



## An ancient bison from the mouth of the Rauchua River (Chukotka, Russia)



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### ABSTRACT

An incomplete carcass of an extinct bison, *Bison* ex gr. *priscus*, was discovered in 2012 in the mouth of the Rauchua River (69°30'N, 166°49'E), Chukotka. The carcass included the rump with two hind limbs, ribs, and large flap of hide from the abdomen and sides, several vertebrae, bones of the forelimbs and anterior autopodia, stomach with its contents, and wool. The limb bones are relatively gracile, which is unusual in bison, and a SEM study of the hair microstructure suggests higher insulating capacity than in extant members of the genus. Additionally, mitochondrial DNA analyses indicate that the Rauchua bison belonged to a distinct and previously unidentified lineage of steppe bison. Two radiocarbon dates suggest a Holocene age for the bison: a traditional <sup>14</sup>C date provided an estimate of 8030 ± 70 <sup>14</sup>C yr BP (SPb-743) and an AMS radiocarbon date provided an age of 9497 ± 92 <sup>14</sup>C yr BP (AA101271). These dates make this the youngest known bison from Chukotka. Analysis of stomach contents revealed a diet of herbaceous plants (meadow grasses and sedges) and shrubs, suggesting that the early Holocene vegetation near the mouth of the Rauchua River was similar to that of the present day: tundra-associated vegetation with undersized plants.

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### Introduction

*Bison* is one of the most abundant fossil representatives of the mammoth faunal assemblage. Bison remains, including bones, soft tissues and carcasses, tend to be the dominant megafaunal species recovered from frozen late Pleistocene sediments of north-eastern Asia and northern North America, and have therefore been important in comparative analyses across the region (Tchershki, 1891; Flerov, 1977; Skarlato, 1977; Filina and Filin, 1980a, 1980b; Guthrie, 1990; Harington, 2007; Boeskorov et al., 2013). Comparison of remains from Alaska and Yakutia has revealed considerable similarities between late Pleistocene bison in Asia and North America, for example, and between ancient bison and the living Canadian wood bison *Bison bison athabasca* (Flerov, 1977; Guthrie, 1990). Many recovered bison carcasses include stomach contents, which can be used to infer the plant community composition at the time of the bison's death (Flerov, 1977; Ukraintseva et al., 1978; Boeskorov et al., 2013); bison have therefore been an important

indicator species in paleontological reconstructions of climate and landscape changes during the Pleistocene (Guthrie, 1990).

In recent years, interest in fossil bison remains has been reignited by new finds in both North America and Russia (Hill et al., 2008; Zazula et al., 2009; Boeskorov et al., 2013; Kirillova et al., 2013; Nikolskiy and Shidlovskiy, 2013; Geel et al., 2014). Here, we describe in detail one of the most recently discovered fossil bison: a well-preserved partial carcass from Chukotka, Russia. Using morphological, isotopic, dietary and genetic data recovered from this partial carcass, we provide new insights into evolutionary history and evolution of bison and a reconstruction of the climate and habitat of western Beringia during the transition into the Holocene.

Using an interdisciplinary approach that takes advantage of the latest techniques in morphological, isotopic, dietary and genetic analyses, we use data recovered from the Rauchua bison carcass to provide new insights into evolutionary history of bison and to reconstruct the climate and paleovegetative habitat of western Beringia. AMS and traditional radiocarbon dates indicate that the Rauchua bison lived around 9000 yr ago, during the transition into the Holocene warm interval. Dating results indicate that the Rauchua bison is the youngest steppe bison carcass yet discovered in Chukotka, and allows inference of the vegetation

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and climate of this part of Western Beringia during the transition into the Holocene. Finally, preliminary genetic analysis of recovered mitochondrial RNA indicates that the Rauchua bison belonged to an old and distinct mitochondrial lineage of steppe bison that never crossed the Bering Land Bridge into North America.

## Material and methods

### Material

During the summer of 2012, Arkadiy Repin, of Bilibino, Chukotka, Russia, discovered a partial carcass of an extinct bovid in the mouth of the Rauchua River (69°18'N, 166°36'E,) (Fig. 1). Today, the average air temperature at the site of the discovery is –10.6 °C, and ranges from averages of –26 °C in January to +7.6 °C in July. Annual precipitation ranges from 150 to 200 mm, with snow melting away in June and covering again at the beginning of October (Treshnikov, 1985; <http://www.fesk.ru/wetlands/246.html>). The present-day floral assemblage includes steppe, boreal, arctic and arcto-alpine elements.

The bison carcass was exposed as the Rauchua River cut through the late Pleistocene and Holocene permafrost silt (edoma). The height of the riverbank in the low water season is only about 0.8 m. The shallowness of the river at this site combined with proximity of the site to the sea cause considerable fluctuations of the water level, as a result of ebb and flow and of rainwater flooding. The estuary region continues to be flooded periodically; such flooding occurred after the discovery of the bison remains, preventing them from being studied *in situ*. By the time of the discovery, the carcass had thawed completely.

The bison remains, including rump, bones, fur and stomach contents (Fig. 2B) were preserved as a compact association. The bones are mainly well preserved and light beige to brownish in color. The coloration is mottled and can vary, even on the same bone, likely due to different amounts of contact with rotting tissues. Bones are variously complete, many of them bear traces suggestive of post-mortem predation. Some bones, and occasionally soft tissues, have stains of amorphous vivianite and whitish tarnish. All samples are housed in the “National Alliance of Shidlovskiy Ice Age Museum,” in Moscow Russia. A complete list of

recovered and examined fragments of the Rauchua bison is provided in Supplement I.

### Morphometric analysis and taxonomy

We measured bones using digital callipers and a measuring box following standard techniques (von den Driesch, 1976; McDonald, 1981). We performed principal component analysis in STATISTICA 6.0 based on a covariance matrix for the standard set of seven measurements of metacarpals (see Lewis et al., 2005).

The absence of the head and primary sexual characters prevented sex determination. Although we attempted sex determination using several techniques (Jusko, 1953; Duffield, 1973; Bedord, 1978; Drees, 2005; Lewis et al., 2005), we were not able to definitively assign sex. The same reasons, as well as some bone features, complicated the taxonomic assignment. Consequently, we use the Latin name *Bison ex gr. priscus*.

### Light and scanning electron microscopy

We studied three samples of fur using light optical microscopy and SEM. As most of the fur was not found attached to the specimen, the exact topography of most of the recovered fur samples is unknown (except for one sample from the hind tibia) as is the seasonality of the fur. To reconstruct hair topography, we compared our data to previously published work on fossil and extant bison (Flerov, 1977; Sokolov, 1979; Guthrie, 1990), including hairs from living *Bison bison* and *Bison bonasus* from the Moscow Zoo.

### Inference of diet and paleoenvironment

To reconstruct the diet of the Rauchua bison, we performed analysis of macrofossils, microfossils and pollen from the preserved stomach content. For macrofossil analysis, we collected and treated two samples of 225 ml each of intestinal content using standard methods (Nikitin, 1969). The stomach contained well-preserved plant remains, nearly all of which were identifiable by comparison to reference collections.

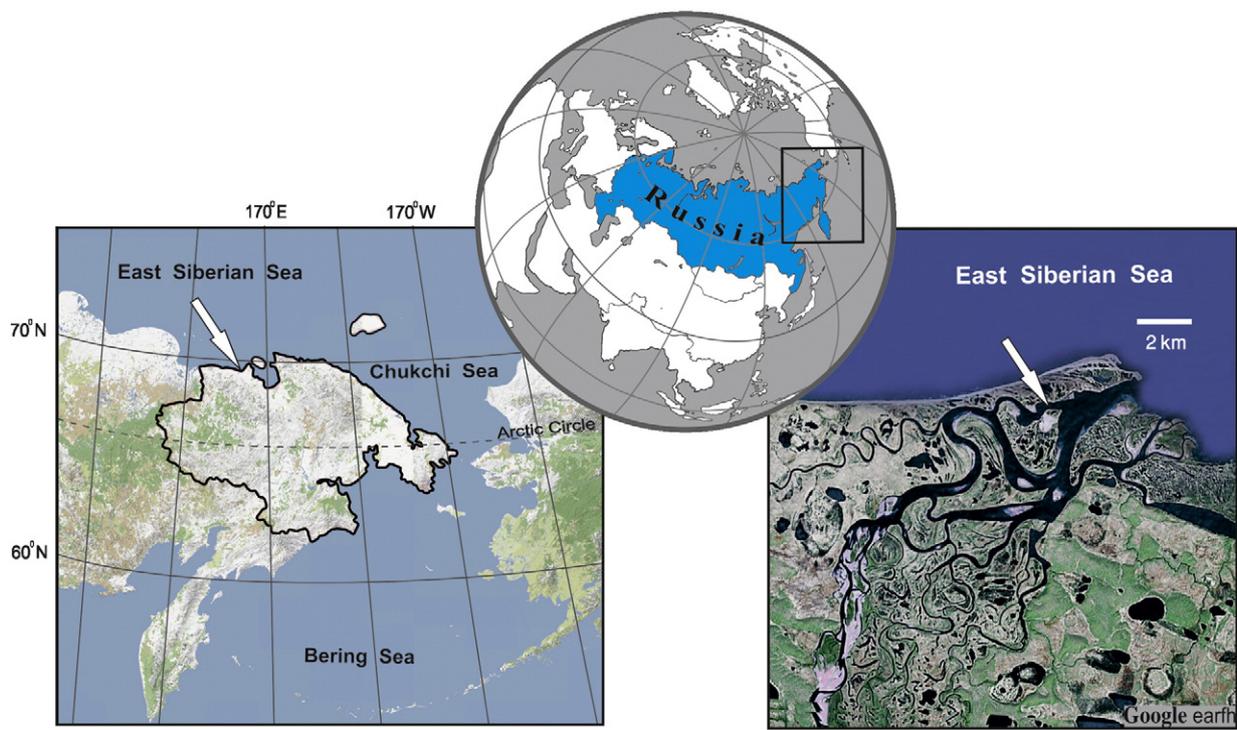
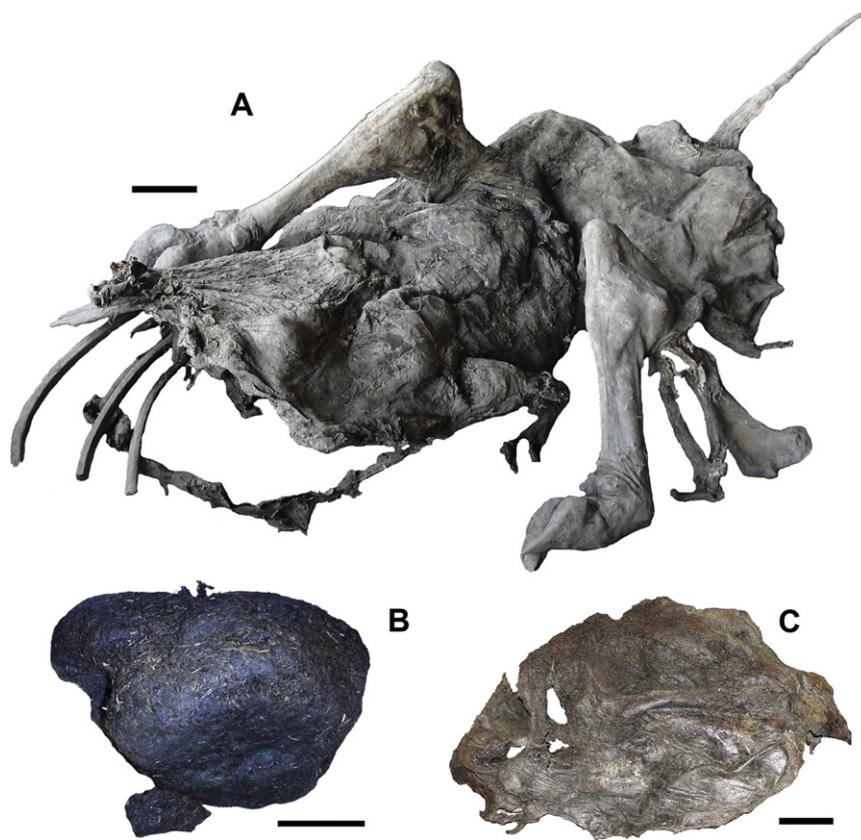


