# A detailed life history of a Pleistocene steppe bison (*Bison priscus*) skeleton unearthed in Arctic Alaska

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**Abstract:**

Detailed paleoecological evidence from Arctic Alaska's past megafauna can help reconstruct paleoenvironmental conditions and can illustrate ecological adaptation to varying environments. We examined a rare, largely articulated and almost complete skeleton of a steppe bison (*Bison priscus*) recently unearthed in Northern Alaska. We used a multi-proxy paleoecological approach to reconstruct the past ecology of an individual representing a key ancient taxon. Radiocarbon dating of horn keratin revealed that the specimen has a finite radiocarbon age ~46,000 +/- 1000 cal yr BP, very close to the limit of radiocarbon dating. We also employed Bayesian age modeling of the mitochondrial genome, which estimated an age of ~33,000-87,000 cal yr BP. Our taphonomic investigations show that the bison was scavenged post-mortem and infested by blowflies before burial. Stable carbon and oxygen isotope ($\delta^{13}C$ and $\delta^{15}N$) analyses of sequentially sampled horn keratin reveal a seasonal cycle; furthermore, high $\delta^{15}N$ values during its first few years of life are consistent with patterns observed in modern bison that undertook dispersal. We compared sequential analyses of tooth enamel for strontium isotope ratios ($^{87}Sr/^{86}Sr$) to a spatial model of $^{87}Sr/^{86}Sr$ ratios providing evidence for dispersal across the landscape. Synthesis of the paleoecological findings indicates the specimen lived during interstadial conditions. Our multi-proxy, paleoecological approach, combining light and heavy isotope ratios along with genetic information, adds to the broader understanding of ancient bison ecology during the Late Pleistocene, indicating that ancient bison adopted different degrees of paleo-mobility according to the prevailing paleoecological conditions and climate.

## 1. Introduction:

### 1.1 Paleoecological context:

Northern Alaska is currently experiencing environmental changes as the result of global warming, which is occurring most rapidly at northern latitudes (Moon et al., 2019). These changes impact the mobility and ecologies of extant megafauna including caribou, moose, and muskoxen (Post and Forchhammer, 2008; Sharma et al., 2009). For example, migratory species are experiencing mismatch in timing of migration and peak resource availability (Post and Forchhammer, 2008), while caribou are losing habitat in the north due to warmer Arctic summers and winters (Sharma et al., 2009). Detailed paleoecological evidence from the remains of past megafauna from this region provides an opportunity to examine how past megafauna lived in this environment (Guthrie, 1989), and therefore help predict responses of living megafauna to present and projected environmental changes.

During the height of the last glaciation (~28-18 thousand years ago (kya)) (Clark et al., 2009), the North Slope of Alaska was part of an expansive land-mass known as Beringia. Sea levels were ~130 meters lower than today (Lambeck et al., 2014), exposing a shallow continental shelf between northeast Asia and North America known as the Bering Land Bridge (BLB). The BLB extended approximately from the Lena River, Russia, in the west and the Mackenzie River, Yukon, Canada, in the east (Elias and Crocker 2008) (Figure 1). The Beringian ecosystem was primarily that of a mammoth steppe, a graminoid-dominated ecosystem that supported a community of large herbivorous mammals, dominated by mammoths (*Mamamuthus primigenius*), horses (*Equus* sp.), and steppe bison (*Bison priscus*) (Guthrie, 2001; Mann et al., 2013; Shapiro and Cooper, 2003; Zimov et al., 2012). The mammoth steppe supported large populations of these herbivores, many of which had larger body sizes than their descendants today at similar latitudes (Zimov et al., 2012). Bison, in particular, had larger body sizes and horns than present-day American bison (*Bison bison*) (Martin et al., 2018), and were present throughout most of Eurasia and North America in what has been termed "The Bison Belt" (Guthrie, 1989). Steppe bison first arrived in North America ~195-135 kya (Froese et al., 2017) and their population began to decline around 37 kya (Heintzman et al., 2016; Shapiro et al., 2004).

Modern bison ecology can provide an analog for inferring ancient bison behavior as well as the basis for comparative (paleo) biology and anatomy. Although modern plains bison (*Bison bison bison*) are often considered grassland grazing specialists (Bamforth, 1987), plains bison in northern habitats (Waggoner and Hinkes, 1986), wood bison (*Bison bison athabascae*) (Larter and Gates, 1991), european wisents (*Bison bonasus*) have been observed to regularly utilize browse in their diet (Kowalczyk et al., 2011). Evidence from macro and micro tooth-wear analysis indicates that steppe bison likely had a broader herbivorous diet and ecological niche that included browsing (Rivals et al., 2010, 2007; Saarinen et al., 2016). The long-distance (>100km) (Berger, 2004; Hanson, 2015; Plumb et al., 2009) migrations of American bison (*Bison bison*) across the American Great Plains were legendary and a key component of bison life history (Bamforth, 1987; Flores, 1991). However, isotopic (strontium) analyses of ancient (~18,500 $^{14}$C yr BP) bison (*Bison priscus*) from a site in Ukraine found no evidence of paleomobility (Julien et al., 2012). Analyses of ancient bison specimens can provide opportunities to flesh out the paleoecological life-history of a taxon that shaped Beringian ecosystems (Zimov et al., 2011).

Fortunately for paleoecologists, bones, teeth, and horns of bison are some of the most numerous fossil remains found in Alaska (Guthrie, 1970; Mann et al., 2013). On rare occasions, high sediment deposition rates along with freezing temperatures can result in preservation of virtually complete carcasses or skeletons of past Beringian fauna, revealing vivid paleoecological snap-shots of life in Beringia (Boeskorov et al., 2016; Kirillova et al., 2015; Van Geel et al., 2014; Zazula et al., 2017; Zazula et al., 2009). These rare and well-preserved glimpses of past megafaunal paleoecology can emerge from eroding river-banks (Mann et al., 2013; Zazula et al., 2009), during mining operations (Guthrie, 1968), and during construction activities (Zazula et al., 2017). In some instances, soft tissue such as hair, skin, organs, and stomach contents are preserved (Kirillova et al., 2015; Van Geel et al., 2014), as well as associated insects. These remains, along with bones and teeth, can retain chemical clues about an individual's paleoecology. Isotopic analyses (Kirillova et al., 2015) and analyses of ancient DNA (aDNA) (Zazula et al., 2017) can reveal past mobility patterns and population interconnectivity, contributing to an understanding of past ecosystems, landscapes, and evolution (Froese et al., 2017; Haile et al., 2009; Marsolier-Kergoat et al., 2015; Shapiro and Cooper, 2003, Heintzman et al., 2016; Shapiro et al., 2004).

118　　　　In this study, we conducted a multi-proxy study, combining isotopic and aDNA analyses,

119　　with supporting paleo-forensic analyses, to investigate the sex, age, paleoecology and life history

120　　of an exceptionally well-preserved and largely articulated steppe bison (*Bison priscus*) found on

121　　the North Slope of Alaska (Figure 1 a-c). We assess peri- and post-mortem events together with

122　　the taphonomic history of skeletal remains using a taphonomic analysis of the skeleton and of the

123　　plant and insect remains present. Our examination of the physical condition of the remains

124　　(bones and teeth) from the specimen provides clues about an individual's age, sex, and

125　　appearance (Fuller, 1959). The taphonomy and geology associated with the specimen provides

126　　information about the context surrounding an organism's death and a possible cause of death.

127　　We used insect (Elias et al., 2000) and plant (Bigelow et al., 2013) macrofossils associated with

128　　the bison's remains to provide valuable paleoecological information. Our multi-proxy,

129　　paleoecological approach adds to the broader understanding of ancient bison ecology during the

130　　Late Pleistocene.

131

132　　*1.2 Stable Isotopes:*

133

134　　Isotopic analyses have become a popular tool in paleoecology for determining the ecological and

135　　life-history traits of ancient fauna (Bocherens, 2003; Britton et al., 2009). Tissues that form in

136　　discrete layers over a period of an individual's life, such as tooth enamel, hair, or horn, can be

137　　subsampled to allow inference of inter- and intra-annual paleo-mobility and paleoecology using

138　　isotopic analyses of these sample types (Balasse et al., 2001; Britton et al., 2009; Stevens et al.,

139　　2011; Zazzo et al., 2012). Intra-tooth strontium isotope ratio ($^{87}Sr/^{86}Sr$) analysis has been

140　　developed as a useful tool to track the mobility of past animals and humans (Balasse, 2002;

141　　Britton, 2009; Britton et al., 2011; Hoppe et al., 1999; Hoppe, 2004; Julien et al., 2012; Koch et

142　　al., 1995; Pellegrini et al., 2008; Radloff et al., 2010; Viner et al., 2010; Widga et al., 2010).

143　　$^{87}Sr/^{86}Sr$ ratios can vary across landscapes depending in part on the age and rock type of the

144　　underlying geology (Bataille et al., 2014; Brennan et al., 2014). These landscape $^{87}Sr/^{86}Sr$

145　　signatures can enter animals through their diet and drinking water, replacing calcium in tissues

146　　such as teeth and bones (Capo et al., 1998). The combination of $^{87}Sr/^{86}Sr$ ratios and oxygen

147　　isotopic ($\delta^{18}O$) values from analyses of animal tissues have proved to be a powerful predictor of

148　　geographic location (Britton et al., 2009; Gigleux et al., 2017; Knudson et al., 2009). The $\delta^{18}O$

149    values from a specimen can indicate location based on latitude and distance from the coast

150    (Hoppe, 2006; Lachniet et al., 2016). The $\delta^{18}$O values from analyses of bison teeth have also

151    been used to determine approximate local climate and seasonal temperature variation, because

152    $\delta^{18}$O values in water can be closely related to temperature (Bernard et al., 2009; Hoppe et al.,

153    2006; Scherler et al., 2014). Examining bison mobility has been one of the more common

154    applications of this isotopic methodology, partly due to the abundance of bison remains in the

155    archaeological and paleontological records (Britton et al., 2012; Julien et al., 2012; Widga et al.,

156    2010).

157            Stable carbon and nitrogen isotope ratios (expressed as $\delta^{13}$C and $\delta^{15}$N values,

158    respectively) from analyses of sub-fossils of animals can add a dietary dimension to a

159    paleoecological reconstruction (Drucker et al., 2008; Stevens and Hedges, 2004). $\delta^{13}$C, along

160    with $\delta^{18}$O, values can be generated from the analysis of inorganic carbon in bones and teeth

161    (Koch et al., 1997). Bison horns, which grow throughout the life of a bison, are a carbon and

162    nitrogen-rich keratin tissue that allows intra- and inter-annual paleoecological inferences. $\delta^{13}$C

163    values can also be generated from analyses of organic carbon preserved as bone collagen and the

164    horn keratin, these methods also produce $\delta^{15}$N values (Iacumin et al., 2001; Schoeninger and

165    DeNiro, 1984). In order to interpret the $\delta^{13}$C and $\delta^{15}$N values of these analyses, potential sources

166    of variability need to be evaluated. One common source of $\delta^{13}$C variation in the diet of

167    herbivores is variation in the proportional contribution $C_4$ vs. $C_3$ plants. However, $C_4$ plants are

168    exceedingly rare or non-existent in the Arctic (Wooller et al., 2007). Furthermore, a lack of trees

169    and even shrubs in Pleistocene Arctic Alaska, even during some warmer interglacials (Willerslev

170    et al., 2014), also excludes "the canopy effect" caused by the concentration of $CO_2$ in dense

171    forest (Drucker et al., 2008) and differences between herbs and shrubs (Schwartz-Narbonne et

172    al., 2019). Thus, the main source of variability in $\delta^{13}$C values we can expect in Arctic vegetation

173    is between wetter and drier environments (Wooller et al., 2007).

174            There are several drivers of $\delta^{15}$N variation in animals, which can make it a challenging

175    system to study although $\delta^{15}$N values can demonstrate important relationships. For example,

176    $\delta^{15}$N values in ancient megafauna have been found to have a strong relationship with the amount

177    of precipitation during the Pleistocene (Carlson et al., 2016; Drucker et al., 2003; Graham et al.,

178    2016; Heaton et al., 1986; Rabanus-Wallace et al., 2017), which is likely due in part to major

179    changes in soil ecology in response to climatic change (Hobbie and Hobbie, 2006; Stevens et al.,

180   2006). However, for higher resolution $\delta^{15}$N we must consider behavioral and physiological

181   explanations for change found in serially analyzed tissues (Drucker et al., 2010). Behavioral

182   explanations including migration or dispersal could explain some of the differences and $\delta^{15}$N

183   values found in relation to aridity (Barbosa et al., 2009) and altitude (Männel et al., 2007). In

184   northern regions, studies have found consistent difference in plants based on mycorrhizal

185   relationships with the soil (Kristensen et al., 2011). However, these are not sufficient to account

186   for the seasonal differences or major regional differences that would be required to explain some

187   of the magnitude of variation in $\delta^{15}$N values we go on to document in this ancient bison and

188   other modern bison in the region (Funck et al., 2020). Alternatively, physiological changes in

189   $\delta^{15}$N values of animals can occur in animals adapted to extreme conditions. Notably, animals

190   who undergo hibernation (Lee et al., 2012), lack sufficient calories or are fasting (Hobson et al.,

191   1993; Hobson and Clark, 1992; Mekota et al., 2006; Voigt and Matt, 2004) as well as animals

192   managing acute physical stress (Delgiudice et al., 2000; Fuller et al., 2005; Habran et al., 2010;

193   Rode et al., 2016) can exhibit relatively large increases in $\delta^{15}$N values. The effect of dietary

194   stress on $\delta^{15}$N values in wood bison was evident in individuals that had undergone nutritional

195   stress during the winter in Northern Alaska (Funck et al., 2020). For this reason, we will focus

196   our interpretation on nutritional stress as the primary factor of intra-tissue $\delta^{15}$N variation but

197   acknowledge that other behavioral and ecological factors may be involved. From our review of

198   the literature, we have noted that changes in $\delta^{15}$N values in herbivores from the mammoth steppe

199   over time have largely not included the possibility that some of the variation could be driven by

200   physiological stress and even starvation. To some degree this is likely obscured by the fact that a

201   majority of the previous research has focused on $\delta^{15}$N values generated from analyses of bone

202   collagen, which provides a more integrated and essentially a life-time measure. Our analyses of

203   horn-sheaths are providing a new a more detailed temporal perspective, which could be

204   translated to the huge abundance of archived bison horn sheaths available. Using a combination

205   of isotopic approaches on different sequentially grown tissues can provide a multi-proxy

206   perspective of an individual's life-history and eventually put this in the context of larger herds.

207

208   *1.3 Ancient DNA:*

209

210 Ancient DNA (aDNA) from ancient bison specimens from Beringia has been used to monitor

211 gene-flow across the BLB and through the ice-free corridor that connected eastern Beringia to

212 the rest of the Americas (Froese et al., 2017; Heintzman et al., 2016). It has also been used to

213 estimate past changes in effective population size (Lorenzen et al., 2011), which has been used to

214 identify the decline of steppe bison since ~37 kya in Beringia (Shapiro et al., 2004). Analyses

215 using aDNA can also add a further perspective on individual steppe bison specimens. They can

216 provide information on an individual's genomic sex and population affinity, and help constrain

217 age estimates for specimens potentially outside the range or towards the limits of radiocarbon

218 dating. For the latter analysis, one such approach uses Bayesian analysis of aDNA sequences

219 from dated specimens that lived at different time periods to calibrate a molecular clock, and then

220 use this calibration to estimate the age of the undatable individual (Shapiro et al., 2011). The

221 mitochondrial genealogy of Pleistocene bison in North America has been relatively well

222 sampled, both geographically and temporally (Froese et al., 2017; Heintzman et al., 2016;

223 Shapiro et al., 2004), and is therefore likely to be well suited for estimating the age of ancient

224 bison specimens.

