the most indicative, such as, in this case, the aquatic plants found in both studied samples from the mammoth tooth: *Nuphar pumila*, *Nymphaea* sp. and *Myriophyllum verticillatum*. Analysis of the modern distribution of plant species comprising the fossil flora shows that the average temperature of the warmest month exceeded the current temperature by at least 8 °C.

A comparison between the palynological record of the Alazeya mammoth and the regional record from the climatic optimum of the Holocene (Anderson & Lozhkin 2002) highlighted a significant difference. In our case, the flora contained relatively more thermophilic boreal plant species, and the larch pollen content was up to 7% of the total spectrum. The pollen spectra of the Holocene climatic optimum from the sedimentation record located in the coastal tundra between Alazeya and M. Kuropatycha rivers are characterized by much higher concentrations of shrub alder, birch, and dwarf pine pollen and the absence of *Larix* pollen (Anderson & Lozhkin 2002).

The deposits in the middle flow of the Alazeya River are dated palynologically to the Kazantsevo Interglacial (MIS 5e) (Lvova 1989). In the palynocomplex, arboreal pollen dominates, in which the amount of pine pollen (*Pinus pumila* and *P. sylvestris*) is significant, and *Larix*, *Picea*, *Alnus*, *Betula* (tree and shrub) and *Salix* pollen are constantly present. The non-arboreal pollen is represented mainly by Poaceae (47–52%). Pollen of aquatic and coastal plants (*Sparganium*, *Nuphar* and *Menyanthes trifoliata*) and remains of algae *Pediastrum* are also present. A similar palynocomplex was discovered by A.I. Tomskaya at the Sergeyev Ruchei exposure on the Alazeya-Kolyma interfluvium (Grinenko 1985). The age of the sediments was determined as Late Pleistocene based on the mammalian record and was attributed, based on the spore/pollen spectra, to the Kazantsevo Interglacial (Grinenko 1985). These palynocomplexes reflect, similar to those from the mammoth's molars, the spread of forest vegetation under more favourable climatic conditions than today, supporting a correlation between the mammoth remains and the Kazantsevo Interglacial.

Late Pleistocene interglacial deposits from the Oyogos Yar section on the shore of the Dmitry Laptev Strait, west of the lower Alazeya region, yielded pollen spectra similar to those obtained from the mammoth tooth, although the pollen flora were somewhat more impoverished, and pollen from thermophilic aquatic plants were not found (Andreev et al. 2011). Macro-remains of vascular plants from the Kazantsevo Interglacial deposits from the same section represent 87 species, 55 of which are not found in the territory today. Based on the modern

distribution of these species, it can be concluded that the average temperature of the warmest month exceeded the current July temperature in the region by 9–10 °C (Kienast et al. 2011). This conclusion supports our proposed correlation of the mammoth remains with the last interglacial period.

Lake El'gygytgyn, located in the west of the Chukotka Peninsula, has so far yielded the only continuous section in the Asian Arctic where palynological data were obtained from the last three interglacial epochs, i.e. the Holocene Climate Optimum, the Kazantsevo Interglacial corresponding to MIS 5e, and the earlier Middle Pleistocene interglacial period corresponding to MIS 7 (Lozhkin et al. 2007; Matrosova 2009). The pollen spectra of the optimal interglacial phases in this section are fairly close to each other. Therefore, we cannot exclude the possibility that the mammoth molars date to an earlier interglacial epoch (e.g. MIS 7). However, the dental characteristics of the described specimens (relatively large lamellar frequency and thin enamel) exclude a Middle Pleistocene age of the find.

Palaeoenvironmental records from various regions in Arctic Siberia clearly indicate that humid and warm conditions (similar to modern conditions and probably warmer) existed during the last (Kazantsevo) interglacial period, while later on the Arctic Siberian climate remained much colder than the current climate until the early Holocene (Grinenko 1985; Lvova 1989; Anderson & Lozhkin 2002; Lozhkin et al. 2007; Matrosova 2009; Andreev et al. 2011; Kienast et al. 2011). Therefore, we conclude that the studied mammoth tooth could not have been buried during the later substages of MIS 5 or the interstadial warming of MIS 3, when the regional climatic conditions were quite harsh.