Figure 1. Site of the bison locality near the mouth of the Rauchua River (Bilibino District of the Chukotka Autonomous District) 69°30'N, 166°49'E.



**Figure 2.** Rauchua bison remains. A. Rump with hind limbs and hide. View from beneath. Collection no. F-3246/2. B. Main mass of the stomach content. Collection no. F-3246/4. C. Stomach wall tissue. Collection no. F-3246/3. Ice Age Museum. Scale: 100 mm.

Seeds were assigned taxonomically by comparison to the carpological reference collection of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences (IPAE, UB RAS, Yekaterinburg) and atlases of seeds and fruits.

We then burned the samples in a muffle furnace at 350°C and extracted microfossils using wet oxidation and flotation. Specifically, we dissolved carbonates via hydrochloric acid oxidation of organic matter with 38% hydrogen peroxide at 90°C, and manually removed any particles of clay. Microfossils were then separated from the residue in a heavy liquid solution with a density of 2.2–2.3 g/cm<sup>3</sup>. We examined the light fraction on slides in glycerine using a Carl Zeiss Axiostar optical microscope at 200–400× magnification, and examined the dry material using a Vega 3 Tescan scanning electron microscope. Phytoliths recovered from the sample were classified in accordance with the International Code for Phytolith Nomenclature 1.0 (Madella et al., 2005).

We performed pollen identification using identification atlases (Kuprianova, 1965; Kuprianova and Alyoshina, 1972; Beug, 2004) and the palynological reference collection of the Laboratory of Paleocology of the IPAE, UB RAS. In total, 13 microscope slides were examined and 200 pollen grains were identified.

#### Isotopic analysis

Bone collagen was extracted from two ribs and a vertebra using a standard protocol (Longin, 1971). Dried and homogenized collagen samples were weighed and wrapped in tin foil (500–600 µg). Stable isotope analysis was conducted using a Thermo-Finnigan Delta V Plus continuous-flow IRMS coupled with an elemental analyzer (Thermo Flash 1112) in the Joint Usage Center at the Institute of Ecology and Evolution, Russian Academy of Science. The isotope composition of N and C was expressed in a δ-notation. The standard deviation of the isotopic measurements of reference materials (n = 8) was <0.2%. Other

materials analyzed included muscular tissue, hide, and a sample of the stomach contents. In addition, a lock of ten hairs (each about 40 cm in length) from the floccus were aligned and cut into fragments of 10 mm. Each of these fragments was then analyzed separately so as to reveal temporal changes in δ<sup>13</sup>C and δ<sup>15</sup>N values. For comparative purposes, we used data on the isotope composition of bone collagen of several species of large Pleistocene herbivores from western Chukotka that are part of the collection at the Ice Age Museum.

#### Radiocarbon dating

We obtained radiocarbon ages from two sources using two different approaches. First, we sent samples from the hide to the Isotope Centre at the Geography Faculty at A.I. Gerzen Russian State Pedagogical University, St. Petersburg, Russia, where the age was estimated using conventional radiocarbon methods. This analysis provided an age estimate of 8030 ± 70 <sup>14</sup>C yr BP, which does not include a correction for isotopic fractionation (SPb\_743). Second, we sent a rib sample to the AMS radiocarbon dating facility at the University of Arizona, USA. Results of this analysis provided an AMS radiocarbon age 9497 ± 92 <sup>14</sup>C yr BP, which is corrected using a δ<sup>13</sup>C = −21.8 (AA101271). The discrepancy between the two age estimates likely reflects the differences in dating methodologies. However, both dates independently suggest an early Holocene age.

#### Genetic analysis

We performed DNA extraction at the UC Santa Cruz Paleogenomics Laboratory in Santa Cruz, CA, following strict protocols for ancient DNA (Shapiro and Hofreiter, 2012). DNA was extracted from 0.5 g of hair following Dabney et al. (2013), and prepped into sequencing libraries following Meyer and Kircher (2010). We performed hybridization

capture of the bison mitochondrial genome using custom RNA biotinylated probes (MYcroarray, MYbaits Vers. 2), according to the manufacturer's protocol. We sequenced the enriched library using an Illumina MiSeq and v3 kit (Illumina, USA).

From the resulting ~2 million (M) reads, we removed sequencing adapters and merged the paired reads using SeqPrep (<https://github.com/jstjohn/SeqPrep>), with a minimum overlap of 10 base-pairs between forward and reverse reads. We then mapped the resulting 1.85 M merged reads against the mitochondrial genome of *Bison bison* (NC\_012346) using BWA 0.7.10 (Li and Durbin, 2009), which provided a complete mitochondrial genome sequence with an average coverage of 164X and a minimum coverage of 7X at each site, with no ambiguous sites. We converted the resulting alignment to a BAM file using SAMtools 0.1.19 (Li et al., 2009) and used Geneious v.8 (Biomatters, NZ) to create a consensus nucleotide sequence, which is deposited in GenBank as accession number (KR350472).

We inferred the evolutionary relationship between the Raichua bison and other previously published bison mitochondrial data using BEAST v1.8.1 (Drummond et al., 2012). Because the majority of published data include only the hypervariable control region, we extracted this portion of the mitochondrial genome for further work (~580 base pairs). We aligned the Raichua bison to a larger data set of 172 bison mitochondrial control region sequences (Shapiro et al., 2004; Zazula et al., 2009; Lorenzen et al., 2011). We assumed the GTR + G model of nucleotide substitution and the skygrid model of the coalescent process (Gill et al., 2013), and used the ages of each ancient bison, calibrated using the IntCal13 calibration curve (Reimer et al., 2013), using OxCal (Bronk Ramsey, 2009), to inform the molecular clock rate. We ran two MCMC chains for 50 million iterations each, sampling states every 5000 iterations. We discarded the first 10% of states as burn-in and combined the remainder, checked for convergence of the MCMC chains using Tracer v1.6 (Rambaut, 2014), and identified the maximum clade credibility (MCC) tree using Tree Annotator v1.8, which is distributed as part of the BEAST software package.

Next, we constructed a maximum-likelihood species-level phylogeny using PHYML (Guindon et al., 2010) to depict the relationships between a randomly selected subset of 30 bison from the above analysis, the Raichua bison, plus previously published, overlapping mitochondrial data from more distantly related bovid species: *Bos indicus* (zebu) JXN40469 and HQ234736, *Bos taurus* (cattle) KF926377 and AY298746, *Bos grunniens* (yak) AY521142, DQ007223, DQ856603, AY521156, and *Bison bonasus* (wisent) AY28860 and U34294. We used the evolutionary model as above and NNI and SPR branch swapping, optimizing both branch length and topology. To assess statistical confidence of the tree topology, we performed 100 full-likelihood bootstrap replicates.

Finally, we constructed a maximum-likelihood species-level phylogeny using complete mitochondrial genome sequences for the Raichua bison, zebu (AY126697), cattle (GU947021, GU947018, GU947013, and DQ124417), yak (KJ463418, KJ704989, and EF494179), wisent (NC\_014044, JN632602, and HQ223450), and American bison (GU947006, GU946989, GU947001, and GU946999). Sequences were aligned using MUSCLE (Edgar, 2004) and then analyzed using PHYML as above.