225

226 **2. Material and methods:**

227

228 *2.1 Specimen and study site:*

229

230 Dr. Dan Mann and Dr. Pamela Grooves found a nearly complete, and partially articulated

231 specimen of steppe bison (*Bison priscus*) eroding out of a bank of the Ikpikpuk River on the

232 North Slope of Alaska (Figure 1 a-c) located at 69.71563 N, -154.863 W (WGS 84) (Figure 1).

233 They excavated and transported to the University of Alaska Museum of the North (UAMN),

234 where the University of Alaska Museum Earth Sciences collections (UAMES) assigned an

235 identification number UAMES 29458. The North Slope of Alaska is delimited by the Brooks

236 Range of mountains to the south and the Arctic Ocean to the north (Figure 1). The southern

237 portion is predominantly low foothills that become a coastal plain at ~69° north. The Ikpikpuk

238 River cuts through Quaternary-aged aeolian sand deposits, known as the Ikpikpuk Sand Sea

239 (Carter, 1981). These deposits preserve an abundance of Quaternary vertebrate fossils that erode

240 from banks of the Ikpikpuk River, though rarely in such excellent and complete condition (Mann

241 et al., 2015). The general geology of this region consists of undifferentiated alluvial and aeolian

242 deposits (organic-rich silt, loess and sand) of Holocene to Pleistocene age. The specimen was

243 discovered and excavated from the eroding banks of the Ikpikpuk River in these unconsolidated

244 sediments. The vast majority of vertebrate remains recovered from here are single isolated

245 elements found in reworked sediments while floating the river by small boat. Unfortunately, a

246 quarry map is not available from the site at the time of collection, in part due to the unexpected

247 nature of the find and constraints of rapidly conducting fieldwork in remote Alaska. The

248 sediment and associated microfossils analyzed in this study were collected from matrix directly

249 surrounding or within cavities of the skeleton.

250

251 *2.2 Fossil Material:*

252

253 Skeletal elements of specimen UAMES 29458 were removed from the encasing sediment,

254 cleaned, and anatomically re-articulated (Figure 2a). Hair, preserved soft tissue, and associated

255 sediment were stored by individual body element and kept frozen. We rearticulated the specimen

256 at the UAMES (Figure 2 a, b) and examined it for signs of scavenging and other taphonomic

257 processes, using methods outlined elsewhere (Binford, 1981; Domínguez-Rodrigo, 1999; Fisher,

258 1995; Haynes, 1980; Hudson, 1993; Lyman, 1994, 1987). We found a large number of

259 invertebrate and plant macrofossils within the interstices of the skull, particularly the brain

260 cavity. These were collected and identified to provide taphonomic and paleoenvironmental

261 context. We removed larger macrofossils and examined them using a dissecting microscope. We

262 wet sieved sediments at 150 µm and 250 µm. All diagnostic plant macrofossils were collected

263 from sediments larger than 250 µm and all invertebrate materials were collected and archived.

264

265 *2.3 Radiocarbon analysis:*

266

267 Radiocarbon dating was conducted on different materials associated with specimen UAMES

268 29458. Previously the bone collagen from the cap of a spinous process, extracted without

269 ultrafiltration, was analyzed at Beta Analytic (Miami, Florida), and found to be non-finite in age

270 >43,500 radiocarbon years (Mann et al., 2013). However, collagen is porous and can be subject

271 to contamination, so we selected additional materials for further analysis: keratin from the horn

272     sheath, along with a fly pupal case and a plant macrofossil (herbaceous stem) that were both

273     recovered from inside the bison skull. W. M. Keck Carbon Cycle Accelerator Mass Spectrometry

274     Laboratory analyzed the samples on a National Electrostatics Corporation (NEC 0.5MV

275     1.5SDH-2 AMS system). The horn sheath keratin was run alongside three non-finite-$^{14}$C aged

276     bison horn sheath samples and the mean blank from these three was subtracted from sample

277     results, with an assumed 30% uncertainty. All of the sample preparation backgrounds were also

278     subtracted, based on measurements of a $^{14}$C-free wood standard, with an assumed 30%

279     uncertainty.

280

281     *2.4 Isotopic analyses:*

282

283     We removed thirty-three intra-tooth subsamples of enamel from the right mandibular molars 1,

284     2, and 3 (M1, M2, M3) of UAMES 29458 (Supplemental Figure 1). We collected samples in a

285     laminar flow hood at the Alaska Stable Isotope Facility (ASIF) at the University of Alaska

286     Fairbanks (UAF). We removed the surface layer of the target region from each molar and

287     subsequently used a Dremel diamond-coated circular saw to divide samples along each tooth

288     parallel to the growth plane (Figure S1). Enamel samples were removed as chips, which has been

289     found to reduce the potential for contamination (Diego Fernendez, University of Utah, ICPMS

290     Facility 2018 personal communication).

291        The University of Utah, Department of Geology and Geophysics, ICPMS facility

292     analyzed half of each sample for $^{87}$Sr/$^{86}$Sr ratios using a multi-collector inductively coupled

293     plasma mass spectrometer (MC-ICPMS - ThermoFisher Scientific, High Resolution NEPTUNE,

294     Bremen, Germany). Strontium isotope analyses followed previously published protocols

295     (Glassburn et al., 2018; Nelson et al., 2018). Additionally, we sampled whole molars from 14

296     modern rodent museum specimens (UAM:Mamm: *Microtus oeconomus*, *Microtus mirus*,

297     *Dicrostonyx groenlandicus*) from within a 250-km radius surrounding the UAMES 29458

298     locality (Figure 1a) to determine the bioavailable $^{87}$Sr/$^{86}$Sr ratios in the region (Bataille et al.,

299     2020). This method has previously been used to determine local bioavailable $^{87}$Sr/$^{86}$Sr ratios for

300     comparison to mobile individuals (Hoppe et al., 1999; Kootker et al., 2016; Radloff et al., 2010).

301     The results of this investigation augment existing spatial models of variability in $^{87}$Sr/$^{86}$Sr ratios

302     in Alaska (Bataille et al., 2014).

303    We chemically pre-treated the remaining half of each bison enamel sample to remove

304    contaminants from gas exchange using the modified method from Pellegrini and Snoeck (2016,

305    2015) in order to produce $\delta^{18}O$ and $\delta^{13}C$ values. To compensate for the use of small (~1 × 2 mm)

306    enamel chips rather than powder we increased the soaking time. We added one milliliter of 2%

307    sodium hypochlorite (NaOCl) to each sample, shaken to mix, and soaked for 48 hours to remove

308    organic particulates. We then rinsed samples with deionized water and soaked them in 1 M

309    acetate buffered acetic acid (0.1 M) ($CH_3CO_2H$) for 48 hours to removed carbonate portion.

310    Finally, we rinsed the samples three times with deionized water before freezing and then freeze-

311    dried them for approximately 10 hours on a VirTiS benchtop Lyo-Centre lyophilizer to remove

312    any moisture prior to isotopic analysis. We analyzed the carbonate fraction using a Thermo

313    Scientific GasBench II carbonate analyzer attached to a Thermo Scientific DeltaV$^{Plus}$ Isotope

314    Ratio Mass Spectrometer at ASIF following previously published protocols (Glassburn et al.,

315    2018). Stable carbon and oxygen isotope ratios are reported in δ notation as parts per thousand

316    (‰) relative to the international standard Vienna Pee Dee Belemnite (VPDB). We ran the

317    samples with laboratory standards of calcium carbonate (Merck, Suprapur 99.95% Lot #

318    B510959 313) every 10 samples to determine analytical precision for $\delta^{13}C$ values (0.3 ‰) and

319    $\delta^{18}O$ values (0.2 ‰) (all errors are expressed as one standard deviations). The $\delta^{18}O$ and $\delta^{13}C$

320    values were initially determined relative to VPDB for oxygen and carbon, but the $\delta^{18}O$ values

321    were subsequently converted to the Vienna Standard Mean Ocean Water (VSMOW) scale to

322    allow comparison of the values to meteoric water values. The $\delta^{18}O$ values were converted to

323    VSMOW using Formula 1 (below) (Verkouteren and Klinedinst, 2004) and then Formula 2

324    (below), a conversion developed by Hoppe et al. (2006) and Velivetskaya et al. (2016) to

325    compare bison enamel to meteoric water $\delta^{18}O$ values:

326

327    Formula 1: VSMOW = 30.92+1.03092*VPDB

328

329    Formula 2: Enamel carbonate = 0.7(±0.12)*VSMOW- 30.06(±1.40)

330

331    We removed horn sheath keratin as a wedge perpendicular to the direction of the keratin

332    growth layers (Figure S2). We selected the location to maximize the years of horn growth

333    covered by the core. We then subsampled the core by peeling off thin layers between 0.1-0.3 mm

334    in thickness with a razor blade, for a total of n = 113 sub-samples. Sub-samples were analyzed to

335    produce $\delta^{15}N$ and $\delta^{13}C$ values (vs. AIR for nitrogen and VPDB for carbon) using a Flash 2000

336    Organic Elemental Analyzer (EA) connected via a Conflo IV to an IRMS (DeltaV Plus) at ASIF.

337    Internal reference checks using peptone (No. P-7750 meat-based protein. Sigma Chemical

338    Company, Lot #76f-0300) were run every 10th sample, and blanks were run every 20th sample.

339    Repeated measurements of standards provided the analytical precisions, which were ±0.1 ‰ and

340    ±0.6 ‰ for $\delta^{15}N$ and $\delta^{13}C$ values, respectively.

341

342    *2.5 aDNA analyses:*

343

344    The first premolar (PM1) of specimen UAMES 29458 was sent to the specialized Paleogenomics

345    Laboratory at the University of California Santa Cruz (UCSC) for aDNA analysis. We followed

346    standard protocols as outlined in Froese et al. (2017) to extract and analyze ancient DNA unless

347    stated otherwise. Briefly, we extracted aDNA using a silica column method (Dabney et al.,

348    2013), and then converted extracts into an Illumina-compatible double-stranded DNA library

349    (Meyer and Kircher, 2010). We enriched an aliquot of this DNA library for bison mitochondrial

350    genomic fragments using a commercial MyBaits target capture kit (Arbor Biosciences, Ann

351    Arbor, MI). We sequenced both the enriched and remaining unenriched library on separate runs

352    of an Illumina MiSeq using v3 150 cycle chemistry75 cyc, with paired-end 75 bp reads. We then

353    merged the paired-end read data, trimmed adapters, and removed short (<25 base pairs (bp) for

354    the enriched library; <30 bp for the unenriched library) and low-complexity sequences (DUST

355    cutoff: 7) using SeqPrep and PRINSEQ-lite v0.20.4 (Schmieder and Edwards, 2011).

356         We aligned the filtered reads from the unenriched library to a reference database that

357    included the cow (*Bos taurus*) genome (Genbank: Btau_4.6.1) and an American bison (*Bison*

358    *bison*) mitochondrial genome (Genbank: NC_012346), using the Burrows Wheeler Aligner

359    (BWA; Li and Durbin, 2009) aln algorithm with the seed disabled (-l 1024). We filtered aligned

360    reads by map quality score (minimum of 20) and removed duplicates using SAMtools v0.1.19

361    (Li and Durbin, 2009). We assessed aDNA damage patterns using mapDamage v2.0.9 (Jónsson

362    et al., 2013). To infer the genomic sex of UAMES 29458, we followed the method of Heintzman

363    et al. (2017), which compares the relative mapping frequency of the X chromosome to the

364  autosomes. A male is inferred if this ratio is 0.45-0.55, whereas the expectation for a female is

365  0.95-1.05.

366     We mapped the filtered reads from the enriched library to a steppe bison reference

367  mitochondrial genome (Genbank: KX269138) using the multiple iterative assembler (MIA;

368  Briggs et al. 2009) and BWA, as above. For aDNA damage assessment of the enriched data, we

369  used the BWA mapping consensus results as the reference sequence for mapDamage. We

370  calculated a mitochondrial genome consensus sequence from the MIA mapping results using the

371  criteria outlined in Froese et al. (2017), and added this sequence to the full mitochondrial

372  genome alignment of Froese et al. (2017), as modified by Zazula et al. (2017). This alignment

373  consisted of four yak and 47 Siberian or North American bison mitochondrial sequences.

374     Before estimating the age of UAMES 29458 with Bayesian time-tree methods, we tested

375  for temporal signal in the data set. Tip-dating methods are only valid if this signal is present, as

376  these methods will usually converge on an estimate whether or not there is a temporal signal

377  present (Firth et al., 2010). We used a linear regression of phylogenetic root-to-tip distance

378  against the sampling date to test for temporal signal (following Murray et al., 2016). We

379  estimated a neighbor-joining tree of the data set (excluding the yak and two radiocarbon non-

380  finite bison sequences) using a K80 nucleotide substitution model with pairwise deletion, using

381  the ape package in R (Paradis et al., 2004), in which the root was fit simultaneously with the

382  regression, so as to minimize the residual mean squares, with the resulting root matching the root

383  obtained by using the yak sequences as an outgroup. Analyses of the full alignment and a

384  reduced alignment, with MS022 omitted (see below), returned positive correlations that are

385  significantly different from random permutations over clusters of samples with similar dates

386  (full: r = 0.50, p = 0.010; reduced: r = 0.44, p = 0.025; Figure S3). We defined similar-date

387  clusters (n=34-35) as monophyletic clades that had the same date after rounding to the nearest

388  thousand years. A Mantel test suggested that this clustering was sufficient to eliminate a

389  correlation between genetic and temporal distances in the data (without clustering: p = 0.001,

390  with clustering: p = 0.18) (Murray et al., 2016), which can result in a false positive result.

391  Overall, these analyses suggest the presence of temporal signal in the bison mitochondrial

392  genome data set.

393     We then estimated a time-tree in BEAST (v1.10.4, Drummond et al., 2012) so as to

394  estimate both the age of UAMES 29458 and its placement in the bison mitochondrial genome

395   phylogeny. We used a strict molecular clock with either finite radiocarbon dates or stratigraphic

396   data associated with the other sequences in the analysis as priors, following Froese et al. (2017)

397   and Zazula et al. (2017). To estimate the age of UAMES 29458, we used a uniform prior

398   distribution of between 30 kya BP (as this specimen is borderline radiocarbon finite; see results)

399   and 195 kya BP (the earliest mitochondrial estimate for the arrival of bison in North America;

400   Froese et al., 2017), following the method of Shapiro et al. (2011). To test the robustness of the

401   oldest age estimates, we also ran analyses with the minimum age prior set at 0, 20, 40, or 50 kya

402   BP. We ran analyses with each set of priors twice, each time with the Markov chain Monte Carlo

403   (MCMC) chains run for 60 million iterations, sampling every 3,000 iterations, and discarding the

404   first 10% as burn-in. Using Tracer v1.6, we observed that all parameters reached convergence

405   with the exception of the tree likelihood, which swapped between two optima in all analyses.

406   This was due to the shifting placement of sequence MS022 (KX269130; Froese et al., 2017).

407   This sequence was therefore removed from the alignment and all analyses were re-run.

408   Convergence was then observed for all parameters. For each prior and alignment result set, we

409   summarized trees and calculated a maximum clade credibility tree. All ages are reported as 95%

410   highest posterior density (HPD) credibility intervals.