The relationship between the tooth enamel microwear patterns and the diets of ungulates and proboscideans is well known (Rivals et al. 2014; Mayte et al. 2016; Semprebon et al. 2016; Smith & DeSantis 2018). The presence of strokes and scratches and the absence of numerous pits and chips on the enamel surface of specimen F-3326 show that this 'semi-dwarf' mammoth subsisted primarily on herbs, which typically contain less silica than grasses. A comparison between the absolute width of scratches on F-3326 and scratches on the teeth of other mammoths cannot be conducted, as only the ratio of scratches of different thicknesses (from 0 to 2 or 4, from 'the thinnest' to 'the coarsest and thickest') is presented in the literature (Rivals et al. 2014; Mayte et al. 2016; Semprebon et al. 2016). The microwear patterns in our samples can be categorized as either 0 or 1 – the predominance of thin, gentle scratches (strokes) or thick, coarse scratches, respectively. The absolute thickness of the scratches on the enamel of F-3326 varies between 0.70 and 12.42 µm; they occur in different parts of the tooth and even different sections of the same sample (Table S2). The widest scratches (grooves) were found in sample 4 on the linguo-medial side of the tooth's

proximal part. Wide scratches are relatively rare, and the thinner ones are numerous. The number of observed scratches does not quite fit with the numbers counted in other species (Semperebon *et al.* 2016; Table 1). In the Alazeya mammoth's case, the average total number of thick/thin scratches was 16.2/0.12 mm² (corresponding to 21.6/0.16 mm²), which is higher than the *M. exilis* molars' average total. However, the specimen F-3326 had nine times fewer grooves than strokes, i.e. the thick, coarse scratches were sporadic. Some individuals of the pygmy mammoth species *M. exilis* had only thin scratches on the tooth enamel, and the enamel itself was polished, which is associated with a less abrasive diet (see Semperebon *et al.* 2016; Fig. 6). This phenomenon was also present for the Alazeya mammoth. The absence of numerous and large pits, as well as a small number of grooves, indicates that it mainly fed on herbs and, to a lesser extent, grasses.

Size reduction

The stable isotope ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) values of the enamel and the associated botanical remains indicate interglacial conditions with temperatures that were probably higher than they are today. During the transition from a glacial to an interglacial period, permafrost degrades, which leads to a landscape with an increasing dominance of lakes and swamps and a decrease of habitable areas for the woolly mammoth (Tomskaya 2000; Ukraintseva 2002; Velichko & Zelikson 2005; Kirillova *et al.* 2016). Currently, tundra, which covers vast areas, cannot provide enough resources for large herds of large herbivores, as was the case during the Pleistocene, as a considerable part of this ecotone is covered by swamps and lakes with their characteristic vegetation. Nevertheless, in elevated places, small, fragmented areas with steppe vegetation and associated fauna are preserved (Sher *et al.* 2005).

The isolation of small Wrangel elephants occurred between 9000 and 3700 years ago (Vartanyan *et al.* 2008), although this time was not sufficient for them to become true dwarfs on this island. A sharp decrease in body size (up to 50%) of large mammals under the conditions of island isolation, limited food resources and the absence of large predators occurred over several millennia (Lister 1989; van der Geer *et al.* 2016).

There are currently a few small populations of relatively small elephants in Africa. Their reduction in body size is associated with a reduction of suitable habitat over the last few centuries (Laursen & Bekoff 1978; Shoshani & Eisenberg 1982; Cranbrook *et al.* 2007). The restriction of resource space led to increased competition and, as a result, accelerated size reduction (Raia *et al.* 2003) or local extinction. However, at the same time, large individuals existed in the neighbouring areas. This scenario (isolation and reduction of habitat) might also explain the reduced size of the mammoths in the region

between the mouths of the Alazeya and Malaya Kuropachya rivers.

Nikolaev *et al.* (2011) reported the coexistence of large and small mammoths along the Laptev Sea coast. The observed differences in the stable isotope composition of the bones of the smaller and larger individuals indicated, according to the authors, that diet and locality (valleys and watersheds) were the major factors determining the size of individuals. However, the authors disregarded the fact that female bones are noticeably smaller than male bones and did not give measurements showing that the sizes are truly small.

A reduction in animal body size over generations often occurs due to the restriction of food and other resources during the juvenile age. Switching to better nutrition after a period of very poor feeding does not compensate the skeletal development lag. Underfeeding affects the ratio between the different parts of the skeleton, and hence the weight and size of different parts of the skeleton can decrease disproportionately (Chirvinsky 1909). The mechanism leading to size reduction is controlled by the thyroid hormone, which, in response to stress, affects reproductive physiology, inducing the earlier maturation of individuals. These animals may have reproductive advantages compared to later-maturing individuals. Moreover, stress-intolerant individuals are quickly eliminated, which gives an advantage to more stress-resistant smaller individuals (Crockford 2008).