## Description and results

### Rump, F-3246/2 (Fig. 2A)

The rump includes both hind limbs as far as the tibia, and also a large (approximately 1.2 × 0.8 m) piece of hide that would have covered the abdomen and part of the sides of the animal. Prior to drying out post-excavation, the hide was soft and flexible with mottled coloration, mostly light-brown with ash colored patches. After drying, the color became dark brown with black patches, and the hide became mummified. After 2 days of repeated soaking of the right leg (to remove the bones), the hide softened once again. However, it was less flexible than it had

been when it was first recovered. This may indicate that the carcass never thawed between the time when it was frozen in the permafrost until it was discovered and removed in 2012. Fatty deposits remained in place in the soft tissues and under the hide, reaching 8 cm in thickness. The claw sheaths of phalanges III are found separately from the hoofs. When the carcass was collected, the right femur was separated from the carcass and the left femur was attached by tendons to the tibia. The hide contained seven ribs of the left side, distally connected with the sternum and unevenly broken (three posterior under the articular head, three anterior and one posterior—in the upper third), several vertebrae, half of the pelvic bone, and tail. The mesentery was aligned to the internal side.

### Isolated bones of the postcranial skeleton

Specific details of the bones are as follows, with measurements provided in mm and abbreviations following von den Driesch (1976):

**Vertebrae**, F-3246/32–41, one cervical, other thoracic (Fig. 3A, B). All spinal processes are broken off near the base, with no traces of gnawing. Many vertebral bones are intensely gnawed.

**Ribs**, F-3246/17–24 left and F-3246/25–31 right. All bones are damaged and fragmented, some with bite marks and/or remains of soft tissues.

**Scapula**, F-3246/8 left (Fig. 4A). The bone is broken distally (vertebral border). GLP: 94.6; LG: 83.9; BG: 66.3; SLC: 82.1.

**Humerus**, F-3246/10 left and F-3246/9 right (Fig. 4B, C). On the left shoulder bone, the large proximal epiphysis is gnawed off and the head is damaged at the base. Bp: 130.2; Sd: 48.3. The right bone is complete, with remains of mummified soft tissue. GLC: 350.0; Sd: 50.0.

**Ulna**, F-3246/13–14 left (Fig. 4D). The proximal part of the ulna bone is broken and the tubercle is covered by mummified soft tissues.

**Foreleg**, F-3246/11 right (Fig. 4E). Both ulna and radius are complete and fused. The diaphyses appear gnawed. Radius: GL: (385.0); Bp: 107.0; Bd: 94.4; SD: 53.8. Ulna: GL: 471.2, LO: 133.3, SDO: 72.5.

**Radius**, F-3246/13, left (Fig. 4F). GL: 383.0; Bp: 105.0; Bd: 95.5; SD: 54.0.

**Metacarpal**, F-3246/15 left, complete (Fig. 5, center). The rough surface at the attachment of metacarpal Y is well developed. GL: 240, Bp: 75, Dp: 45, Bd: 80, Dd: 45.

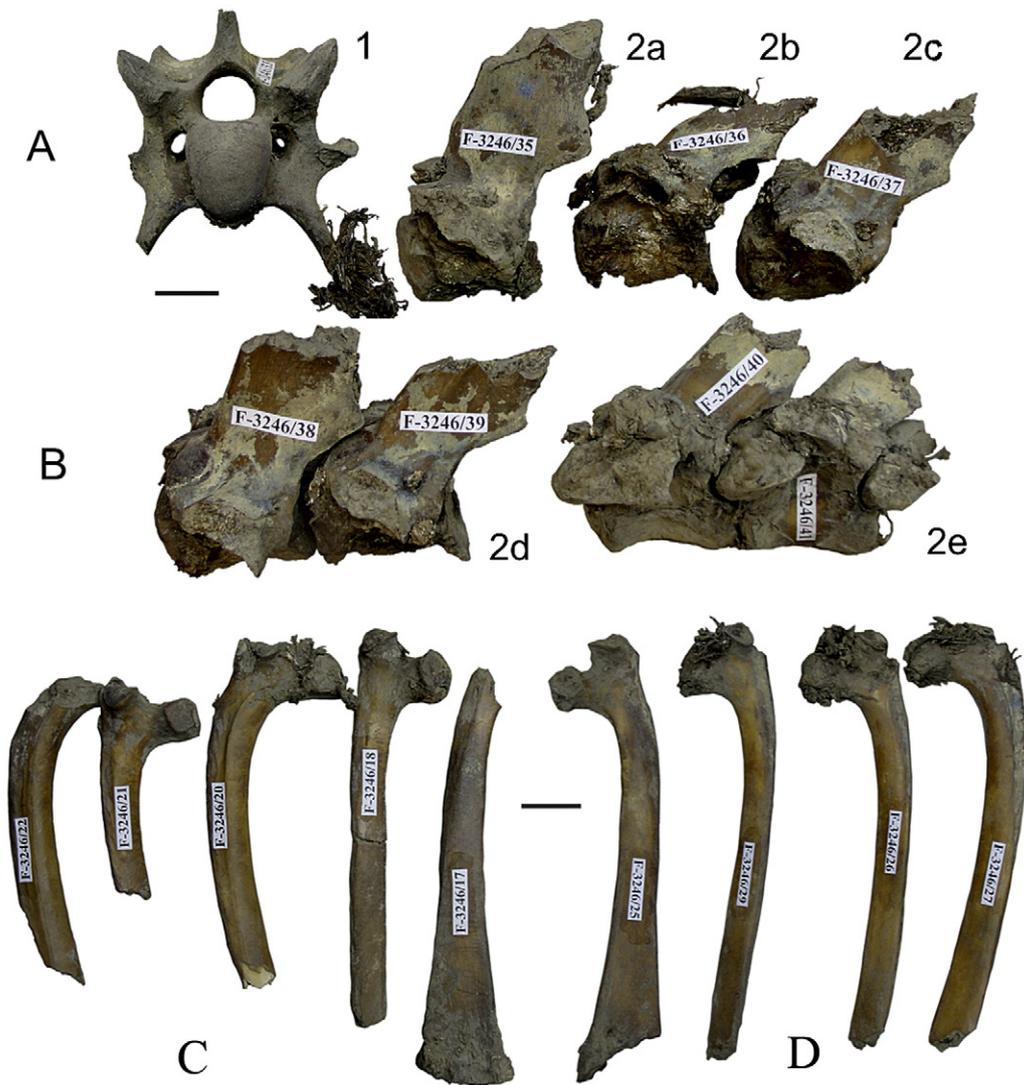
**Fore autopodia**: F-3246/12 right and F-3246/16 left. The right autopodia includes the metacarpal, carpal, and phalanges and is covered by hide stained by vivianite and patches of short reddish fur. The left autopodia, lacks the metacarpal and is covered by hide (Fig. 4G, I).

**Hoof sheath**, F-3246/43–45 (Fig. 4H).

**Pelvis**, F-3246/5 right (Fig. 6A). Right and left sides are fused but broken almost along the suture. Remains of soft tissues are preserved, especially in the acetabulum. The ilium is gnawed. The lowest height of the ilium shaft (SH): 53.5, LFo: 106.5.

**Femora**, F-3246/6 left and F-3246/7 right (Fig. 6B). The left femur has the distal joint strongly gnawed, with soft tissue remaining on either end; only a few bite marks are present on the diaphysis. On the right femur, the large trochanter with a preserved tendon and the distal joint are gnawed. Spongy tissue on both ends of the bone has deep grooves left by canine teeth. The diaphyses have numerous surface scratches. GLC:454.3; SD:48.7.

**Tibia**, F-3246/2–1 right, complete (Fig. 6D). Medially, short and shallow predator tooth marks run across the long bone axis on the diaphysis. On the proximal epiphysis, the knee cruciate ligament tubercle is oval and extends to the diaphysis below the proximal



**Figure 3.** Vertebrae and ribs of the Raichua bison. A. Cervical vertebra. Anterior view. Collection no. F-3246/33. B. Thoracic vertebrae with soft tissue remains, spinal processes broken off. Deep gnawing scars are visible on the vertebral bodies. Collection numbers from left to right F-3246/34–41. C. Left ribs. D. Right ribs. Collection numbers F-3246/17–31. Ice Age Museum. Scale: 40 mm.

articular surface. A small posterolateral area of the epiphysis bears a suture where it fused to the diaphysis. The bone is relatively gracile, as shown by a narrow diaphysis. GL: 447, Bp: 130, Dp: 121, Bd: 82, Dd min: 53.

**Calcaneus**, F-3246/2–3 right, complete (Fig. 6E). GL: 182. The bone is noticeably elongated and narrow (bone width: 35.8).