411

412   **3. Results:**

413

414   *3.1 Physical description:*

415

416   Overall, we observed specimen UAMES 29458 to be relatively complete and well preserved

417   (Figure 2). Based on the observed number of annual growth cycles visible in the horn sheath, we

418   estimated the bison specimen to be minimally 12 years old, which is considered a mature

419   individual (Fuller, 1959). The specimen's horn span was 90 cm at the widest point and the

420   comparative angle and length of the horns indicate that it was a male (Guthrie, 1966). Much of

421   the hair had sloughed off the specimen and was found in the surrounding sediment. In some

422   areas, hair and skin had dried to the bone and were still attached. Hair from the front and hind

423   limbs was yellow ochre in color, as were the shorter undercoat hairs from the body. The longer

424   hairs were a reddish-brown or dark brown and tail hairs were black to dark brown. Long hairs

found in the surrounding sediment, which likely came from the cape (hair on the shoulders), beard (long hair on the chin) or cap (long hair on the top of the head), were light to dark brown.

The skull was in excellent condition and the left and right mandibles were fused at the symphysis. The incisors were missing from a pre-burial break. There were no gnaw marks on the surrounding bone to indicate another animal had gnawed them off. Evidence of root etching was observed on the ventral surfaces of the mandible with vivianite deposits observed on the articular surface. Vivianite was identified visually, it is commonly found on fossils found in these environments, and is unique in its blue appearance. We observed that the cervical vertebra 2 (C2) through thoracic vertebra 7 (T7) had the dorsal portion of the spinous process gnawed (Figure 3b) and bitten off (Figure 3a). We also observed T4 and T5 had evidence of damage from a carnivore, including puncture marks (Figure 3 a). Lumbar vertebra 1 (L1) to the sacrum also had evidence of carnivore damage on the ventral surface of the vertebrae (Figure 3 b). The distal ends of four thoracic ribs (towards the anterior portion of the body) also had puncture marks and gnawing. There were several pre- and post-burial breaks, and several medial portions of the ribs were missing. One rib on the right side had a pathology consistent with a healed break (Figure 3c). The left side was missing two thoracic ribs. The costal cartilage had carnivore gnawing damage on two fragments and the manubrium was missing one section.

The right appendicular skeleton was complete and we observed no evidence of carnivore damage. In addition, there was soft tissue (keratinous hoof sheathes, leather-like flesh and connective tissue) and vivianite present. There were gnaw and puncture marks observed on the proximal end of the left humerus (lateral tuberosity) near its articulation with the scapula; the scapula was missing. There was root etching on the medial surface of the humerus where it would have rested on the ground after the specimen's death and we observed soft tissue adhering to the bone. The left metacarpal, carpals, and proximal, medial, and distal phalanges were missing, which could be consistent with loss during taphonomic processes upon emerging from the riverbank because the bones would have been exposed first and eroded out of the bank. In addition to the lack of carnivore marks near the articulations, they do not possess much food value for a carnivore and would not have been a primary target. On the left femur there was a pre-burial break at the greater trochanter, but no obvious carnivore damage. The left patella, calcaneus, several left tarsals, one sesamoid, one proximal, medial and distal phalanx was

455    missing, which is also consistent with secondary loss upon the specimen eroding out of the

456    riverbank.

457

458    *3.2 Radiocarbon analysis:*

459

460    We generated three new radiocarbon dates associated with specimen UAMES 29458 (Table 1).

461    The background-subtracted fraction modern values for both the keratin and insect chitin are

462    different from zero by ~6 standard deviations, which indicates the ages are finite. The age of the

463    keratin from the bison horn sheath was $46,000 \pm 1,100$ $^{14}$C yr BP (46,962 cal yr BP using CALIB

464    7.1; (Stuiver et al., 2019)), which was very similar to the radiocarbon date produced from the

465    keratinous fly puparium (Table 1 , Figure 4) taken from inside the bison skull cavity ($46,800 \pm$

466    $1,200$ $^4$C yr BP, just outside the range for calibration using CALIB 7.1 (Stuiver et al., 2019). The

467    dated plant macrofossil found in the skull, along with the puparia, had a radiocarbon date of

468    >49,900 radiocarbon years, which was outside the range for calibration (Table 1).

469

470    *3.3 Macrofossils:*

471

472     *3.3.1 Fossil plant remains*

473

474    The contents of the neural canal of the spine and skull from specimen UAMES 29458 included a

475    sand-rich matrix with abundant moss, wood, and we could identify other plant fragments to

476    species in some instances (Figures 4 and 5). The plant macrofossil assemblage from inside the

477    skull is consistent with a mesic tundra or a wet flood plain surrounded by a shrub tundra (Figure

478    5). The presence of *Daphnia* spp. ephippia indicate that the sediment was also, at least partially,

479    aquatic in origin. Bryophytic material, likely from wet tundra and rivers, was abundant and well

480    preserved in the skull cavity. Wood was very common and possibly came from the shrubs

481    identified from seeds, leaves, and other materials in the skull cavity, including *Salix* spp.

482    (willow), *Betula* spp. (birch), and *Andromeda polifolia* (bog rosemary) (Figure 4 n). These

483    shrubs are typical of wet tundra and tend to be more abundant in more protected areas (Cody,

484    2000; Hulten, 1968), suggesting an interstadial environment. In addition, *Potentilla palustris* and

485    *Juncus* spp. were also present and are typically associated with riparian habitats and bogs (Cody,

486    2000). In contrast, the remains of *Papaver* spp. (poppies) and *Polygonum bistorta* (Figure 4 l),

487    which favor drier open slopes (Hulten, 1968), were also present in the bison skull cavity. The

488    largest number of plant macrofossils from the skull cavity was the mustard and *Draba*-type seeds

489    (Figures 4 m and 5), which are from a large and very diverse family making it difficult to use

490    these specimens to characterize paleoecological conditions (Cody, 2000; Hulten, 1968).

491    However, many of the species from this group are typical of open slopes, gravel and/or sandy

492    river banks (Cody, 2000). In addition, there is a portion of grasses (Poaceae) (Figure 4 k) (and

493    *Carex* Figure 4 i and j) that are typical of tundra or steppe ecosystems in the Arctic, and are

494    consistent with an open landscape with no large shrubs (Hulten, 1968). The burial occurred in a

495    time scale that prevented lots of skeletal disarticulation by scavengers but allowed some

496    activities by insects in an energy regime allowed deposition of sand but not coarser sediment.

497

498    *3.3.2 Fossil insect remains*

499

500    Analysis of the skull cavity of UAMES 29458 revealed the presence of insect remains, including

501    complete or incomplete blowfly puparia (Calliphoridae) (n = 15, UAMES 52319-52330). From

502    their excellent state of preservation, a determination at the species level was possible and the

503    taxon that colonized the bison at the time of its death was identified as the northern blowfly

504    *Protophormia terraenovae* (Robineau-Desvoidy) (Figure 4 a-e). With the exception of 4

505    fragmentary specimens, all the puparia were complete and unhatched indicating that the life

506    cycle was interrupted before adult emergence. An attempt to open two fossil puparia (#29458c,

507    (#29458g), in order to find a possible nymph and to observe its maturity stage, proved

508    unsuccessful since the pupa had disintegrated inside.

509        Partial abdomen remains of a carabid beetle (Pterostichinae: cf. *Pterostichus* sp.) were

510    also found inside the skull (UAMES 52334; Figure 4 f). Thirty-five *Pterostichus* species occur in

511    Alaska (Bousquet et al., 2013). Some representatives of this genus (i.e. *Pterostichus costatus*

512    Ménétriés), live in the damp peaty areas of lowland tundra regions (Lindroth, 1966). Other insect

513    remains belonging to several distinct orders were also recovered from inside the skull: a

514    complete wing of Psylloidea (Homoptera) (UAMES 52331; Figure 4 g); a cephalic capsule of a

515    larval Chironomidae (Diptera), an incomplete elytron of Elaphrinae (Coleoptera, Carabidae)

516    (UAMES 52332; Figure 4 h) and finally, some disarticulated coleopteran remains, too

17

517     fragmented to be identified. The presence of a psylloidean species in this context is not

518     surprising since fossil remains of the three main plants (*Salix*, *Betula*, *Polygonum*) exploited by

519     these insects were preserved evidenced within the skull cavity of the bison. The larval stages of

520     chironomids develop in almost any aquatic or semiaquatic habitat, both standing and flowing

521     waters, but also occur in tree-holes, rotting vegetation, and damp soils. Finally, the presence of

522     *Elaphrus* sp. (*cf*. *trossulus* Semenov) (UAMES 52333; Figure 4 h), another ground beetle, is

523     recorded. The species belonging to this genus are representative of riparian communities. Adults

524     of all species of *Elaphrus* live along rivers, small streams, swamps, sloughs, or bogs, which is

525     fully consistent with the bison discovery site. Overall, these taxa are typical of mesic to wet

526     tundra habitats at the time of burial.

527

528     *3.4 Isotopic analyses:*

529

530     The $\delta^{13}$C and $\delta^{15}$N values from the collagen sample were -20.0 ‰ (±0.6) and 4.2 ‰ (±0.1),

531     respectively. The $\delta^{13}$C value is consistent with a diet of vegetation consists of plants using $C_3$

532     photosynthesis in a relatively open environment (Drucker et al., 2008). The $\delta^{15}$N value is

533     consistent with values from other bison specimens dated to interstadial conditions, and contrast

534     with stadial conditions, which can have higher values (Hedges et al., 2004; Rabanus-Wallace et

535     al., 2017). Based on an 8-10 year collagen turn-over rate (Hedges et al., 2007), the collagen

536     would exclude the higher $\delta^{15}$N values from this individual's early life based on analyses of the

537     horn sheath (described below), and thus the bone collagen and horn can be considered in the

538     same range. The mean horn keratin $\delta^{13}$C value was slightly lower than the collagen values (mean

539     $\delta^{13}$C value -21.3 ‰ ±1.1; -20.0 ‰ respectively), which is consistent with the difference in

540     fractionation factors associated with the two different tissue types (keratin Δ=3.1 ‰ ±0.3;

541     collagen Δ=5.1 ‰ ±0.3 (Drucker et al., 2008)).

542         The mean $\delta^{15}$N value from analyses of the horn keratin (4.6 ‰ ±1.1) was similar to the

543     $\delta^{15}$N value from the collagen value (4.2 ‰ ±0.1). The periodicity of the isotopic fluctuations in

544     the horn sheath (Figure 6) appears to reflect annual cycles because the number of oscillations (n

545     = 11) is consistent with the number of observed annual growth layers observed from the horn

546     (11-12). The first two oscillations (~2 years) likely correspond with the period covered by the

547     tooth record (~2.5 years) from the same specimen (described below). These apparently annual

548 fluctuations would be consistent with the peaks in $\delta^{15}N$ values reflecting a seasonal shift to
549 greater nutritional stress and a more water-limited plant diet during the winter 2020). Shortly
550 before the death of the bison, the $\delta^{15}N$ values from the horn sheath increases (Figure 6), which
551 would correspond with a transition from summer to winter that is observed in modern bison from
552 Alaska (Funck et al., 2020), indicating the bison may have died in the late summer/early fall.
553 Two peaks in the $\delta^{15}N$ values from the horn sheath occurred towards the start of the life of the
554 bison and the second of these corresponds with a decrease in $\delta^{13}C$ values from the horn sheath.
555 These features are consistent with periods of nutritional stress (Funck et al., 2020). Most notably,
556 this pattern seems consistent with catabolism and the use of lipid reserves respectively (Funck et
557 al., 2020). A marked decrease in $\delta^{13}C$ values is evident in the year prior to the bison's death,
558 which also seems consistent with the use of the animal's lipid reserves (Funck et al., 2020).
559      The results of the $^{87}Sr/^{86}Sr$ ratio analyses (n = 33) from specimen UAMES 29458 (Table
560 2), with an analytical precision of 0.00001, show a mean $^{87}Sr/^{86}Sr$ ratio from the first molar (M1)
561 of 0.71139 ($\pm$0.00028). These values are consistent with the rodent teeth values from the Arctic
562 Coastal Plain, which range from 0.70940 to 0.71107 (Table 3, Figure 7). The mean $^{87}Sr/^{86}Sr$ ratio
563 from the M2 was higher compared to the values from the M1 ($p < 0.000$, t.test), averaging at
564 0.71206 ($\pm$0.00025). The mean $^{87}Sr/^{86}Sr$ value from the M3 was 0.71308 ($\pm$ 0.00008) and was
565 higher than the values from both the M1 and M2 ($p < 0.000$, t.test). The range of the M3 values
566 was similar to the values found from the modern rodents found in the foothills of the Brooks
567 Range mountains (Table 3) (from 0.7137 to 0.7205) (Figure 8). Based on the bedrock $^{87}Sr/^{86}Sr$
568 model (Bataille and Bowen, 2012), the expected $^{87}Sr/^{86}Sr$ ratio at the place of death of specimen
569 UAMES 29458 was ~0.70982 (Figure 8). Overall, the M1, M2 and M3 sequential data show a
570 marked increase in $^{87}Sr/^{86}Sr$ ratios throughout the tooth sequence ($p < 0.000$, ANOVA) (Figure
571 7).
572      The mean $\delta^{18}O$ value across all teeth samples from specimen UAMES 29458 (n = 30)
573 was -21.1 ‰ ($\pm$0.4) vs. VPDB (with an analytical precision of 0.2 ‰) (Table 4). Values were
574 highly variable across the M1-M3 sequence (Figure 7) ranging from -18.4 ‰ to -26.5 ‰, but
575 were not significantly different between teeth ($p = 0.34$, ANOVA). The values appear to cycle
576 through approximately two full years, with three peaks representing summers, which seasonally
577 have higher $\delta^{18}O$ values (Velivetskaya et al., 2016) and separated by two cooler periods with
578 lower values (Figure 7).

579         The mean $\delta^{13}C$ value of the enamel calcium carbonate from the teeth of specimen

580 UAMES 29458 was -11.0 ‰ (±2.0) (with an analytical precision of 0.03) and had a relatively

581 small range of values (-10.3 ‰ to -11.7 ‰) (Table 4), which are consistent with a $C_3$ diet.

582 Typical values for $C_3$ plants are ~-27 ‰ (Wooller et al., 2007) and the difference between animal

583 diets and tooth calcium carbonate is $\Delta+14.6$ - (Cerling and Harris 1999; Passey et al. 2005).

584 Overall the $\delta^{13}C$ values started at their lowest during early life (M1) and gradually became higher

585 in the M2 (-11.1 ‰ ±0.2) and M3 (-10.5 ‰ ±0.1) ($p < 0.000$, ANOVA), a trend that appears to

586 correlate with the temporal shift from lower to higher $^{87}Sr/^{86}Sr$ ratios from the same teeth (Figure

587 7).

588

589 **_3.5 aDNA analyses:_**

590

591 We generated 1.15 million reads from the unenriched library of UAMES 29458 (raw reads

592 available at the NCBI Short Read Archive under BioProject PRJNA61324),which had an

593 endogenous DNA content of 15.4% based on reads aligning to the cow genome. The relative

594 mapping frequency ratio between the X chromosome and autosomes was 0.528, with a range of

595 0.493-0.561 across all 29 autosomes (Table 5). This is consistent with UAMES 29458

596 representing a genomic male individual.

597         A full mitochondrial genome (JK319) was generated from the enriched library, with an

598 average coverage of 139× (Genbank: MN549280). The phylogenetic placement of the UAMES

599 29458 mitochondrial genome was marginally impacted by the minimum age prior used, and was

600 found either to fall at the base of Clade 2 (prior of 50 kya BP) or to be sister to MS002 within

601 bison mitochondrial Clade 2 (all other tested priors) (Figure 9, Table 6). The inclusion or

602 exclusion of MS022 did not affect the phylogenetic placement of UAMES 29458. Across all

603 analyses, the age of UAMES 29458 was estimated to be ~33-87 kya BP (Table 6). Analyses with

604 MS022 excluded generally yielded slightly older age estimates, but varying the minimum age

605 prior did not greatly impact this individual's maximum estimated age (range of ~81-87 kya BP

606 across all analyses). This suggests that the priors did not drive the estimated age results.