The complex structure of elephant teeth predetermines the way the teeth change due to skull and body size reductions. This structure allows the bending of the posterior part of the tooth, including pathological cases such as plate twisting (Maschenko & Shpansky 2005) and displacement (Kirillova 2009). The curvature of the posterior plates can partially compensate the pressure on the growing tooth in the alveoli. Underdevelopment of the posterior plates at an early stage of tooth development may lead to the formation of a specific structure of the posterior part of the last molar. In our opinion, an extreme example of the size reduction process can be a decrease in the number of plates. It is notable that a decrease in tooth size due to the reduction of the posterior part of the molars is also observed in captive lemmings because of inbreeding (Markova *et al.* 2019).

The reduction in the number of plates along with crown size reduction could be due to the decrease in size of the elephant's jaws and body. The number of plates in insular dwarf proboscids is lower than in the ancestral continental larger forms. The morphology of the teeth of the true dwarf *Palaeoloxodon cypriotes* from Cyprus appears the same as the original mainland *P. antiquus*. However, its lamellar frequency is similar to the deciduous teeth of their mainland ancestor. The enamel thickness of the teeth of the island form is relatively more and the number of plates is reduced: the average plate number at the third molars is 11 instead of 18, as in the ancestral form. Hence, the loss of the tooth's plates in the

teeth of the Cypriot dwarf elephant is more significant than that in the other island dwarf, *P. falconeri* (Davies & Lister 2001).

A similar situation is observed in the case of the Alazeya region mammoth. The loss of plates (17–19 plates excluding talons in specimens F-3326, F-3327 and F-3889), compared with the average number of plates in M3 of mid- and large-sized *M. primigenius* from the region (average number of plates = 24, Table 1), is 20–29%. This reduction in the number of plates in M3 is not unique. It is also observed in some mammoth teeth from the region (Table S3; Fig. 4), suggesting the regional existence of specific conditions leading to the development of this feature.

The process of size reduction in woolly mammoths largely occurred in different territories and was a natural reaction to environmental changes. For example, slight reduction in the tooth crown size due to a reduction in the number of plates correlating with the cold MIS 4 was noted in the Late Pleistocene locality of Aghnadarragh, Northern Ireland (Lister & Grün 2015). In this case, the decrease in the size of mammoths was also explained by the change in environmental conditions. Despite the diverse conditions in north Eurasia, cases of body size reduction occurred in different periods of the Late Pleistocene during both warm and cold epochs.

There is no reason to assume that the Alazeya region mammoth reduced in size because it lived on an island. The geographical position of the coastline during the Kazantsevo Interglacial was close to its position today, and the sea level of the area between the Indigirka and Kolyma rivers was more or less the same as the current levels (Treshnikov 1985; Atlas of Paleoclimates and Paleoenvironments of the Northern Hemisphere 1992; Pavlidis *et al.* 1998). We assume that the described specimens from the Alazeya region were characteristic of some mammoth populations inhabiting the region, which had a mosaic landscape, limited food sources, and reduced pressure from large carnivores (cave lions, polar bears and brown bears). These circumstances led to the reduction of body size and, as a result, the modification of tooth crowns in some groups of local mammoths.

Conclusions

The results of this comprehensive study of diminutive mammoth teeth from the East Siberian Sea coast indicate the regional occurrence of a mammoth population with a reduced body size during the early Late Pleistocene. The main characteristics of the teeth (width, lamellar frequency and enamel thickness) exclude a Middle Pleistocene or earlier age. Palaeobotanical data and stable isotope data suggest that this animal lived in warm, interglacial conditions: the Kazantsevo Interglacial (= Eemian, MIS 5e), the only Late Pleistocene interglacial episode. The widespread degradation of permafrost due

to interglacial warming caused the increase and extension of lakes, swamps and rivers. It changed the landscapes and reduced the productivity of biocoenoses, which resulted in the reduction of the mammoth's size (island effect in mainland conditions of isolation: Pianka 1974). The decrease of the teeth's dimensions was accompanied by a marked decrease in the number of plates. Most likely, the mammoths from this region represent a local incomplete 'attempt' towards dwarfing. The newly obtained data clarify the mechanism of the reduction of a mammoth's teeth sizes as a response to body reduction that is correlated with environmental changes and reducing the resource space.

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Supporting Information

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

Fig. S1. Incremental stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope records of structurally bound carbonate of treated and untreated samples with their uncertainty limits (1σ) plotted against distance at a millimetre scale for specimen F-3327.

Fig. S2. Variability of the elephants of the mammoth lineage in Eastern Siberia (according to M3 parameters).

Table S1. The results of pollen analyses of the sediments filling the roots of the mammoth molar F-3327.

Table S2. Metric data of strokes and scratches on the enamel from samples 1–7 of the M3 of the Alazeya mammoth (specimen F-3326).

Table S3. Measurements of the upper M3 teeth of *Mammuthus primigenius* from the lower Alazeya region (NE Russia).