**Talus**, F-3246/2–2 right, complete (Fig. 6F). Length: 86, upper and lower trochleae: 61 each.

**Malleolar bone**, F-3246/2–4 right, complete. GD: 40.1.

#### Stomach, F-3246/3 (Fig. 2C)

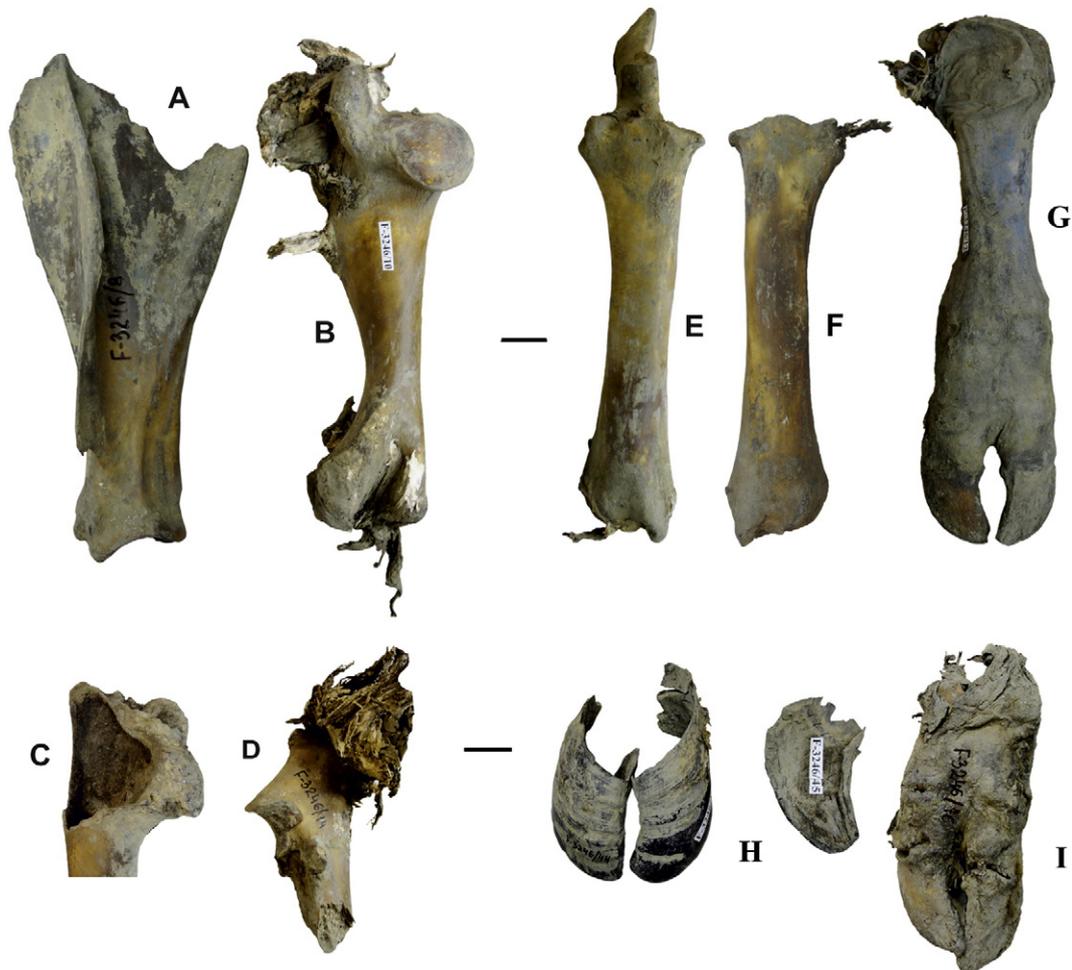
The stomach tissue covering the stomach contents is up to 0.5 m<sup>2</sup>, and the main fragment is 45 × 45 cm. In places, the tissue periphery retained the mammillate layer and a narrow strand of fat deposits up to 40 cm in length and with an expansion area of 14 × 15 cm.

#### Stomach contents, F-3246/4 (Fig. 2B)

Macrofossils and microfossils recovered from the semi-digested stomach content of Raichua bison were mostly well-preserved

remnants of plants, dark-brown to black color. We recovered numerous vegetative parts of herbal plants, generally sedges and grasses; sedge seeds, grasses pollen and phytoliths, shrub pollen and macrofossils were also found. In addition to these, a few bison hairs and single quartz grains were noted. Complete descriptions of the analysis and data recovered are provided in Supplement II.

Macrofossil analyses identified fragments of vegetative parts of plants, including stalks and leaves of herbs, grasses and sedges (Fig. 1, see Supplement II). Crushed shrub branches with split ends (112 pieces, length 20–65 mm and diameter 1–3 mm), a fragment of a charred branch with length of 13 mm and diameter of 5 mm, small quantities of the moss *Polytrichum* sp. (40 units), shrub and subshrub buds (45 units), and seeds and leaf fragments of herbaceous plants and shrubs were also identified. The stalks and leaves of grasses were more abundant than shrub materials (99:1 by volume). Among the plant macrofossils, the most dominant forms were sedge nutlets (*Carex*) and caryopses of grasses (*Arctagrostis latifolia*, cf. *Calamagrostis* and other Poaceae). Shrubs (*Alnus fruticosa*, *Salix* and *Betula* sect. *Nanae*) and subshrubs (*Rubus arcticus*, *Vaccinium vitis-idaea*, *Ledum*) were also common, indicating a shrub tundra paleoenvironment, however species that tend to be found in humid habitats were also present, including *Comarum palustre*, *Ranunculus* cf. *hyperboreus*, and *Menyanthes trifoliata*. Detailed results are provided as Table S1, Supplement II.



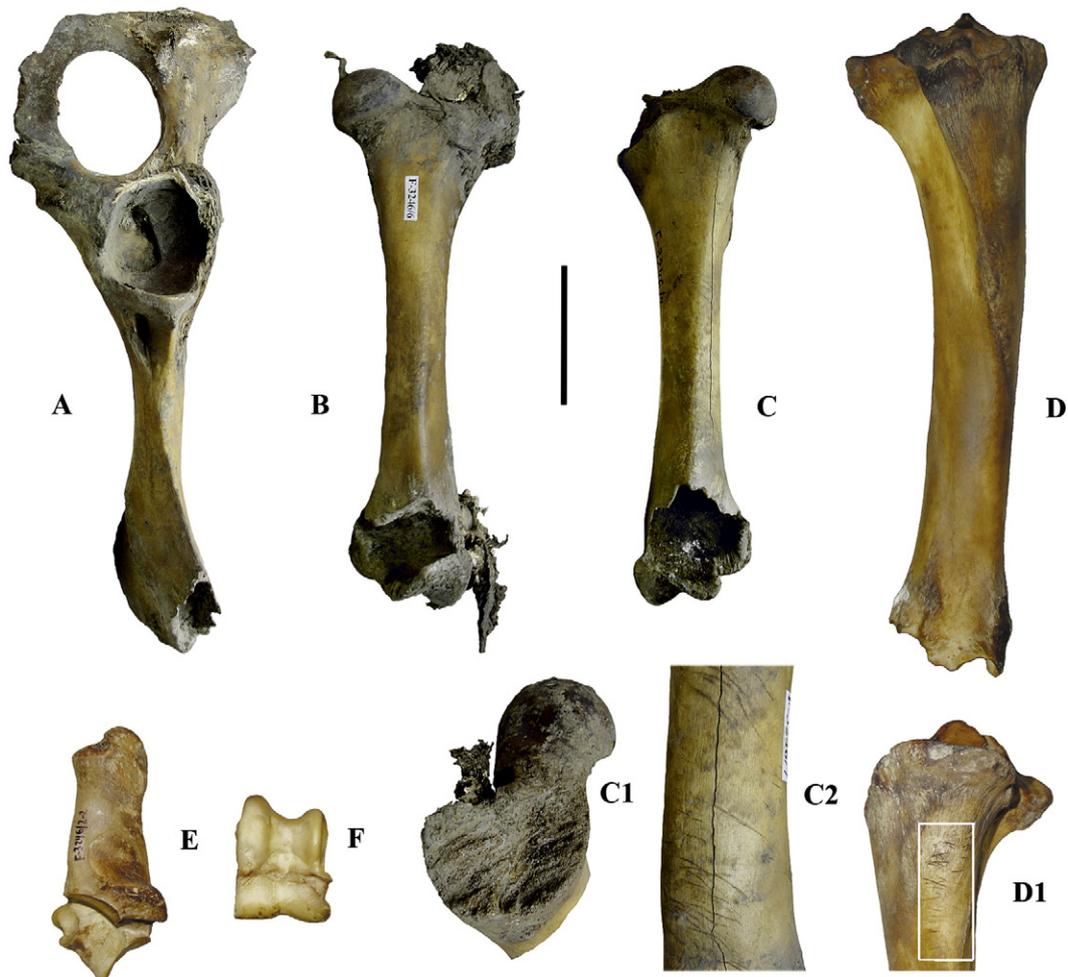
**Figure 4.** Bone of the pectoral girdle of the Raichua bison. A.Scapula. Collection no. F-3246/8. B.Left humerus with soft tissue remains. Collection no. F-3246/10. C.Proximal joint of right humerus gnawed by a large predator. Collection no. F-3246/9. D.Proximal part of the left ulna with remains of soft tissue. Collection no. F-3246/14. E.Right forearm. Collection no. F-3246/11. F.Left radius. Collection no. F-3246/13. G.Right fore autopodia (metacarpal and digital phalanges). Collection no. F-3246/12. H.Hoof sheaths. Collection numbers F-3246/43–45. I.Left distal limb without the metacarpal. Collection no. F-3246/16. Ice Age Museum. Scale: 40 mm.

The microfossil complex includes a large quantity of phytoliths (553–620 units), moss and shrub tissues, cuticle casts of herbs and shrubs, grass and sedge epidermis, epidermis with stoma, and remains of diatoms. We found some large ( $\gg 150 \mu\text{m}$ ) plant tissue remains and a low mineral content. No arboreal plant remains or wood tissues were found. One sample contained intact shells of diatom algae.

The dominant phytolith morphotypes were acicular forms (trichomes) and trapeziform phytoliths. Various types of trichomes were found, including trichomes with a wide base and trichomes with smooth and sinuate spines. Among the trapeziforms, polylobate trapezoids were dominant. These forms prevail in the genera *Poa* and *Bromus* and are common in *Festuca* and *Calamagrostis* (Carnelly et al., 2004).



**Figure 5.** Sexual dimorphism of metacarpals of the Quaternary bison from northeastern Russia. In the centre, metacarpals of the Raichua bison, collection no. F-3246/15. To the left, female bones; from left to right, F-1353, F-1339, F-1348. To the right, male bones; from left to right, F-3072, F-1155, F-1275. Nos. F-1339 and F-3246/15 are on the left; the remaining bones are on the right. Ice Age Museum.



**Figure 6.** Pelvic girdle of the Rauchua bison. A. Pelvis. Collection no. F-3246/5. B. Left femur. Collection no. F-3246/6. C. Right femur. Collection no. F-3246/7. C1 and C2. Canine marks left by a large predator, on the diaphyses, proximal, and distal joints, respectively. D. Tibia. Collection no. F-3246/2-1. E. Calcaneus. Collection no. F-3246/2-2. F. Astragalus. Collection no. F-3246/2-3. Ice Age Museum. Scale: 100 mm.