607         Mapped reads from both the unenriched (primarily nuclear) and enriched (mitochondrial)

608 DNA libraries exhibit damage patterns characteristic of authentic aDNA, including short DNA

609 fragments and elevated relative deamination frequencies at the ends of reads (Figure S4).

610

**4. Discussion:**

611

612

*4.1 Constraining a chronological age for UAMES 29458:*

613

614

Specimen UAMES 29458 provides several lines of evidence that can be used to constrain the

615

individual's chronological age (Figure 11). The radiocarbon dates from the keratin and the blow

616

fly puparium (chitin) are nearly identical (46,000 ±1100 ^{14}C yrs and 46,800 ±1200 ^{14}C yrs –

617

inside and outside the range for calibration, respectively). Keratin is a structurally dense tissue

618

and less susceptible to contamination than collagen (Taylor et al., 1995). The blow flies *P*.

619

*terraenovae*, which colonizes a corpse within hours or days following death, seemed a good

620

candidate for precise ^{14}C dating of specimen UAMES 29458. The congruence of the keratin and

621

chitin ^{14}C dates lends support for a finite age of approximately 46,900 ^{14}C yrs. In contrast, the

622

radiocarbon dates from collagen and from plant material are non-finite. Collagen, from porous

623

bone material, can be contaminated or degraded. The sample from the bone of UAMES 29458

624

was also run on a lower energy ^{14}C instrument, which cannot discriminate low levels of ^{14}C from

625

old samples compared with the chitin and keratin, which were run on a more powerful

626

instrument. The radiocarbon date of the plant material and its apparent older age compared to the

627

puparium and keratin is difficult to interpret. The plant material recovered from the skull was

628

specifically selected because it was a delicate herbaceous structure that would not have

629

experienced substantial reworking or be influenced by variations in carbon sources that can

630

occur in aquatic plants (Marcenko et al., 1989). However, the radiocarbon date of the plant was

631

determined to be non-finite (>49,000) and could have been reworked from older sediments.

632

Given that the dates from keratin and chitin are on the margins of radiocarbon limits we must

633

consider two possibilities; first, that the finite dates are accurate, or second, that these dates are

634

not distinguishable from non-finite dates.

635

Other evidence supports the hypothesis that UAMES 29458 dates are finite in age.

636

Environmental information from the $\delta^{18}O$ values from the bison specimen and plant macrofossils

637

add further dimensions that help constrain the chronological age estimation for UAMES 29458.

638

The mean $\delta^{18}O$ value (as VSMOW) from analyses of the bison's molars is -3.9 ‰ (±1.2) lower

639

than the mean modern precipitation values. In contrast, full stadial $\delta^{18}O$ values for precipitation

640

tend to be around -8 % lower than modern precipitation values (Bowen, 2018; Gaglioti et al., 2017; Meyer et al., 2010; Rasmussen et al., 2014). The $\delta^{18}O$ values from UAMES 29458 therefore indicate that although the climate was slightly colder than modern it was not full stadial (Figure 11). The finite radiocarbon date from the keratin coincides with a period of time that had an offset in $\delta^{18}O$ values of $\Delta$ -3.9 ‰ (±1.2), between 44,380 cal yrs BP and 46,880 cal yrs BP (Rasmussen et al., 2014). This inference that the bison specimen may have lived during a more moderate (interstadial) climate is also supported by the plant macrofossils and insect remains found in the skull, which represent a typical flood plain in tundra ecosystems of the Arctic. However, as stated above, the plant remains may not be exactly contemporaneous with the specimen.

The Bayesian molecular age estimate for the specimen was between ~33-87 kya BP, which is consistent with the radiocarbon ages and corresponds to Marine Isotope Stage (MIS) 3 through to MIS 5b (Lisiecki and Raymo, 2005). Although the results of this analysis are not informative as to whether UAMES 29458 is of older radiocarbon finite or non-finite age, they do suggest that, if the individual were radiocarbon non-finite, it lived after MIS 5e. The finite radiocarbon age from the bison's keratin is within the range of this molecular-clock derived age estimate, which could narrow the age estimate to within MIS 3 (29-57 kya BP). Our phylogenetic analyses show that UAMES 29458 belonged to bison mitochondrial clade 2 (Heintzman et al., 2016). This lineage did not contribute to extant bison diversity, and instead became extinct during the late Holocene, by as long as ~400 years ago (Heintzman et al., 2016; Shapiro et al., 2004). Given the varied methods used for dating this specimen, it is expected that there might be some disagreement between results. However, the two nearly identical dates from the chemically stable portions associated with the specimen (i.e. keratin and insect chitin, 46,000 ±1100 ^{14}C yr BP and 46,800 ±1200 ^{14}C yr BP, respectively) provide support for this as a finite-aged specimen very close to the limit of radiocarbon dating. This age is congruent with an appropriate climatic period suggested by the $\delta^{18}O$ values (Figure 11) and the macrofossil assemblage of flora.

*4.2 Life history of an individual steppe bison:*

671    Multiple lines of evidence suggest that specimen UAMES 29458 was a large bull that was 11 to

672    12 years old at the time of death. Present-day male bison of this age are typically lone bulls,

673    either in or just past their prime (Maher and Byers, 1987; Soper, 1941). During his life, this

674    individual incurred injury to a rib and the bone callous clearly indicates it healed (Figure 3c).

675    This type of injury typically occurs in present-day bison during the rut when bison compete for

676    access to females (Lott, 1971). In addition to this evidence of injury, the early stages of this

677    bison's life, recorded as the $\delta^{15}N$ values from the horn sheath (Figure 6), could indicate some

678    periods of nutritional stress. Increases in $\delta^{15}N$ values in the tissues of bison can represent

679    stressors, such as starvation, illness, or long-distance movement (Funck et al., 2020). Shifts in

680    $\delta^{15}N$ values are generally used to determine changes in the trophic level (Post, 2002), an

681    interpretation that is not appropriate for a herbivore, except during breast feeding when an

682    juvenile is essentially a trophic level above their mother (Gadbury et al., 2000; Reitsema and

683    Muir, 2015). However, during nutritional stress, such as a hard winter (Funck et al., 2020) or

684    nutritional transition like weaning (Fuller et al., 2003), an animal can break down its muscles to

685    build new proteins, during which tissues fractionate and lead to elevated $\delta^{15}N$ values (Lee et al.,

686    2012). The bison specimen analyzed here exhibited two periods of elevated $\delta^{15}N$ values towards

687    the start of its life (Figure 6). Horn stubs begin developing in utero but do not solidify into horn

688    spikes until the calves are older (Wiener et al., 2015). The two periods of higher $\delta^{15}N$ values

689    likely occurred in the first 2-3 years of life, overlapping with some of the time periods

690    represented by the molar development, which was used to produce the $\delta^{18}O$ values and $^{87}Sr/^{86}Sr$

691    ratios. This allows us several lines of evidence for interpreting what early life was like for this

692    bison.

693         The interpretation of intra-tooth serial samples as a measure of change over time requires

694    an understanding of how teeth develop and mineralize. For example, the molars of bison have

695    been shown to grow over 2 to 2.5 years (Gadbury et al., 2000; Higgins and MacFadden, 2004;

696    Velivetskaya et al., 2016) and the pattern of molar eruption occurs in a particular sequence and

697    time in an animal's life. As each molar develops, discrete layers of enamel are laid down and

698    retain the isotopic composition of conditions at each point in time. However, as a tooth develops

699    it continues to mineralize over 6 to 7 months leading to a degree of isotopic averaging (Balasse,

700    2002; Montgomery et al., 2010). As a result, changes that may appear progressive could in fact

701    occur over much shorter periods of time and the exact timing of tooth development and

702  mineralization can be subject to some degree of variation between individuals and species.

703  However, Velivetskaya et al. (2016) used high-resolution sampling for analysis of $\delta^{18}O$ values to

704  pinpoint the timing of tooth development in two late-Pleistocene steppe bison from the Middle

705  Urals, Russia and found it to be close to those of present-day bison. Seasonal oscillation in $\delta^{18}O$

706  values can also be compared to those of present-day animals to track the speed of tooth

707  development.

708  The M1 is formed in utero and shortly after birth (Bernard et al., 2009; Widga et al.,

709  2010), and thus represents the mother's home range and the calving grounds. The M1 formation

710  likely corresponds with the timing of the first $\delta^{15}N$ value peak (Figure 6). The $^{87}Sr/^{86}Sr$ ratios

711  from the M1 had less variation than the M2 suggesting the mother remained in a relatively

712  consistent geological area. When the M1 $^{87}Sr/^{86}Sr$ ratios are compared to bioavailable $^{87}Sr/^{86}Sr$

713  ratios from the region, it appears that this bison began life on the Alaska coastal plain (Figure 8).

714  Contemporary caribou from similar regions of Alaska currently use the coastal plain as calving

715  grounds, taking advantage of the emerging graminoids and open terrain (Fancy et al., 1990; Post

716  and Forchhammer, 2008). Subsequently, they move to higher ground to avoid insects and to take

717  advantage of abundant lichens that sustain them during non-calving seasons (Fancy et al., 1990).

718  Bison calves are dependent on milk for the first ~5 months and gradually stop suckling over 9-21

719  months (Green et al., 1993). So the first peak in $\delta^{15}N$ values from the horn (Figure 6) likely

720  corresponds to this M1 period and could be interpreted as a maternal/weaning signal (Gadbury et

721  al., 2000; Reitsema and Muir, 2015), either attributed to the bison being at a higher trophic level

722  than its mother from which it was nursing, or the effect of weaning and the nutritional stress that

723  it may have imparted (Fuller et al., 2003).

724  After the period of initial relative geographic stability inferred from the $^{87}Sr/^{86}Sr$ ratios in

725  the M1, which likely represented the first half-year of life, the bison seems to have dispersed into

726  a new geographic area during its second summer according to the $^{87}Sr/^{86}Sr$ ratios from the M2

727  and M3. The M2 development starts at ~2 to 3 months of age and continues for 12-15 months

728  (Gadbury et al., 2000; Velivetskaya et al., 2016). The M3 subsequently develops from the

729  beginning of the second summer after weaning, ~10-11 months until the age of about 2 to 2.5

730  years (Gadbury et al., 2000; Velivetskaya et al., 2016). Comparisons of the bison's $^{87}Sr/^{86}Sr$

731  ratios from the M2 and M3 to bioavailable $^{87}Sr/^{86}Sr$ ratios from the region indicate that the bison

732  may have moved into the foothills of the Brooks Range (Figure 1 and Figure 8). The second peak

733   in $\delta^{15}$N values from the analyses of the horn sheath (Figure 6) could correspond to mobility on

734   the landscape, which seems to have occurred during this period. A study on present-day wood

735   bison in Alaska (Funck et al., 2020) found that bison that traveled long distances, or experienced

736   nutritional stress, produced elevated $\delta^{15}$N values due to the energetic costs of travel. The horn

737   $\delta^{13}$C record begins relatively low shortly before this point, which could be related to the bison

738   beginning to draw on the bodies lipids which have lower $\delta^{13}$C values (DeNiro and Epstein, 1977;

739   Rode et al., 2018). This offset follows the same pattern found in a modern wood bison

740   experiencing a dispersal related dietary stress (Funck et al., 2020). In the present study, the tooth

741   carbonate $\delta^{13}$C values show an overall increase (+1 ‰) during this same period (~2.5 years),

742   consistent with a change from a wetter environment to a drier one (Wooller et al., 2007), which

743   also seems to correspond with a shift towards the higher and drier elevations of the foothills

744   compared to the wetter, lower reaches, of the coastal plain. Later in the bison's life, after the

745   record preserved in the molars is fully mineralized (~2.5 years), we lose track of the specimen's

746   geolocation based on the $^{87}$Sr/$^{86}$Sr record. However, this bison must have eventually returned to

747   the coastal plain to the location where he eventually died and was found (Figure 1).

748         In contrast to the tooth record, the horn sheath continues to develop over approximately

749   the lifetime of the individual. The $\delta^{15}$N fluctuates through what appear to be seasonal oscillations

750   of slightly more elevated $\delta^{15}$N values in the winter, likely due to nutritional stress during this

751   season, then lower $\delta^{15}$N values during more favorable summers, interpreted based on isotopic

752   patterns exhibited in present-day bison from Alaska (Funck et al., 2020). Present-day wood bison

753   south of the Brooks Range in Alaska only had changes in $\delta^{15}$N values during particularly hard

754   winters (Funck et al., 2020). Thus, these winters were likely harder than the conditions

755   experienced by present-day analogous populations. Applying this seasonal pattern implies that

756   the sample closest to the horn core (i.e. the period leading to the animal's death) represented the

757   start of the transition from the summer to winter. This indicates that the bison was not

758   experiencing unusual nutritional stress and did not appear to have been in a weakened state prior

759   to death. Other potential causes for changes in $\delta^{15}$N values in herbivores could include changes

760   in the seasonal $\delta^{15}$N values of forage and seasonal movement to regions with very different

761   baseline $\delta^{15}$N values. Our data indicates that this bison individual did move substantially across

762   the landscape. However, the tooth record of paleomobility is not long enough to cover the longer

763   record represented by the horn sheath data.  We find that our interpretation of the $\delta^{15}$N values as

764 a marker in terms of changes in the degree of nutritional stress is in some ways supported by the

765 $\delta^{13}C$ data from the horn sheath. For example, the low $\delta^{13}C$ values from the horn sheath in the last

766 year of life, relative to the rest of the record from the horn, could indicate that the animal may

767 have begun to draw on its lipid reserves (Funck et al., 2020). Although in some animals these

768 isotopic shifts occurs only at extreme thresholds of starvation this is a more common strategy in

769 animals that have large fat and muscle reserves for winter use, such as bison (Funck et al., 2020).

770 The degree of mobility of the bison specimen analyzed, based on the $^{87}Sr/^{86}Sr$ ratio data

771 from the North Slope specimen, is relatively high compared to data from other ancient and

772 present-day bison (Figure 10, Table 7; Britton et al., 2011; Glassburn, et al., 2015; Julien et al.

773 2012; Widga et al., 2010). Although the range of $^{87}Sr/^{86}Sr$ ratios cannot be directly compared,

774 because variability is highly dependent on the geological heterogeneity of a landscape that

775 individuals inhabit it is worth considering this bison in the context of others analyzed using the

776 similar methods. Britton et al. (2011) examined a single bison from western France dating to

777 49,000 ±5000 BP and demonstrated high fidelity to an area, with almost no variability in

778 $^{87}Sr/^{86}Sr$ ratios despite a variable geological environment. Julien et al. (2012) found that steppe

779 bison from the Last Glacial Maximum (LGM) (~20.5 kya BP) in Amrosievika in Eastern

780 Ukraine had a $^{87}Sr/^{86}Sr$ range of 0.00074 (Julien et al., 2012). This range was attributed to the

781 low degree of variability to minimal mobility on the landscape because there was no signals from

782 mixed geology as close as 20 km to the south-west of the site where the bison were found (Julien

783 et al., 2012). A study of bison herds on the Great Plains of North America from the Middle

784 Holocene indicated that bison also had limited seasonal mobility (<50 km), while inter-annual

785 movement of herds over ~4-5 yrs moved further afield (<500 km) (Widga et al., 2010a). In

786 contrast, present-day *Bison bison* from the interior of Alaska, with an observed seasonal and

787 regional migration route of about a 100km, had a $^{87}Sr/^{86}Sr$ ratio range from 0.71714 to 0.71540

788 (0.00174) (Glassburn et al., 2018). Although these regions and studies cannot be quantitatively

789 compared because of difference in local geology (Bataille et al., 2020) we can still draw some

790 qualitative comparisons. The variability in $^{87}Sr/^{86}Sr$ ratio ranges among bison from different

791 localities and periods suggests that bison utilize different mobility strategies that are dependent

792 on (paleo)ecological conditions. The range of $^{87}Sr/^{86}Sr$ ratio variation from the North Slope bison

793 specimen analyzed here (0.00237) is relatively large compared to all these previous measures,

794 indicating that he was likely a gregarious individual who traveled some distance during his early

795    years of life. There is a large geological range in this region (Bataille et al., 2020) that this bison

796    appears to be utilizing. Future research could integrate genetic testing of sex from specimens to

797    determine if males and females used different mobility strategies.