Globular, smooth phytoliths of *Poa* sp. and some mosses were observed, as were elongate smooth and long, smooth, fine wavy forms, plates, and parallelepipedal castellated. Silicified stomata complexes (about 25–30  $\mu\text{m}$ ) were present in grass epidermal fragments. Elongate phytoliths were sub-epidermal columnar or rectangular cells. Smooth elongate phytoliths are produced by a large number of grasses and are of little use for interpretation of either paleoenvironment or diet. The conical forms are the most distinctive for sedges. The tissues with stomata had a complex of elongate cells lying parallel to the stomata, similar to what has been described for sedges (Carnelly et al., 2004). Detailed results of the microfossil analyses and data standardized as a percentage of the total phytolith count for each form are provided as Table S2, Supplement II.

The pollen spectrum has low pollen and spore contents background and is composed of mainly grasses (Poaceae) and sedges (Cyperaceae). Shrub pollen (*Betula* sect. *Nanae* and *Alnus fruticosa*) is also found in relatively high amounts, and pollen of *Pinus* and *Betula* is present in small amounts. Pollen of mixed grasses is absent. Spores of green mosses (Bryales) are numerous. Redeposited and recent pollen-grains were not found. Singular ascospores of coprophilous fungi are also present. Detailed results of the pollen analysis are given in Table S1, Supplement II.

#### Hair

Almost all fur was found separately from the hide (F-3246/1), except for small areas of short reddish fur that were attached to the distal ends

of the limbs (F-3246/2-1). Preserved hairs varied in length, firmness, thickness and color (Fig. S1, Supplement III). Several types of hair were sampled for further analysis. The first type included long, up to 35–40 cm, coarse black clumps (Sample 1). The second included black, firm, slightly curled clumps up to 16 cm long with brownish underfur at the base (Sample 2). The third included reddish soft clumps with somewhat denser firm black hairs, up to 7 cm long (Sample 3). The fourth included brownish-black or soft dark gray hairs up to 7–9 cm long. Hairs of the second, third, and fourth types constitute the main bulk of the fur. The hairs of a fourth type have been pulled from the level of the medial side of the upper tarsal. This is short firm fur with light-brownish underfur up to 3.2 cm long (Sample 4).

To identify the unattached hairs, we studied descriptions of ancient bison from the Indigirka, Vilyui, and Yana rivers and from the vicinity of Fairbanks (Alaska), and extant American and European bison (Flerov, 1977; Sokolov, 1979; Guthrie, 1990). We concluded that hairs of the first type, based on their length, firmness and jet-black color, come from the tail. The hairs of the second type could be from the lower areas of the body. Reddish hairs are likely to have come from the back and sides, and the brownish-black and dark-gray hairs are most probably underfur.

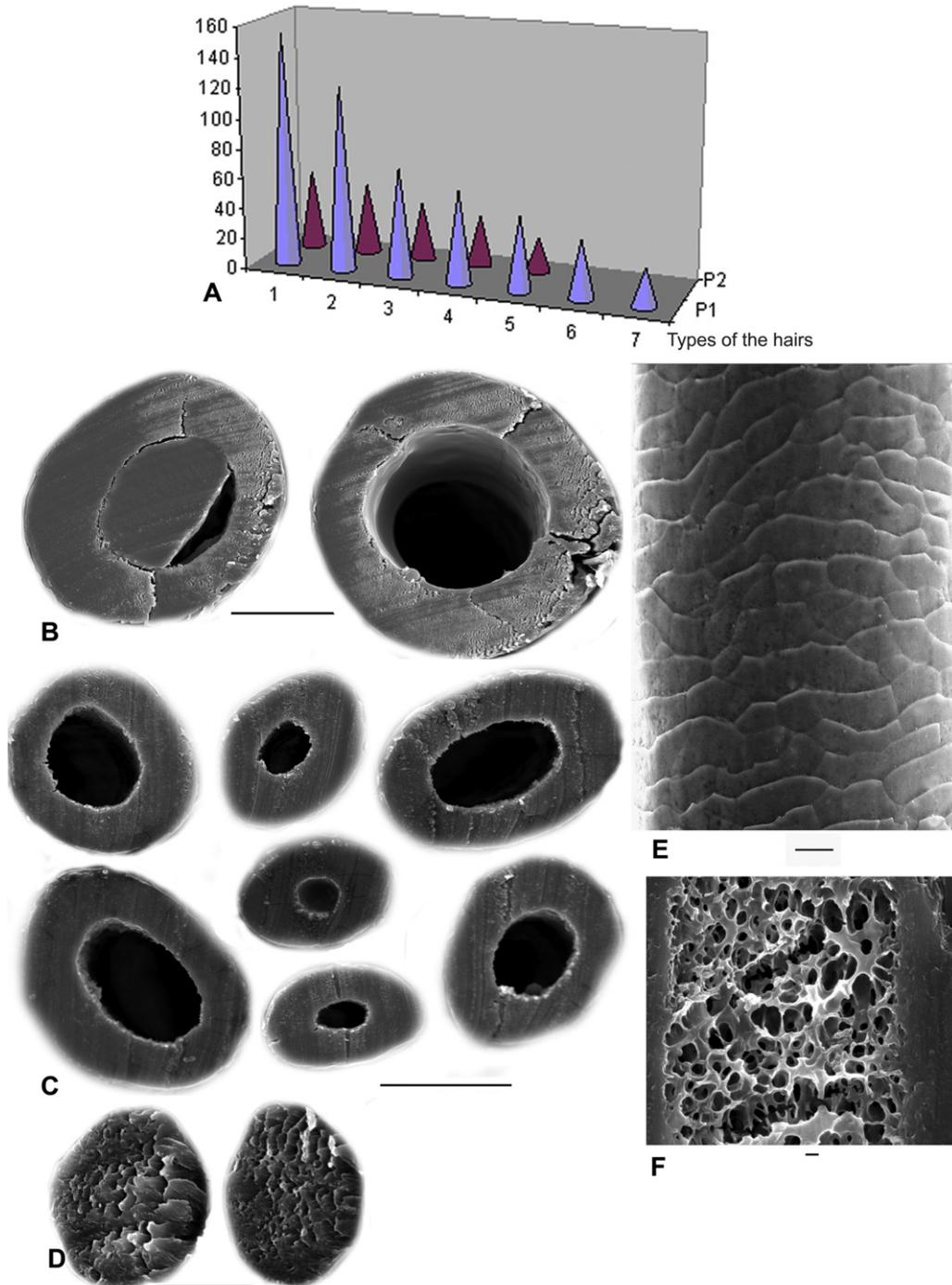
Metrically, we distinguished several types and categories of hairs: the largest and longest guard hairs (overhair), three categories of smaller, so called “zigzag hairs”, and two categories of smallest wavy woolly hairs (underfur). These results indicate that the fur is very well differentiated, and is comprised of an upper tier and a dense undercoat. Guard

hairs are hard, black and straight but with two to three waves (or bends) at the base of the shaft. The zigzag hairs are black or light brown, light or dark or light gray. They have two to five bends. The woolly hairs are light gray and have up to five to seven bends. The width of the different categories of hairs is very different, judging from the average values (Fig. 7, P1). The guard hairs are the thickest (up to 245  $\mu\text{m}$ ); the zigzag hairs I: up to 185  $\mu\text{m}$ ; the zigzag hairs II: up to 101  $\mu\text{m}$ ; the zigzag hairs III: up to 84  $\mu\text{m}$ ; the zigzag hairs IV: 50  $\mu\text{m}$ ; the woolly hairs I: 39  $\mu\text{m}$ ; the woolly hairs II: 37  $\mu\text{m}$ . Although the highest tier of the ancient bison's fur consists of a few

hard, thick guard hairs, the lowest, dense tier is formed by numerous waved woolly hairs.

#### Isotopic composition

The samples examined had rather homogenous isotopic composition of nitrogen ( $\delta^{15}\text{N}$  from 6.2 to 9.6‰), but differed considerably in  $\delta^{13}\text{C}$  (Fig. 8A). Compared to the stomach contents, the hairs, muscular tissue, skin and bone collagen were enriched in  $^{13}\text{C}$  by 4–6‰. Relatively narrow C:N mass ratio (on average  $23.4 \pm 1.5[\text{SE}]$ ) suggests that a large



**Figure 7.** Morphometric and microstructure of the ancient bison's hairs (sample F-3246/1). A. Diagram of some metrics of different types of hair from the ancient bison. B, C, D. Transversal sections of different parts of the shaft of the guard and zigzag hairs (from metatarsus, probe 4). E. Cuticle of a guard hair (as in the previous). F. Medulla of a guard hair on longitudinal section (from a side, probe 2). Legend: P1, absolute width of the hairs, mean value, microns; P2, the relative width of medulla of the hairs, mean value, % of the hair width,  $n = 10$  for each type of the hairs; 1, guard hairs; 2, zigzag hairs I; 3, zigzag hairs II; 4, zigzag hairs III; 5, zigzag hairs IV; 6, woolly hairs I; 7, woolly hairs II; D, a woolly hair I. SEM. Scale bars are B, C, 100  $\mu\text{m}$ ; D, E, 10  $\mu\text{m}$ ; F, 1  $\mu\text{m}$ .

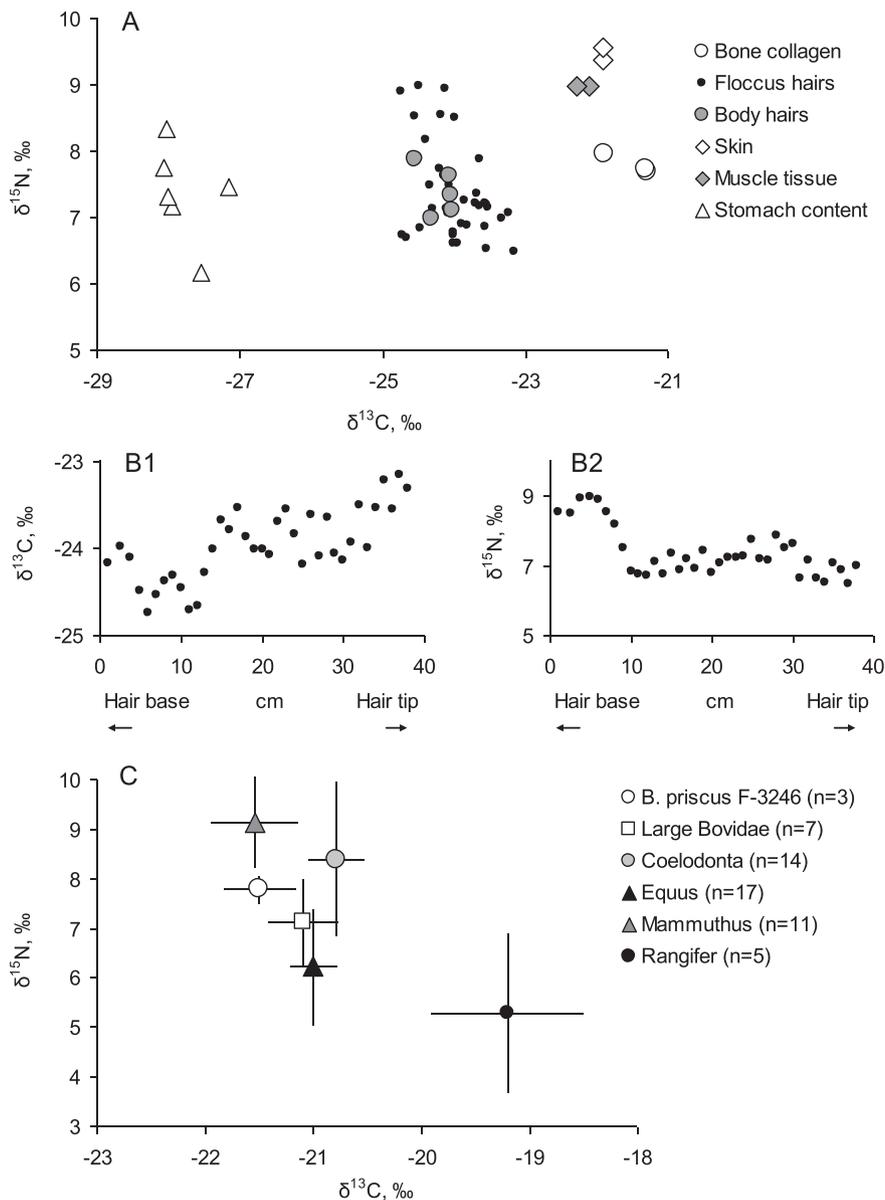
proportion of the nitrogen in the food bolus came from the decaying soft tissues of the bison. Indeed,  $\delta^{15}\text{N}$  values of the stomach content barely differed from the  $\delta^{15}\text{N}$  values of the animal tissues. In contrast, the carbon isotope composition in the stomach content (ca.  $-28\text{‰}$ ) is typical for C3 vegetation.

The  $\delta^{13}\text{C}$  values fluctuated along the length of the floccus hairs rather weakly, with a slight decrease from the tip to the base (growing point) (Fig. 8B). On the contrary, the  $\delta^{15}\text{N}$  values remained nearly constant in the distal part of the hairs (from 10 to 40 cm from the base) and approximately corresponded to the  $\delta^{15}\text{N}$  values of the body hair. In the “youngest” part of the floccus hairs (from 0 to 10 cm from the base) the  $\delta^{15}\text{N}$  values increased sharply, by approximately 2‰.

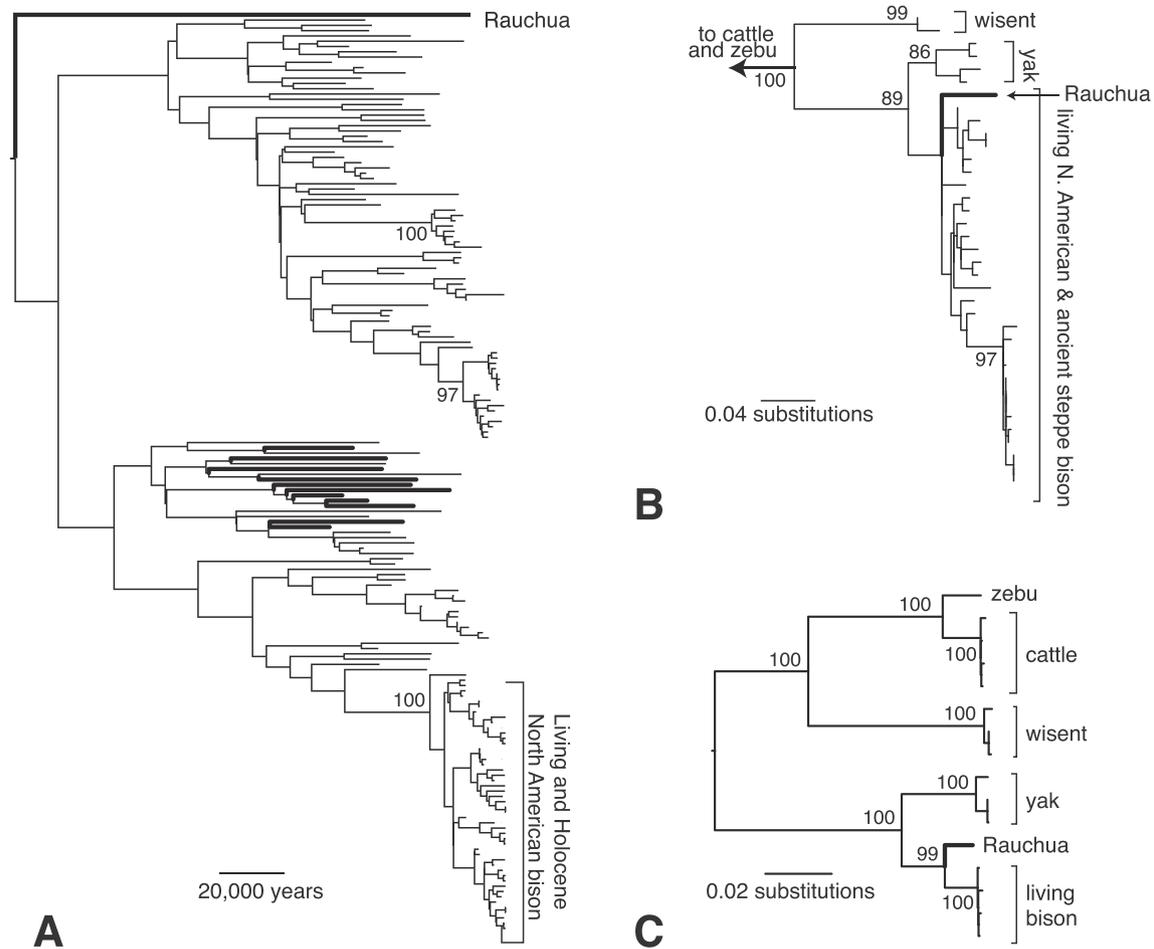
#### Mitochondrial DNA relative to mitochondrial sequences of bison from Asia and North America

Figure 9A describes the placement of the Rauchua bison mitochondrial control region sequence within a more extensive genealogy of

living and late Pleistocene bison mitochondrial sequences from Asia and North America (Shapiro et al., 2004; Zazula et al., 2009; Lorenzen et al., 2011). As shown previously, all living wood bison and plains bison cluster into a clade that also includes bison from Alberta and other locations south of the Cordilleran Ice Sheet (Shapiro et al., 2004). These bisons share a common ancestor around the time of the last glacial maximum (the 95% Highest Posterior Density estimate for the age of this node is 14–24 ka). Apart from the Rauchua bison, all Russian bisons cluster into a single clade, which also includes some bison from North America (Fig. 9). Although the branching order at the root of the tree remains unresolved, the Rauchua bison stands out as potentially distinct from all previously published bison mitochondrial sequences. The trees depicted in Fig. 9B and C describe the relationships between bison (including the Rauchua bison) and other, closely related species. Figure 9B depicts a phylogeny generated using only the control region data (as in Fig. 9A), and Fig. 9C shows a phylogeny estimate using complete mitochondrial genomes. In both trees, the Rauchua bison mitochondrial haplotype falls within the diversity of steppe, wood, and



**Figure 8.** Isotopic composition. A. The isotopic composition ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values) of stomach content, tail and body hairs, skin, muscles and bone collagen of *Bison priscus* F-3246 (each point shows the result of a single analysis). B. The isotopic composition of carbon (B1) and nitrogen (B2) of the floccus hairs of *B. priscus* F-3246 (each point shows the result of a single analysis). C. The isotopic composition of bone collagen of the F-3246 specimen, and other large Pleistocene herbivores of the region (all analyzed samples homed in the Ice Age Museum, Moscow). Points are mean values  $\pm$  1 SD.