798

799    *4.3 Necrology and Biostratinomy:*

800

801    Evidence from the specimen UAMES 29458 helps shape a paleoecological picture leading up to

802    the individual's death, decomposition, and the mechanism of burial. The bones from the bison

803    specimen were overall in a state of excellent preservation as evidenced by the presence of intact

804    horn, hooves, fur, spinal cord, cartilage, and possible brain tissues. Specimens of this level of

805    completeness are extremely rare in Quaternary deposits. There were no obvious signs of the

806    cause of death, such as bite marks around the nose or neck, and all carnivore marks were related

807    to scavenging (Andersson et al., 2011) but predation cannot be ruled out. After death, the

808    specimen came to finally rest on his right side, which protected that side from scavenging, this is

809    further supported by the presence of vivianite. Vivianite deposits tended to be on the bone

810    surfaces that were exposed to the ground surface and root etching also tended to be present on

811    the surfaces of the bones that rested on the ground (Supplemental data).

812          Carnivore tooth marks are present at various locations on the specimen, indicating

813    scavenging of the bison carcass occurred post mortem (Figure 3 a and b and Supplemental data).

814    There are four major carnivore taxa present contemporaneously that could cause the type of

815    damage seen on UAMES 29458: *Arctodus simus* (short-faced bear), *Canis Lupus* (wolf),

816    *Homotherium serum* (scimitar cat), and *Panthera atrox* (American lion) (Fox-dobbs et al., 2008;

817    Schubert, 2010). The dentition marks (Figure 3) were consistently narrow punctures, which are

818    not consistent with the wide teeth of *A*. *simus* (Sorkin, 2006) or *H*. *serum* (Ewald et al., 2018).

819    The incisor punctures indicated that the space between the canines is at least 6 cm apart (Figure

820    3a, which is consistent with *P*. *atrox* (Baryshnikov and Boeskorov, 2001; Christiansen and

821    Harris, 2010). This may be out of the range of the smaller *C*. *lupus* (Sorkin, 2006), leaving large

822    *felidae* as the most likely scavenger. Further analysis of dentition morphometrics in predator

823    species would be useful for this type of taphonomic analysis. Indication of lion scavenging have

824    also been found on other preserved bison specimens from in Alaska (Guthrie, 1989). It is likely

825    that only one individual scavenger caused all of the damage based on the consistency in size of

826   the tooth marks of the 14 tooth marks with punctures. The 11 instances of gnawing are less

827   diagnostic but also appear consistent. The limited scavenging also supports a single scavenger, as

828   more individuals would require less time to remove meat, disarticulate the corpse, and scavenge

829   from a greater area of the carcass (Blumenschine, 1986). The carnivore appears to have

830   consumed the bison carcass and ate portions of the backstrap (meat along the top of the spine)

831   based on observed damage along the spinous processes of several vertebrae (Figure 3 a and b).

832   The carnivore also seems to have consumed the carcass from the inside of the body and likely ate

833   the internal organs and tenderloin based on damage to the costal cartilage, the distal ribs, the

834   transverse processes of the lumbar vertebrae, and the sacrum. In addition, the carnivore gnawed

835   the left humerus and likely removed the left scapula, in an attempt to get at the flesh of the left

836   fore-limb. Scavenging only seems to have occurred in high-value areas, supporting an inference

837   that the carcass was likely buried rapidly. In most contexts a carcass on an open landscape with

838   carnivores can be consumed and disarticulated within hours to a few days (Blumenschine, 1986).

839   It is for this reason that complete specimens are extremely rare. Thus, for this specimen to

840   preserve, something exceptional must have occurred to protect it. During the erosion that re-

841   exposed the bison it seems the left extremities of the front and hind limbs (phalanxes, carpals,

842   tarsals, etc.) may have been lost due to erosional processes (Figure 2). These skeletal elements

843   would be the first to be exposed and vulnerable to gravity, weathering, and would have been

844   preferentially removed via taphonomic agents (e.g., eroded into the river and lost). These skeletal

845   elements of the lower extremities are also not associated with high food value flesh and likely

846   would not have been a target for scavenging.

847        The presence of the blow fly puparia recovered from inside the skull made it possible to

848   propose some "paleoforensic" hypotheses associated with postmortem events. Blow flies figure

849   among the most relevant witnesses in forensic entomology in order to determine the time elapsed

850   since death, namely the postmortem interval (PMI) because blow flies (Calliphoridae) are the

851   first and predominant organisms to colonize a body after death. Within hours of death, these

852   insects are attracted to the smell of the decomposing remains, which are both a site for laying

853   eggs and a source of protein for larval development. Under normal circumstances, egg laying

854   occurs soon after death (1–3 days) (Gomes et al., 2006). The favored egg-laying sites are the

855   natural openings of the body (mouth, eyes, anus) as well as any wounds present on the corpse

856   (Gomes et al., 2006). The species preserved on the carcass *Protophormia terraenovae* (Robineau

857 Desvoidy) is a Holarctic, cold-adapted species, present throughout northern Europe and Asia.

858 Very common in the cooler high latitude regions and notably in the Arctic, representatives of this

859 species are found within 890 km of the North Pole (Smith, 1986). Experiments conducted by

860 Marchenko (2001) found that the development period of *P. terraenovae* (from egg to adult) is

861 relatively long. According to Warren and Anderson (2013), egg-carrying females of *P.*

862 *terraenovae* do not lay eggs at temperatures lower than 10.3°C. In the North Slope region,

863 temperatures only reach above 10°C during the summer period (https://www.weatherbase.com).

864 Insects, like all arthropods, are coldblooded and the duration of their life-cycle is primarily

865 temperature driven. Rate of development is species-specific and influenced by biotic (e.g.

866 maggot mass that can significantly accelerate rate of development) and environmental factors

867 (exposure of the carcass to sunlight or shade, rain, and wind). Following the biological data

868 provided by Marchenko (2001), and focusing on temperatures ranging from 11 to 18°C

869 (respectively the average minimal temperature required for laying eggs and the current maximum

870 temperatures recorded on the paleontological site), *P. terraenovae* development extends from 15

871 to 50 days (egg to pupal stage) and adult emergence from 24 to 78 days. In the case of UAMES

872 29458, all of the puparia were intact with no evidence of adult emergence.

873    The fact that the bison's skeleton was almost complete and articulated, and not fully

874 scavenged by carnivores suggests that the fly pupal stage intervened fairly quickly, indicating

875 relatively high temperatures at the time of death (e.g., at 18°C, the pupal stage would have

876 started on the 15th day). The bison carcass was then quickly covered with sediment or snow

877 precluding further access to predators; however, a few centimeters of soil cover would not

878 prevent the development and emergence of flies (Balme et al., 2012). Trapped in the skull, the

879 pupae would have preserved in situ. The presence of unhatched fly puparia of *P. terraenovae*

880 recovered from the bison individual would suggest that its carcass had been subaerially exposed

881 for at least 2 weeks before the life cycle was interrupted either due to a more complete burial or

882 freezing. The fact that the carcass was little affected by scavengers over this period might be

883 explain by low scavenger density on site, high carcass availability or because the bison's remains

884 were only accessible to flying insects and not by terrestrial scavengers (e.g. carcass partially

885 exposed in river water). Finally, we can argue that the ambient temperature was very likely over

886 10°C when the fly infestation occurred, requiring the events to occur during a warm period of the

year. This warm period seems to have been at the transition from summer to winter, based on the isotopic evidence from the horn sheath.

Fluvial sediments including plant macrofossils likely entered the skull after this initial burial during which the *P. terraenovae* puparia developed. The plant macrofossils recovered from inside the skull and neural canal are unlikely penecontemporaneous with the death of this bison individual, but could indicate an overall glimpse of the surroundings. The macrofossil assemblage of plants is consistent with an Arctic flood plain. The immediate surrounding of the river was probably covered in moss, low shrubs, and bogs (Figure 5). Further away from the banks of the river were likely drier tundra with grasses, sedges, and a variety of tundra flowers including *Papaver* sp., *Polygonum bistorta*, and *Draba* type (Figure 5). Overall, the plant assemblage is more typical of a mesic tundra than a steppe and possibly originated from an inter-glacial or interstadial environment (Gaglioti et al., 2018).

Overall, we conclude that this bison died on a flood plain during the warm period prior to the onset of winter and fell on to its right side. A carnivore, possibly a large *felidae*, quickly consumed high-value areas of meat and blow flies swiftly laid eggs within the skull. Alluvial sediments or possibly snow then quickly buried the carcass before the carcass could be further disarticulated. At least two weeks passed before temperatures inside the carcass or the oxygen availability fell too low for the puparia to continue developing.

**5. Conclusion:**

Our multi-proxy paleoecological evidence from UAMES 29458 fills out the details of an individual bison's life and death in the Arctic, where bison were once a dominant herbivore. Combining serial isotope analyses with aDNA allowed us to combine mobility information with genealogical information, and to place the individual within bison meta-population dynamics over millennia. This augments a paleoecological picture based on the physical evidence of the skeletal remains alone, providing a more vivid image of a highly mobile individual moving across the North Slope of Alaska. The mitochondrial lineage of this bison is one that thrived in Beringia but ultimately died out. Our multiproxy evaluation indicates that this bison likely lived during an interstadial period, which in some ways may have been somewhat similar to today. Strontium isotope data from the specimen indicates that he dispersed across the Northern Alaska

918 landscape from possible calving grounds located on the Arctic coastal plain to the foothills of the
919 Brooks Range in early life and ultimately back to his place of death on the Arctic coastal plain.
920 Nitrogen isotopes from the horn sheath indicate that the mobility of his early life may have
921 resulted in significant nutritional stress, and that this individual suffered somewhat harsher
922 winters than those on the North Slope today. The taphonomic analysis revealed that this bison
923 was scavenged in parts of high nutritional value, which was followed by a rapid burial in a
924 riverine environment.. In this case, a multiproxy approach has uncovered a life history and
925 detailed examination of a member of a dominant Pleistocene species in the Arctic.
926

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1497

1498    **Figure titles:**

1499

1500    Figure 1. a) A map on northern Alaska, with the provenance of steppe bison (*Bison priscus*)

1501    specimen UAMES 29458 indicated by the red star. Yellow dots show rodent specimen localities

1502    and strontium isotope ratios measured from their teeth. The underlying map is modified from

1503    Bataille et al. (2016). b) UAMES 29458 skull in situ during excavation. c) UAMES 29458

1504    articulated thoracic vertebrae attached with connective tissue, in situ during excavation.

1505

1506    Figure 2. a) Specimen UAMES 29458 rearticulated for taphonomic analysis. b) Skeletal

1507    elements missing from specimen are indicated in gray and elements with carnivore marks

1508    indicated in red. All elements from the right side were present.

1509

1510    Figure 3. Scavenger dentition marks on the a) thoracic vertebral processes of *Bison priscus*

1511    specimen UAMES 29458 with bites indicated by arrows, and b) ventral side of lumbar vertebrae

1512    with gnaw marks indicated by arrow c) Vertebrae with healed pathology indicated by arrow.

1513

1514    Figure 4. The macrofossil assemblage taken from skull of specimen UAMES 29458:

1515    *Protophormia terraenovae* puparium UAMES 52319. a), dorsal view b), lateral view c), ventral

1516    view d), posterior view, the posterior spiracles surrounded by a rectangle e), the posterior

1517    spiracles in close-up view. (photos: J.-B. Huchet, 2018), f) Partial abdomen sternites of a ground

1518    beetle UAMES 52334 (Carabidae: Pterostichinae) (photo: J.-B. Huchet, 2018), g) Psyllid

1519    forewing recovered from inside the bison skull UAMES 52331 (photo: J.-B. Huchet, 2018), h)

1520    Right elytron of a ripicolous ground beetle of the genus *Elaphrus* Fabricius UAMES 52333

1521    (Carabidae: Elaphrinae) (photo: J.-B. Huchet, 2018), i) *Carex* seed lenticular, j) *Carex* seed

1522    Trigonal, k) Poaceae caryopsis, l) *Polygonum bistorta*, m) *Draba*-type seed, n) *Andromeda*

1523    *polifolia*, o) *Bryophyta sp*.

1524

1525    Figure 5. The relative abundance of plant macrofossil specimens in the skull and spine of

1526    specimen UAMES 29458, categorized by characteristic eco-type.

1527

1528    Figure 6. Carbon and nitrogen stable isotope values of serial horn sheath samples (n=113) with

1529    dotted trend-line of weighted moving averaging of the nearest 3 samples and collagen carbon and

1530    nitrogen stable isotope values. * Indicate lowest $\delta^{15}$N values associated with summer. Labels on

1531    the bottom indicate approximate timing of identifiable life events.

1532

1533    Figure 7. Isotope data from analyses of molar 1 (M1), molar 2 (M2), and molar 3 (M3) from

1534    specimen UAMES 29458. a) Strontium $^{87}$Sr/$^{86}$Sr ratios, b) Oxygen stable isotope ratios

1535    expressed as $\delta^{18}$O values and c) Stable carbon isotope ratios (expressed as $\delta^{13}$C values). Shading

1536    represents estimates of winter, based on the $\delta^{18}$O values. * Indicate highest $\delta^{18}$O values

1537    associated with summer.

1538

1539     Figure 8. Rodent $^{87}$Sr/$^{86}$Sr ratios grouped by region, compared to $^{87}$Sr/$^{86}$Sr ratios from specimen

1540     UAMES 29458 over time and a model-predicted $^{87}$Sr/$^{86}$Sr ratio for the death location of

1541     specimen UAMES 29458.

1542

1543     Figure 9. A Bayesian time-calibrated genealogy of bison mitochondrial genomes, with major

1544     well-supported Clades (1, 1A, 2, 2A, 2B) highlighted (following Heintzman et al., 2016 and

1545     Zazula et al., 2017). All living bison fall within Clade 1A, whereas the specimen UAMES 29458

1546     falls near the base of Clade 2. Purple bars are 95% highest posterior density intervals for node

1547     heights and are shown for nodes with posterior probability >0.95. This maximum clade

1548     credibility tree resulted from the analysis that excluded MS022 and had a minimum age prior of

1549     30 kya BP for UAMES 29458. Results from the other analyses can be found in Table 6. The

1550     diverged yak tips have been removed.

1551     Figure 10. Comparison of the ranges ($\Delta$) of $^{87}$Sr/$^{86}$Sr ratios recorded within the teeth of different

1552     bison including, present-day plains bison (*Bison bison*) from interior Alaska (Glassburn et al.,

1553     2018); Holocene plains bison (*Bison bison*) from the American Plains (Widga et al., 2010); Late

1554     Pleistocene steppe bison (*Bison priscus*) from Ukraine (Julien et al., 2012) and Late Pleistocene

1555     steppe bison (*Bison priscus*) from France (Britton et al., 2011).

1556     Figure 11. Summary of all radiocarbon dates ($^{14}$C), molecular clock estimates, and compatible

1557     $\delta^{18}$O value periods based on Greenland Ice core values (Rasmussen et al., 2014) and a $\Delta$4‰

1558     lower values than present. *dates are calibrated radiocarbon dates where possible, otherwise they

1559     are before present.

**Supplementary materials**

Figure S1. Intra tooth sampling of molar 1 (M1), molar 2 (M2) and molar 3 (M3) from *Bison priscus* specimen UAMES 29458, number indicates sample number.

Figure S2. Serial sampling scheme for bison horn sheath from *Bison priscus* specimen UAMES 29458.

Figure S3. Results of the tests for temporal signal in the bison mitochondrial genome data set. a) Full alignment data set, and b) reduced alignment data set (excluding MS022). Left panels: linear regression of phylogenetic root-to-tip distance against sampling date. Center panels: similar-date clusters (rounded to the nearest thousand years). Right panels: testing the results against random permutations over the clusters presented in b).

Figure S4. Assessment of damage patterns in nuclear (A-C) and mitochondrial (D-F) DNA fragments from *Bison priscus* specimen UAMES 29458. (A, D) DNA fragment length distributions, with means of 90 bp (nuclear) and 127 bp (mitochondrial). (B, E) The relative frequency of cytosine to thymine deamination (red line) and observed guanine to adenine misincorporation (blue line) from cytosine deamination on the opposite DNA strand. Deamination is more prevalent at the ends of ancient DNA fragments. (C, F) DNA fragmentation plots showing an elevated occurrence of purines (guanine, adenine) immediately upstream of the ancient DNA fragment (to the left of the grey box) and the opposite signal immediately downstream of the fragment (to the right of the grey box).

1    **Tables**

2    Table 1. Summary of radiocarbon dates.

| Material | ¹⁴C yrs | Error | Cal yr BP CALIB | Laboratory | Accession Number |
|---|---|---|---|---|---|
| Collagen | >43,500 | NA | | BETA | 324600 |
| Keratin | 46,000 | 1100 | 46,962 | Keck | 209861 |
| Chitin | 46,800 | 1200 | | Keck | 209862 |
| Plant | >49,990 | NA | | Keck | 209863 |

3      Table 2. Results of isotopic analysis of strontium, carbon and oxygen of UAMES specimen

4      29458.

| Tooth | Sample # | Distance from base of enamel (cm) | $^{87}Sr/^{86}Sr$ | $\delta^{13}C$ ‰ (VPDB) | $\delta^{13}C$ ‰ Std dev | $\delta^{18}O$ ‰ (VPDB) | $\delta^{18}O$ ‰ Std dev |
|---|---|---|---|---|---|---|---|
| M1 | 1 | 1.8 | 0.71117 | -11.4 | 0.1 | -19.0 | 0.1 |
| | 2 | 1.7 | 0.71087 | -11.5 | 0.3 | -20.2 | 0.3 |
| | 3 | 2.55 | 0.71116 | No data | No data | No data | No data |
| | 4 | 1.3 | 0.71132 | -11.3 | 0.4 | -21.0 | 0.5 |
| | 5 | 1.15 | 0.71125 | -11.4 | 0.5 | -23.8 | 0.9 |
| | 6 | 1 | 0.71138 | -11.0 | 0.2 | -21.0 | 0.2 |
| | 7 | 0.8 | 0.71144 | -11.2 | 0.3 | -22.1 | 0.4 |
| | 8 | 0.65 | 0.71158 | -11.3 | 0.1 | -22.2 | 0.2 |
| | 9 | 0.5 | 0.71162 | -11.2 | 0.1 | -22.2 | 0.2 |
| | 10 | 0.3 | 0.71172 | -11.7 | 0.4 | -23.2 | 0.4 |
| | 11 | 0.2 | 0.71182 | -11.4 | 0.2 | -22.1 | 0.3 |
| M2 | 1 | 2.1 | 0.71172 | -10.7 | 0.1 | -18.8 | 0.3 |
| | 2 | 1.95 | 0.71184 | -10.9 | 0.2 | -19.7 | 0.6 |
| | 3 | 1.8 | 0.71198 | -11.0 | 0.1 | -19.6 | 0.1 |
| | 4 | 1.65 | 0.712 | -11.5 | 0.3 | -22.7 | 0.4 |
| | 5 | 1.45 | 0.71189 | -10.7 | 0.2 | -20.2 | 0.4 |
| | 6 | 1.35 | 0.71191 | -10.9 | 0.2 | -20.5 | 0.5 |
| | 7 | 1.1 | 0.71195 | -11.4 | 0.2 | -21.7 | 0.3 |
| | 8 | 0.95 | 0.71195 | -11.5 | 0.5 | -26.5 | 0.9 |
| | 9 | 0.75 | 0.71214 | -11.3 | 0.1 | -21.2 | 0.3 |
| | 10 | 0.6 | 0.71242 | -11.4 | 0.1 | -21.5 | 0.3 |
| | 11 | 0.45 | 0.71236 | No data | No data | No data | No data |
| | 12 | 0.3 | 0.71255 | No data | No data | No data | No data |
| M3 | 1 | 2.25 | 0.71297 | -10.9 | 0.1 | -22.3 | 0.3 |
| | 2 | 2.05 | 0.71324 | -10.5 | 0.1 | -21.0 | 0.1 |
| | 3 | 1.8 | 0.71315 | -10.5 | 0.4 | -21.0 | 0.1 |
| | 4 | 1.60 | 0.71314 | -10.9 | 0.2 | -22.3 | 0.2 |
| | 5 | 1.4 | 0.71307 | -10.5 | 0.2 | -21.1 | 0.3 |
| | 6 | 1.2 | 0.71302 | -10.3 | 0.1 | -19.7 | 0.1 |
| | 7 | 1 | 0.71303 | -10.4 | 0.2 | -20.0 | 0.2 |
| | 8 | 0.85 | 0.71298 | -10.4 | 0.2 | -20.0 | 0.2 |
| | 9 | 0.6 | 0.71303 | -10.4 | 0.1 | -18.4 | 0.2 |
| | 10 | 0.45 | 0.71304 | -10.6 | 0.2 | -20.0 | 0.2 |

5    Table 3. Rodents use for characterizing $^{87}$Sr/$^{86}$Sr isoscape.

| UAM: Mamm | Species | Locality | Environment | Lat | Long | 87Sr/86Sr |
|---|---|---|---|---|---|---|
| 4650 | *Microtus oeconomus* | Meade River village | Coastal Plain | 70.481 | -157.417 | 0.71007 |
| 8163 | *Microtus oeconomus* | Umiat region | Coastal Plain | 69.367 | -152.133 | 0.71309 |
| 11149 | *Microtus oeconomus* | Kikitaliorak Lake | Mountain Drainage | 68.125 | -156.233 | 0.71721 |
| 11166 | *Microtus oeconomus* | Feniak Lake | Mountain Lake | 68.250 | -158.333 | 0.71372 |
| 13614 | *Microtus oeconomus* | Barrow, NARL | Coastal Plain | 71.283 | -156.783 | 0.70940 |
| 56327 | *Microtus oeconomus* | Desperation Lake | Mountain Lake | 68.338 | -158.728 | 0.70619 |
| 66866 | *Microtus miurus* | May Lake | Foot Hills | 68.617 | -153.000 | 0.71274 |
| 78833 | *Microtus miurus* | Agiak Lake | Mountain Lake | 68.078 | -152.924 | 0.71502 |
| 79046 | *Microtus miurus* | Nanushuk River | Mountain River | 68.275 | -150.655 | 0.71695 |
| 79102 | *Microtus oeconomus* | Agiak Lake | Mountain Lake | 68.081 | -152.944 | 0.71661 |
| 82113 | *Microtus oeconomus* | Lake Tulilik | Mountain Lake | 68.117 | -154.120 | 0.72047 |
| 125703 | *Microtus oeconomus* | Colville River | Foot Hills | 69.007 | -158.268 | 0.71107 |
| 125706 | *Dicrostonyx groenlandicus* | Colville River | Foot Hills | 68.899 | -156.470 | 0.71494 |
| 125713 | *Microtus oeconomus* | Colville River | Foot Hills | 69.060 | -154.244 | 0.71312 |

6

7    Table 4. Summary of isotopic results ($\delta^{13}C$ and $\delta^{18}O$ reported here vs. VPDB in ‰).

|  | Mean | Max | Min | Range |
|---|---|---|---|---|
| $^{87}Sr/^{86}Sr$ | 0.71214 | 0.71324 | 0.71087 | 0.00237 |
| $\delta^{13}C$ | -11.0 | -10.3 | -11.7 | 1.5 |
| $\delta^{18}O$ | -21.2 | -18.4 | -26.5 | 8.1 |

8　Table 5. Results of the genomic sex determination analysis. X:A ratio is the ratio of the relative

9　mapping frequency of the X chromosome to that of an autosome (1-29, all). Chr.: chromosome.

10　The minimum and maximum X:A ratios are highlighted in bold.

| Chr. | Length | Reads mapped | X:A ratio | Chr. | Length | Reads mapped | X:A ratio |
|---|---|---|---|---|---|---|---|
| 1 | 161428367 | 10474 | 0.543 | 17 | 76280064 | 4915 | 0.547 |
| 2 | 141965563 | 9334 | 0.536 | 18 | 65811054 | 4640 | 0.500 |
| 3 | 126844711 | 8357 | 0.535 | 19 | 64845320 | 4500 | 0.508 |
| 4 | 123809850 | 8237 | 0.530 | 20 | 75686341 | 4995 | 0.534 |
| 5 | 125249322 | 8237 | 0.536 | 21 | 69078422 | 4622 | 0.527 |
| 6 | 122519025 | 8008 | 0.539 | 22 | 61598339 | 4384 | 0.495 |
| 7 | 113029157 | 7598 | 0.525 | 23 | 52334015 | 3652 | 0.505 |
| 8 | 116846264 | 7802 | 0.528 | 24 | 64508398 | 4447 | 0.511 |
| 9 | 108503706 | 6828 | 0.560 | 25 | 44081797 | 3137 | 0.495 |
| 10 | 105982576 | 7023 | 0.532 | 26 | 51826547 | 3480 | 0.525 |
| 11 | 109987751 | 7605 | 0.510 | 27 | 48460478 | 3046 | **0.561** |
| 12 | 85119472 | 5420 | 0.554 | 28 | 45964680 | 3144 | 0.516 |
| 13 | 84213851 | 6029 | **0.493** | 29 | 51812796 | 3432 | 0.532 |
| 14 | 81216349 | 5748 | 0.498 | all | 2541187220 | 169841 | 0.528 |
| 15 | 84472747 | 5548 | 0.537 | | | | |
| 16 | 77710258 | 5199 | 0.527 | X | 88654062 | 3126 | NA |

11    Table 6. Summary of the Bayesian molecular analyses of JK319/UAMES 29458, with overall

12    maximum age ranges highlighted in bold

| Analysis variables | | Phylogenetic placement | | Estimated age | | |
|---|---|---|---|---|---|---|
| **Min. age prior** | **MS022** | **Placement** | **Posterior probability** | **Minimum** | **Maximum** | **ESS** |
| 0 | Included | 1 | 0.276 | **32,653** | 85,157 | 11376 |
| 0 | Excluded | 1 | 0.410 | 36,022 | **86,643** | 20465 |
| 20,000 | Included | 1 | 0.261 | 34,300 | 85,618 | 15546 |
| 20,000 | Excluded | 1 | 0.409 | 34,929 | 85,827 | 18525 |
| 30,000 | Included | 1 | 0.268 | 34,708 | 83,346 | 19814 |
| 30,000 | Excluded | 1 | 0.407 | 36,696 | 85,376 | 18945 |
| 40,000 | Included | 1 | 0.241 | 40,021 | 81,074 | 19367 |
| 40,000 | Excluded | 1 | 0.391 | 40,227 | 82,423 | 19013 |
| 50,000 | Included | 2 | 0.678 | 50,000 | 82,285 | 20687 |
| 50,000 | Excluded | 2 | 1.000 | 50,007 | 82,935 | 18967 |

13    Phylogenetic placements are: 1) sister to MS002, and 2) at the base of Clade 2 (see Figure 9).

14    Minimum and maximum ages are based on 95% highest posterior density credibility intervals.

15    Note that, for analyses with a minimum age prior of 40 and 50 kya BP, the estimated minimum

16    ages are likely to have been truncated by the prior. ESS: estimated sample size.

Table 7. Comparison to other Bison strontium data. See Figure 10 *Stratigraphically determined to be from MIS4 **Molecular clock.

| Context | Species | N | Date | Average Range | Citation |
|---|---|---|---|---|---|
| Present-day Interior Alaska | *Bison bison* | 3 | 2014 | 0.00111 | Glassburn et al. 2018 |
| Holocene American Plaines | *Bison bison* | 12 | 8930-6980 cal yr BP | 0.00077 | Widga et al. 2010 |
| Late Pleistocene Ukraine | *Bison priscus* | 24 | 20557-20,491 cal yr BP | 0.00016 | Julien et al. 2012 |
| Late Pleistocene France | *Bison priscus* | 1 | 49,000±5 yr BP* | 0.00010 | Britton et al. 2011 |
| Bison Bob | *Bison priscus* | 1 | 33-87,000 yr BP** | 0.00237 | This paper |