**Figure 9.** Mitochondrial genetic relationships between the Rauchua bison and previously published data from ancient steppe bison from Asia (bold branches) and North America, living bison from North America, and several other bovid species. A. The maximum clade credibility tree resulting from a BEAST analysis of 179 bison. Branches with posterior support >95% are indicated at the nodes. B. A maximum likelihood tree depicting the relationships between bison (including the Rauchua bison), wisent, yak, cattle and zebu (the latter two are not shown). Bootstrap support values >85% are given at the nodes. The base of the bison tree is a polytomy, which results in poor support values for any particular branching order. C. A maximum likelihood tree generated from complete mitochondrial genome sequences of the same taxa, but lacking data from ancient bison from either Asia or North America (no such data are available to date).

plains bison mitochondrial haplotypes, but in a basal position. Unsurprisingly, the support values are significantly higher when complete mitochondrial genomes are used in the analysis. However, as there are no published complete mitochondrial genome sequences yet available for ancient bison, it is not possible to fully evaluate the amount of divergence between the Rauchua bison and other ancient steppe bison

## Discussion

### *Taphonomy and cause of death*

Some bones, including the metacarpal, are completely free from soft tissues but lack signs of predation. This suggests that these bones were defleshed (and hoof sheaths came off the third phalanges) as the bison decayed. Decay of the soft tissues was, however, only partial. When the remains were discovered and transported to Moscow, they did not produce a specific putrid odor as would be expected for decaying flesh. This suggests that maceration occurred before the carcass was preserved in the permafrost. The utilization of the carrion by carnivores was considerable but not complete, judging from the absence of flesh and by the split and torn tendon ends at the proximal ends of the tibiae and other bones. However, the decay of the skeleton and its elements is less significant than of the soft tissue, and can be estimated as stage 1–2 (after Haynes, 1982). In this stage, bones gnawed by wolves primarily

include the pelvis, femur, ribs, and vertebrae (Haynes, 1981), as is observed in this instance.

Some bones from the Rauchua bison retained tooth marks left by a large predator. Thin, sometimes parallel canine marks on the diaphysis of the large tubular bones (humerus, radius, and femur) most likely resulted from a predator feeding on fresh prey. The composition and preservation of the remains (rump with some hide; articulated and disarticulated limb bones, including weakly damaged anterior autopodia with soft tissue, almost complete absence of flesh; split and torn tendons; vertebrae anatomically joined and isolated, with dried spinal cord and broken off spinal processes; broken, slightly gnawed ribs; stomach left with its contents but absence of other internal organs), resemble the remains of bison after wolf pack feeding (Haynes, 1981, 1982, 1988; Fosse et al., 2012).

The bones studied have considerable tooth marks, but the epiphyses of the large bones and vertebrae are never completely destroyed. This could suggest that the predators were satiated and finished feeding before the entire prey was utilized, which happens when food is abundant (Haynes, 1981, 1982); it could also happen if the prey suddenly became inaccessible (e.g. the carcass sank into swampy or muddy ground). It is certain that the bison carrion was utilized for food and, judging from the above, most likely by wolves. A cave lion attack (if cave lions survived to the end of the Holocene in Chukotka) leaves claw marks on the hide, as in the Blue Babe carcass (Guthrie, 1990), or deep canine marks (e.g., on the cervical vertebrae; see Kirillova, 2009), which are not observed in

the Rauchua bison. Feeding by bears is usually accompanied by considerable damage to and often complete destruction of the bones of the prey (Pazhetnov, 1990), which also is not observed in the Rauchua bison.

#### Comparative morphometrics of the Rauchua bison bones

Comparison of the sizes and proportions of the metacarpals of the Rauchua bison with those of other middle- late Quaternary bison of northeastern Russia and northern North America (Sokolov, 1979; Widga, 2006; Lewis et al., 2007; Wilson et al., 2008) and materials from the collection of the Ice Age Museum (sample of 43 metacarpals) showed that the Rauchua metacarpals are different from all other specimens. There are only two similar exemplars: from Yakutia—metacarpals of a male from the middle Pleistocene deposits (Rusanov, 1975) and from the USA—metacarpal of a large male bison of late Pleistocene/early Holocene age (Wilson et al., 2008). However, the proportions of bone F-3246/15 have no equivalents. Other long Rauchua bison bones also differ from those of other fossil bisons being less robust. However, these differences are not connected with gender, but rather characterize its taxonomic status (Table 1). The results of the principal component analysis based on seven measurements of metacarpals demonstrate that the Rauchua bison is an outlier along the second axis (Fig. 10). While the first component (~77% of total variance) is strongly correlated with all variables and, hence, reflects overall size, the second axis (~16% of total variance) is positively correlated with the width of the bone and negatively correlated with its length. This pattern suggests that the metacarpal of the Rauchua bison is pronouncedly more gracile.

#### Sex and determination of age at death

Extant bison show a clear sexual dimorphism, which is observed on the skull and postcranial skeleton. Males are larger than females. The same is observed in ancient bison, as noted by Tcherskii (1891). Rusanov (1975) noted massive metacarpals in adult males with wider diaphysis at both the proximal and distal ends of the bones than observed in females.

Methods of sex determination based on the metacarpal bones are well developed (Schertz, 1936; Empel and Roskosz, 1963; Bedord, 1974, 1978; Drees, 2005; Lewis et al., 2005). Although we performed several tests on the Rauchua bison remains (Supplement IV), our results should be interpreted with caution, as the Rauchua bison is an evident morphological outlier (see above). Future genetic work, and in particular deeper sequencing of the nuclear genome of the Rauchua bison, may lead to a more conclusive sex determination.

The absence of a skull and teeth precludes age determination based on tooth structures, which are the most reliable indicators of age. The well-

differentiated fur found around the carcass suggests that the individual was an adult. All epiphyses of the large tubular bones are completely fused with the diaphyses. The times of their fusion in modern *Bison bonasus*, *Bos taurus*, and ancient bison are different. In the ancient bison, both epiphyses of the femur, the proximal epiphysis of the tibia, the calcaneal tubercle, olecranon, and distal epiphysis of the radius become fused to their respective bones by the age of 5.3 yr (Duffield, 1973; Bement and Basmajian, 1996). The bones of the Rauchua bison show complete fusion, and the sutures cannot be traced along the entire length. However, the fusion of the epiphyses on the vertebrae differed—they fused completely anteriorly and only partially posteriorly. In modern *Bison bonasus*, complete fusion of vertebral epiphyses occurs by the age of 6–7 yr (Koch, 1935; Roskosz, 1962). There were no definite age-related changes or pathologies on the bones, which excludes the possibility of an old and mature age for the animal. We conclude, therefore, that the age of the Rauchua bison at the time of its death was at least 5–6 yr but not more than 7–8 yr.

#### Differentiation and structural features of the hair

The hair of the ancient bison is similarly differentiated to those of the recent aurochs and bison, but contains more categories of zigzag and woolly hairs. All hair types and categories of the ancient bison (besides woolly hairs) are thicker than those of the recent bison (Sokolov, 1979; Alaska fur ID project, 2009). The hairs of all types and categories except the woolly hairs have an averagely developed medulla (Fig. 7A, P2; B). The medullar canal is not situated in the center of the shaft but it is moved to the ventral side of the shaft (Fig. 7B). The dorsal side of the shaft is therefore very strong, due to the thicker dense cortical layer on it. This feature is typical of representatives of Bovinae (Chernova and Tzelikova, 2004; Alaska fur ID project, 2009). In the ancient bison, the degree of medulla development is similar to that of the recent bison, but in some guard hairs of the first of the species it reaches 70% of the width of the shaft. The better-developed medulla in the ancient bison's hair probably provided improved insulation properties (Chernova and Kirillova, 2013).

The microstructure of the medulla is typical for Bovinae (Fig. 7C) (Chernova and Tzelikova, 2004). It consists of numerous relatively small air cavities, which have thick walls. In some places, the walls' square are significantly increased. The walls are permeated by numerous oval or round perforations. The microstructure is evidence of the mechanical endurance of the medulla at the cost of its insulation properties, as the air cavities are small but the partitions are thick.

The cuticular ornament and configurations of the scales are similar in the ancient bison's guard and zigzag hairs (Fig. 7D). Also, they are similar to those of the Recent bison and are characteristic for Bovinae (Sokolov, 1979; Chernova and Tzelikova, 2004; Alaska fur ID project, 2009). The cuticular scales differ in a base and in a middle of the shaft. Their height, configuration, the degree of flattening and indentation of the free edge and folding of the front surface are more brightly expressed in the ancient bison's hair.

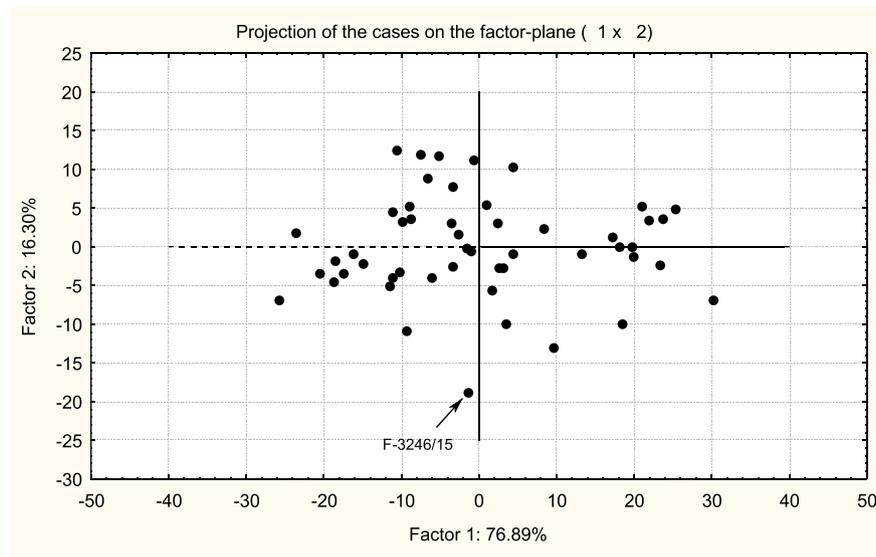
#### Isotopic composition

The difference in the carbon isotopic composition between the plant remains preserved in the stomach ( $\delta^{13}\text{C} = 27.8 \pm 0.2\text{‰}$ ) and the hair ( $-24.0 \pm 0.1\text{‰}$ ) closely matches the "trophic enrichment" in  $^{13}\text{C}$  in hair of herbivores which usually ranges from 3‰ to 4‰ (Sponheimer et al., 2003). The considerable  $^{15}\text{N}$  enrichment (about 1‰) of muscular tissue and skin as compared to bone collagen can be attributed to differences in the amino acid composition of different tissues (Hilderbrand et al., 1996; Martinez del Rio et al., 2009). However, the  $\delta^{15}\text{N}$  values of the collagen extracted from the skin did not differ from those in the bulk skin samples (data not shown). On the other hand, the relative enrichment of muscle and skin samples in  $^{15}\text{N}$  corresponds to the pattern

**Table 1**

Measurements and indices of large tubular bones of the Rauchua bison in comparison with other ancient bisons (mm).

Measurements and indices	Region of Russia	
	Rauchua mouth (Chukotka)	North East Siberia (collection of the Ice Age Museum)
<i>Radius</i>		
1. Greatest length	384	327.0–363.0
2. Breadth of the diaphysis	54	47.2–66.8
Index 2:1	13.8	13.8–18.3, mean = 16.54
<i>Metacarpus</i>		
1. Greatest length	239	207–233
2. Breadth of the diaphysis	49	40.4–61.2
Index 2:1	20.5	18.5–27.8, mean = 23.3
<i>Tibia</i>		
1. Greatest length	450	388.0 = 457.0
2. Breadth of the diaphysis	55.5	49.3–58.7
Index 2:1	12.3	11.0–14.0, mean = 12.7



**Figure 10.** PCA score plots of bison metacarpal bones for the first and second principal components. The position of the *Rauchua* bison is indicated with an arrow.

of changes in  $\delta^{15}\text{N}$  values along the floccus hairs, as the turnover rates of C and N are slower in bone collagen than in soft tissues (Dalerum and Angerbjorn, 2005).

The bone collagen isotopic composition of the ancient bison does not differ much from that of other large herbivores of Chukotka, except for *Rangifer* (Fig. 8C). The deviation towards a small decrease in  $\delta^{13}\text{C}$  in comparison with other Bovidae analyzed does not fall much outside the bounds of a normal dispersion.

#### The diet of the *Rauchua* bison

The *Rauchua* bison appears to have had a broad diet comprised of herbs—sedges (60%), grasses (13.1%), mixed grasses with subshrubs (12.8%), shrubs (3.8%) and moss (10.3%). We observed a wide diversity of phytoliths, including those mosses, dicotyledons herbs, sedges and meadow grasses (Table S2, see Supplement II), including *Poa* sp., *Calamagrostis* sp., *Bromus* sp., *Carex* sp., *Festuca* sp., all of which are common forage grasses in the meadows of North-East Yakutia in the present day. *Festuca* sp., *Poa* sp., and *Calamagrostis* sp. in particular are known to be important forage species for bison in northern-latitude mixed prairies (Van Vuren, 1984; Plumb and Dodd, 1993).

The large amount of macrofossils (10.3%) and microfossils of mosses (Table S1, Supplement II) observed in the stomach contents of the *Rauchua* bison is similar to that observed in the gastrointestinal tract of a late-Pleistocene bison mummy from Indigirka River (Ukrainitseva et al., 1978). Mosses lack nutritional value for ungulate animals (Thieret, 1956; Ukrainitseva et al., 1978; Tomskaya, 2000) and, as they grow very close to the ground, would only have been ingested in large quantities if the bison bit the grass off very near the soil surface and/or if the eaten plants were small. The observation of mosses in the gastrointestinal contents is therefore indicative of the state of forage at time of death.

Previous analyses of vegetative remains from gastrointestinal tracts of fossil bison from northeastern Siberia and Yakutia (Ukrainitseva et al., 1978; Filina and Filin, 1980a, 1980b; Korobkov and Filin, 1982; van Geel et al., 2014) have suggested a diet dominated by grasses and herbs. Reconstructed diets of fossil steppe bison from Interior Alaska differed only slightly from those in Siberia, and were composed of herbaceous plants (90%), trees and shrubs (10%) and mosses (3%) (Guthrie, 1990).

#### Paleoenvironment

Together, the composition of macro- and microfossils in the stomach contents of the *Rauchua* bison indicate that the animal grazed on

mesophytic meadows dominated by sedges and grasses, as well as on relatively drained lands with vegetation consisting of mixed grasses and subshrubs (*Rubus arcticus*, *Vaccinium vitis-idaea*) and on shrubs of willows, dwarf birches, and sedges. On the whole, the nutrition spectrum of the *Rauchua* bison concurs with the summer nutrition spectrum of bison that live in high-latitude locations in present day Canada and Alaska, where habitats are also characterized by sedges, grasses, shrubs, and herbs (Guthrie, 1990; Larter and Gates, 1991, 1994; Plumb and Dodd, 1993; Fortin et al., 2003; Gardner et al., 2007). Apparently, wet sedge-grass meadows with mixed grasses and shrubs were the main summer pastures of bison in the early Holocene of Chukotka, as they are for extant bison in Canada.

Similar paleoenvironments have been reconstructed using paleobotanical remains from the rumen of a frozen Yakutian bison (*Bison priscus*) that lived ca. 10,500 cal yr BP (van Geel et al., 2014). The identified vegetation is composed of species and genera that are typical components of tundra associations of the present subzone of Northern subarctic tundra in the area of the *Rauchua* River (Yurtsev, 1973, 1994).

The phytoliths recovered from the stomach contents are small (~50  $\mu\text{m}$ ), suggesting that the vegetation may have been undersized. In pollen spectra, the proportion of sedge pollen is not high (8.7%), but instead grains of grasses (45.3%) and shrubs (17.6%) and moss spores (23.8%) dominate. Single pollen grains of trees (*Pinus* sp. and *Betula* sp.) were also observed, presumably carried from some distance away.

Similar pollen data were obtained from early Holocene deposits of section Exposure 1, zone 2, which is situated near the *Rauchua* River mouth. In this area, Poaceae dominated the pollen spectrum, *Artemisia* and *Betula* spp. and *Alnus* shrub forms were numerous, and Cyperaceae were rare. Bryales and *Sphagnum* spores were numerous, comprising up to 35% and 6% of the pollen spectrum, respectively (Anderson et al., 2002). Low abundance of mosses of the Sphagnaceae family indicates the lack of over-moistened bog habitats of *Rauchua* bison. In general, the vegetation regime under which the *Rauchua* bison lived was similar to that of both today and the Pleistocene-Holocene transition.

#### Season of death of the *Rauchua* bison

Analysis of the recovered phytoliths enables a tentative reconstruction of the paleoenvironment and the time of year that the bison died. The majority of phytoliths appear to have formed in humid conditions, however hygrophyte and psychrophyte elements were not found. Nonetheless, specific phytolith forms with spiny walls that would

indicate arid conditions (Twiss, 1992) were absent in the grass tissue and the phytoliths were not mature, suggesting that the season of death may have been mid-summer.

The considerable variation between the amount of preserved sedge versus grass material in the stomach contents (Table S1, Supplement II) may be due to differences between these families in their timing of reproduction, and therefore useful to reconstruct the season of death. In the Arctic, sedges blossom from the end of April to the beginning of July, and heavy sedges fruits ripen within the period of grasses blossoming from June to August (Shamurin, 1966). The combination of ripe fruits of sedges and a large amount of grass pollen is characteristic of the second half of summer. This timing agrees with the observation of immature phytoliths.

Changes in the isotopic compositions of C and N along the floccus hairs length allow cautious assumptions about the season of the animal's death. A sharp increase in  $\delta^{15}\text{N}$  and some decrease in  $\delta^{13}\text{C}$  values near the base of the hairs (Fig. 8B) can indicate changes in diet or seasonal stress. The isotopic composition of the body hairs correspond to that of the distal part of the floccus hairs. This suggests that the floccus hairs increased in length by at least 10 cm since the last moult. Bison have a single late-spring moult (Sokolov, 1979) and the floccus hair growth rate of large herbivores amounts to about 1 mm per day (Schwertl et al., 2003; Zazzo et al., 2007). It follows that the death occurred at least 100 days after the last moult date, although the maximum time period cannot be defined. The preserved fur does not resemble that from the winter coat. In accordance with the paleobotanical data, the latest pasturage and the death of the bison correspond to the second half of summer.

#### Mitochondrial DNA

The analyses of mitochondrial data indicate that the *Rauchua* bison falls within the mitochondrial diversity of other steppe bison from Asia and North America (Fig. 9). However, despite considerable sampling across both continents (Shapiro et al., 2004; Zazula et al., 2009), mitochondrial haplotypes similar to the *Rauchua* bison have not been observed. The *Rauchua* bison may therefore belong to a population that was somehow isolated from other steppe bison in Russia, and one that did not disperse across the Bering Land Bridge to North America. The divergence between the mitochondrial haplotype of the *Rauchua* bison and other, previously sequenced bison mitochondrial haplotypes is notable in the context of the specimen's distinct morphology. At this time, nuclear genomic data are not available from any living or extinct bison, which precludes a formal analysis of the level of evolutionary distinctiveness of the *Rauchua* bison. Clearly, future work will be required to fully evaluate how distinct this bison is from other extinct and living bison species.

#### Conclusions

The *Rauchua* bison—the most recent in Western Beringia—lived after the disappearance of the Bering Bridge, which promoted the faunal exchange between Asia and America. The bone proportions put it apart from bisons of North-East Russia due to relative gracility of limbs. Paleobotanical analysis reconstructs treeless landscapes occupied by under-sized meadow mesophytic vegetation. The mitochondrial genetic analyses indicate that it falls within the diversity of other Asian and North American steppe (and living) bison, but in a basal position. Further genetic work, including nuclear genetic analysis and more comprehensive sampling of ancient bison from across Beringia, will be required in order to resolve questions about the *Rauchua* bison's taxonomic status.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.yqres.2015.06.003>.

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