# Figure 1

Figure 2



a)

b)
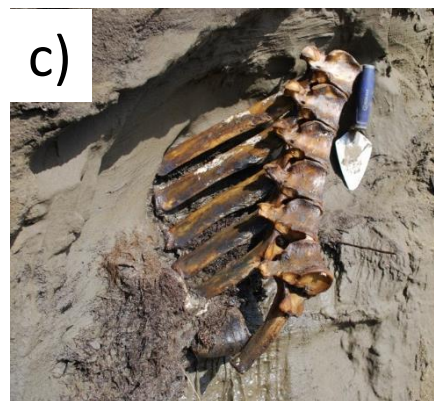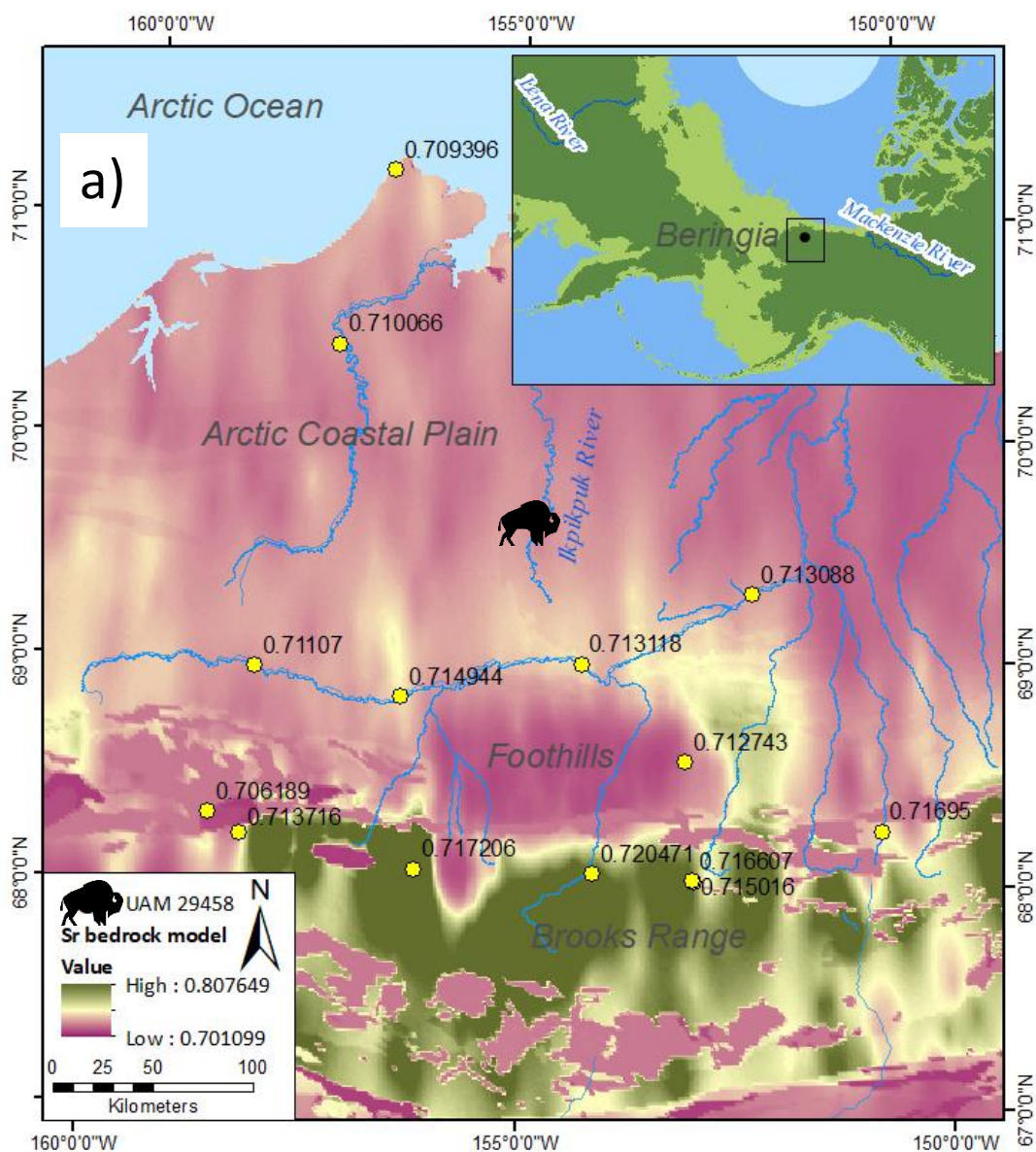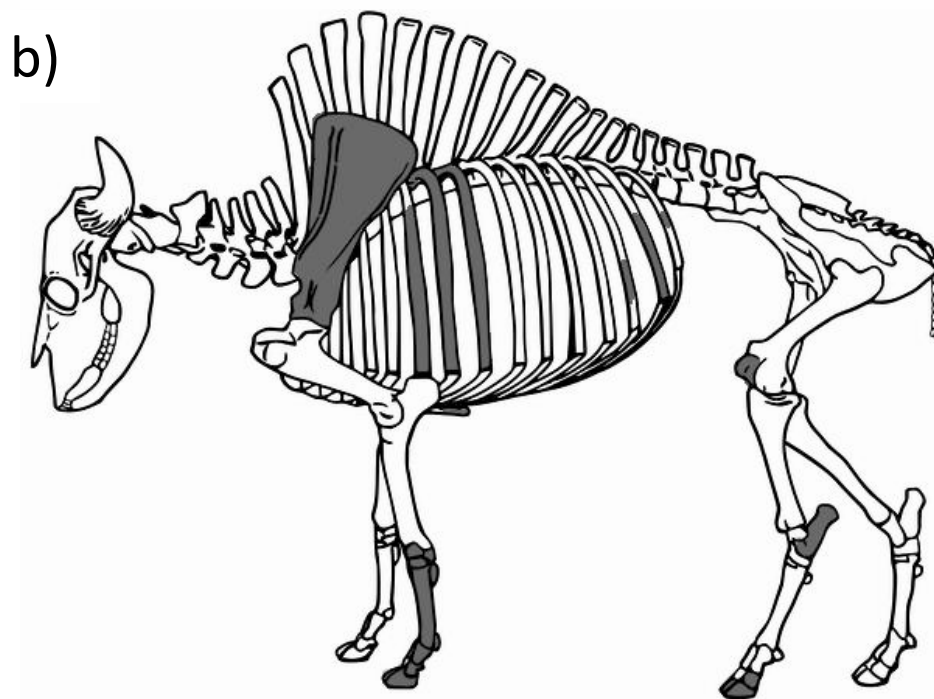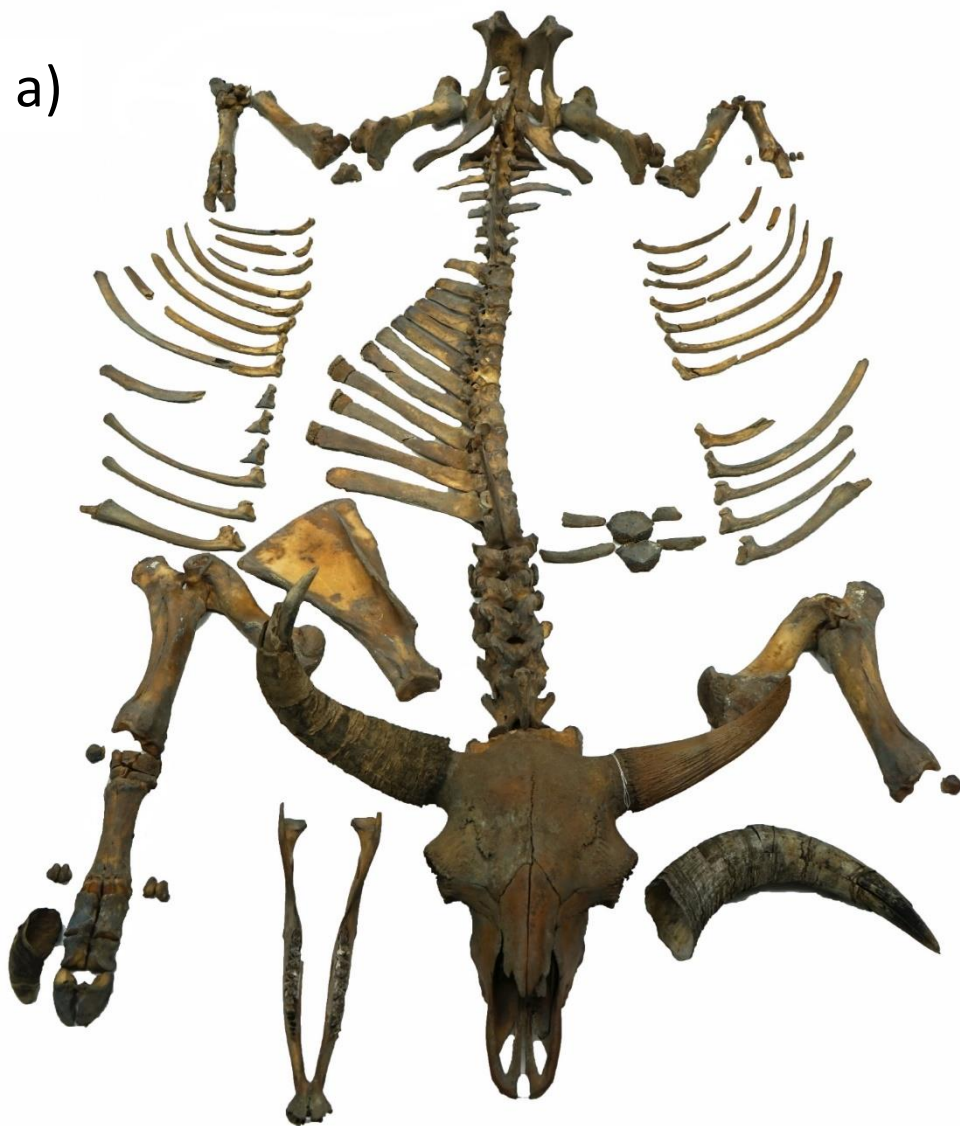
# Figure 3

# Figure 4

# Figure 5



**Shrubs**
- ■ *Salix* Fragment
- ■ *Betula nana* leaf

**Grasses and sedges**
- ■ *Carex* seed lenticular
- ■ *Carex* seed trigonal
- ■ *Poacea* seed

**Open tundra flowers**
- ■ *Drabs* type seed
- ■ Mustard type seed
- ■ *Polygonum bistort* seed
- ■ *Papaver* sp.
- ■ *Asteracea cf. solidago* seed
- ■ *cf. Caryophyllaceae sp.* seed

**Wet indicators**
- ■ *Potentillia Palustre* seed
- ■ *Andromeda polifolia* leaf
- ■ Juncus
- ■ Shells
- ■ *Daphnea* ephippia
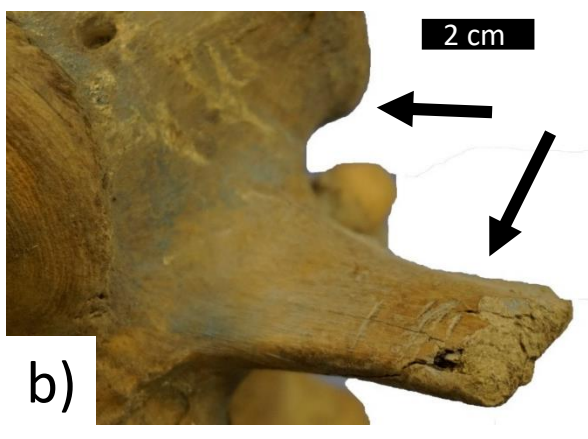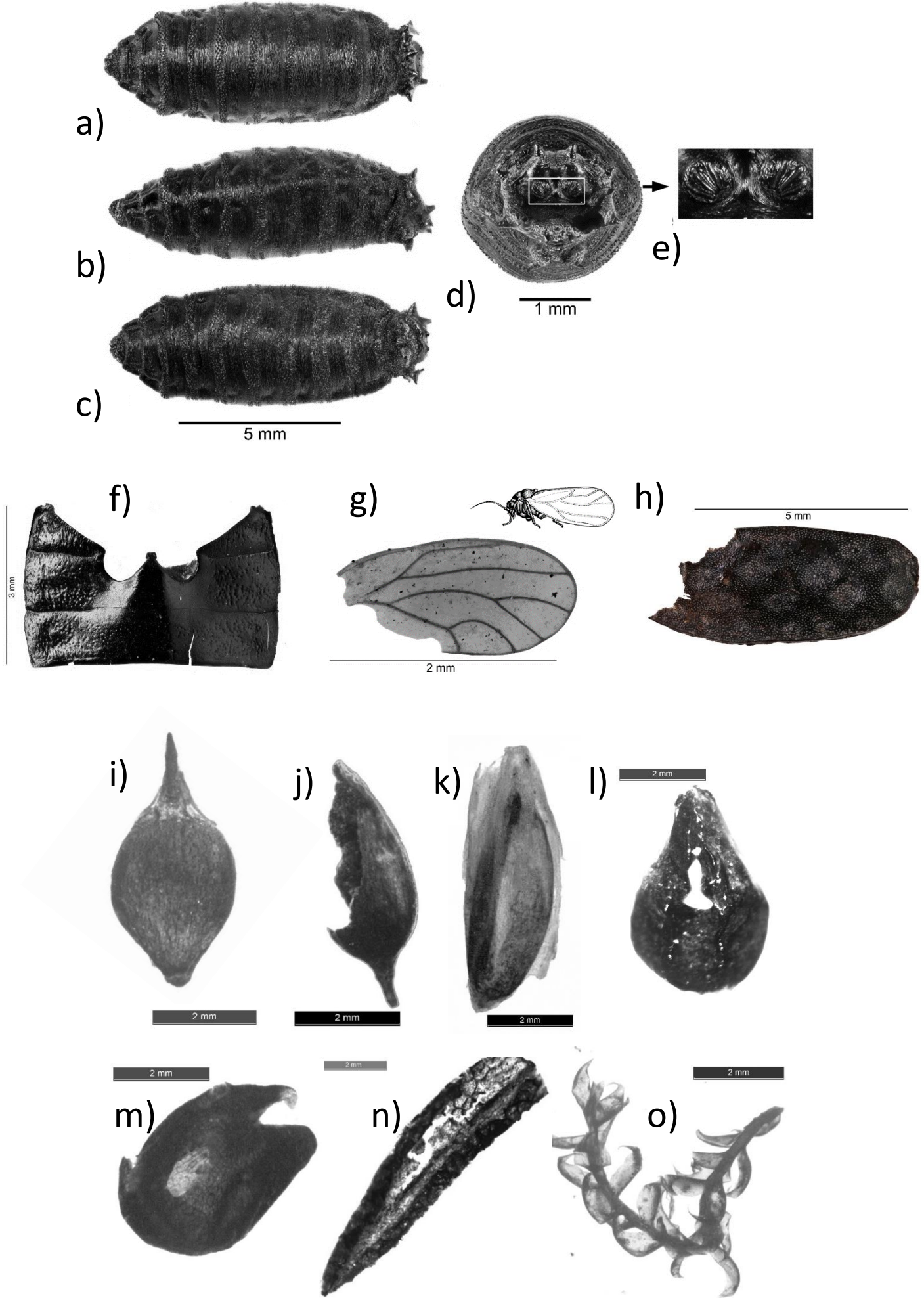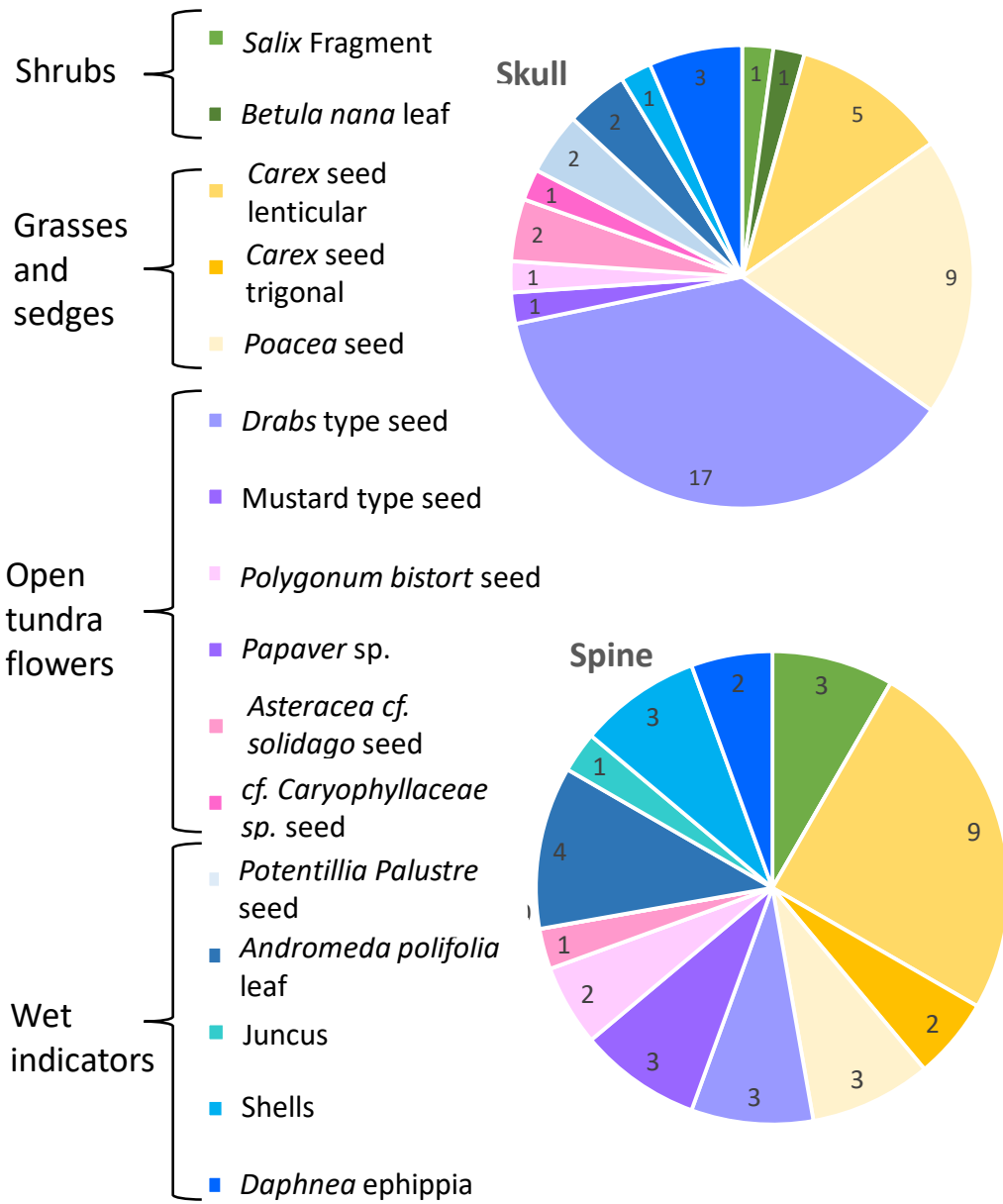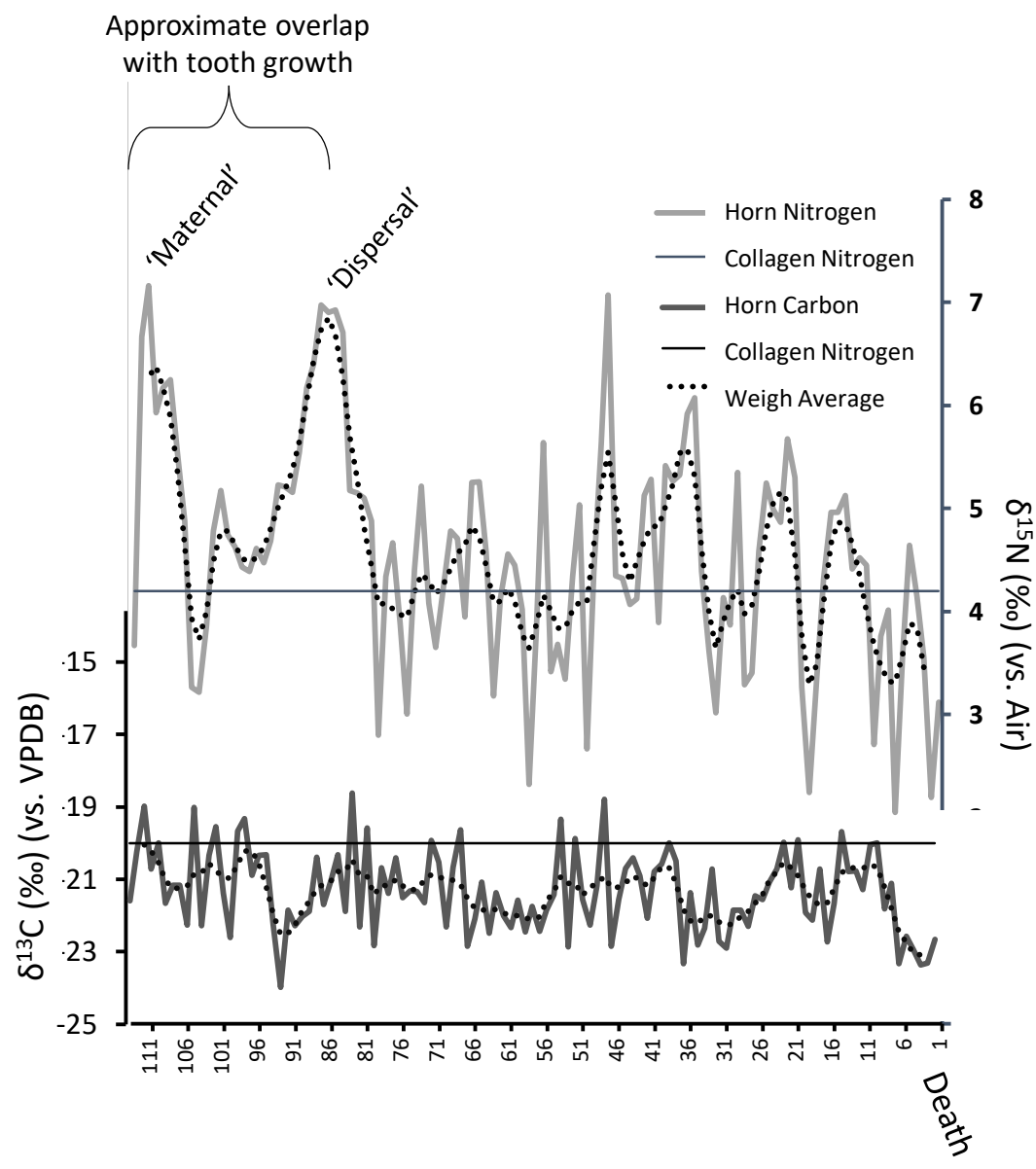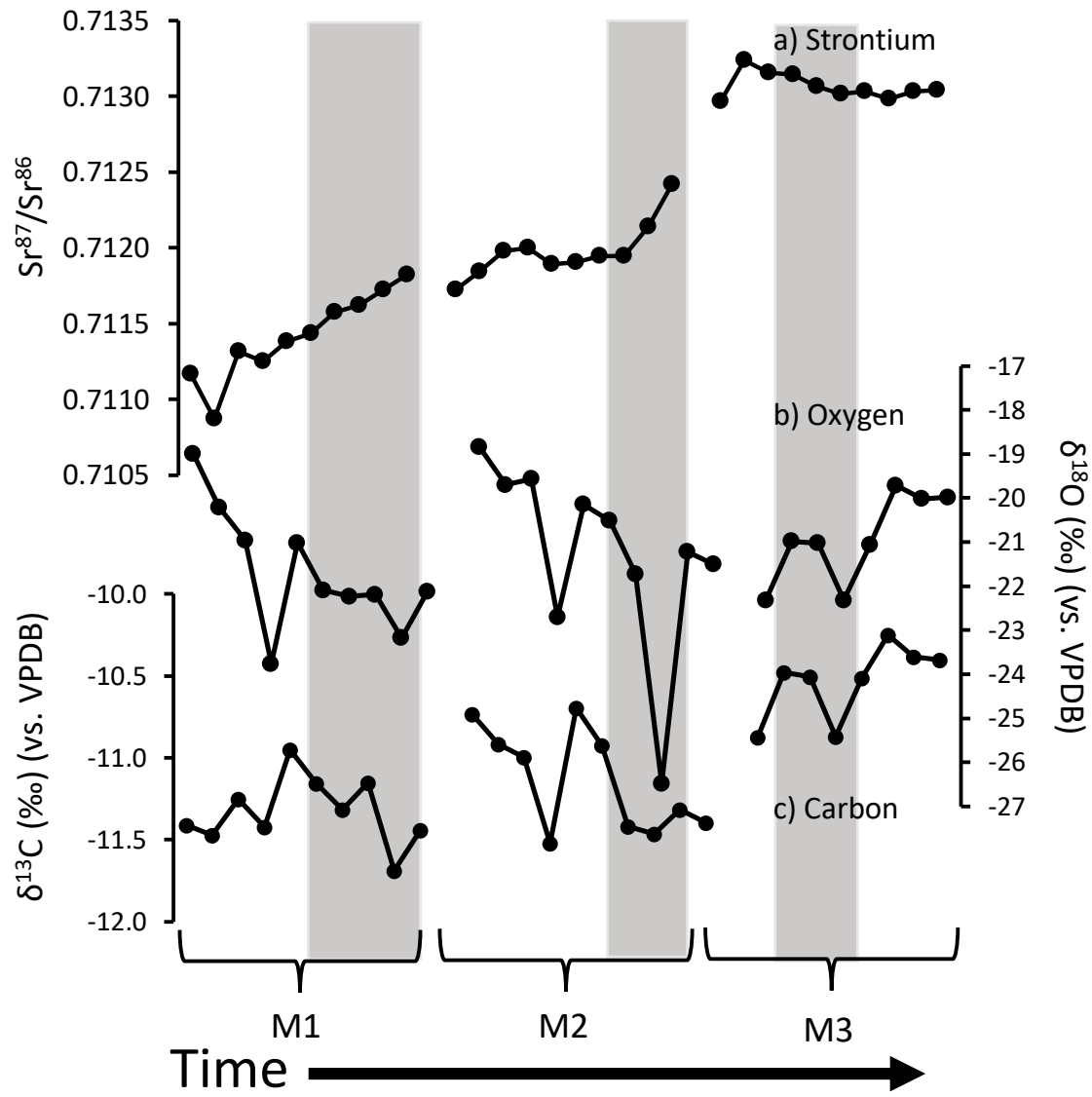
# Figure 6

# Figure 7

# Figure 8
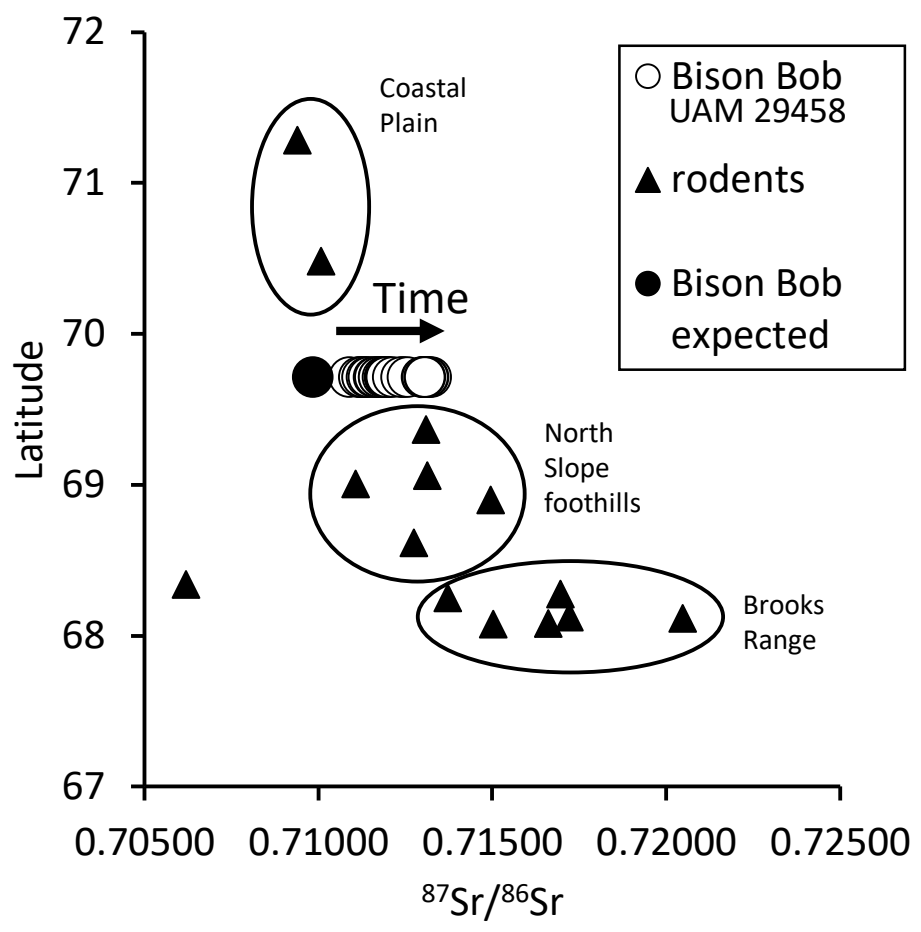
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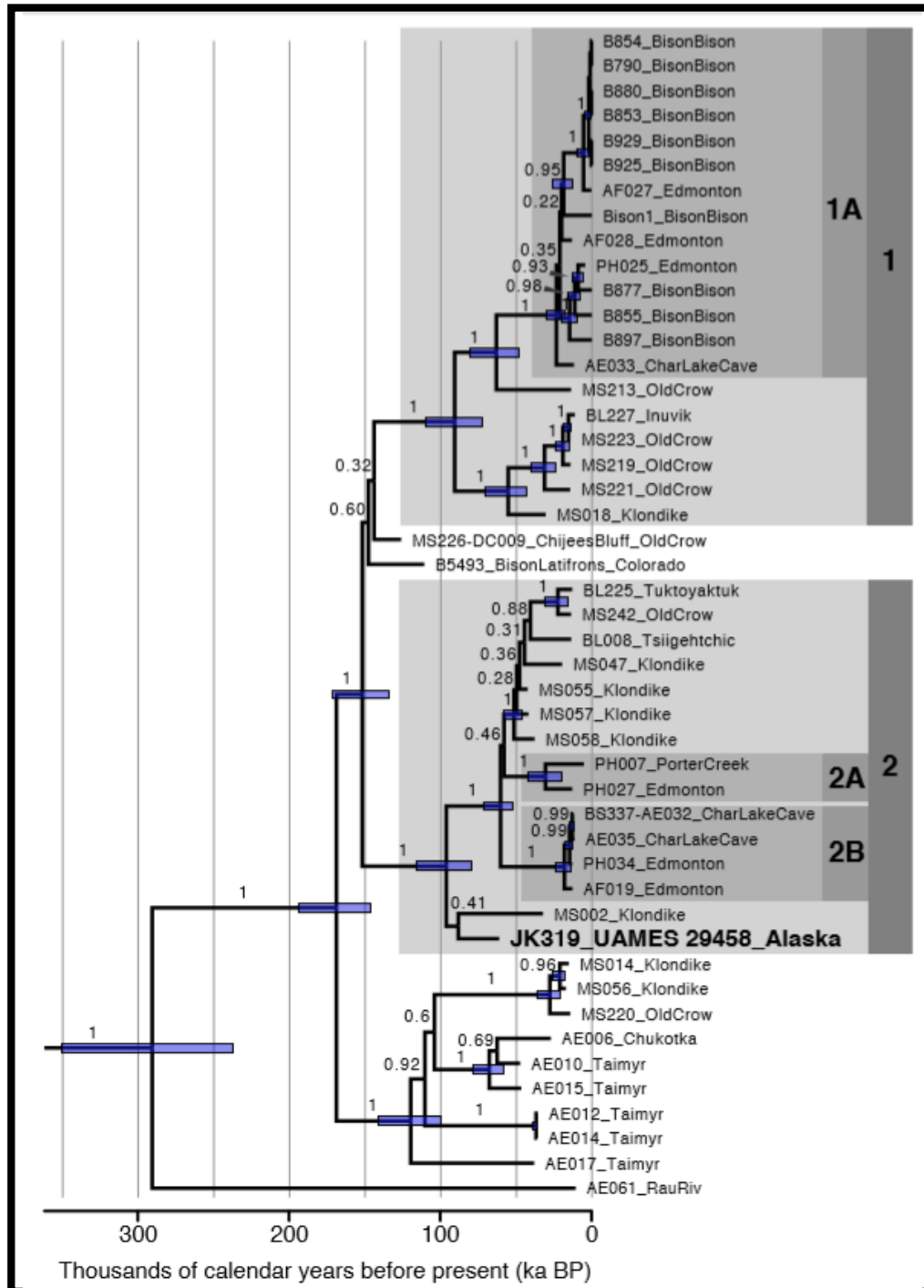
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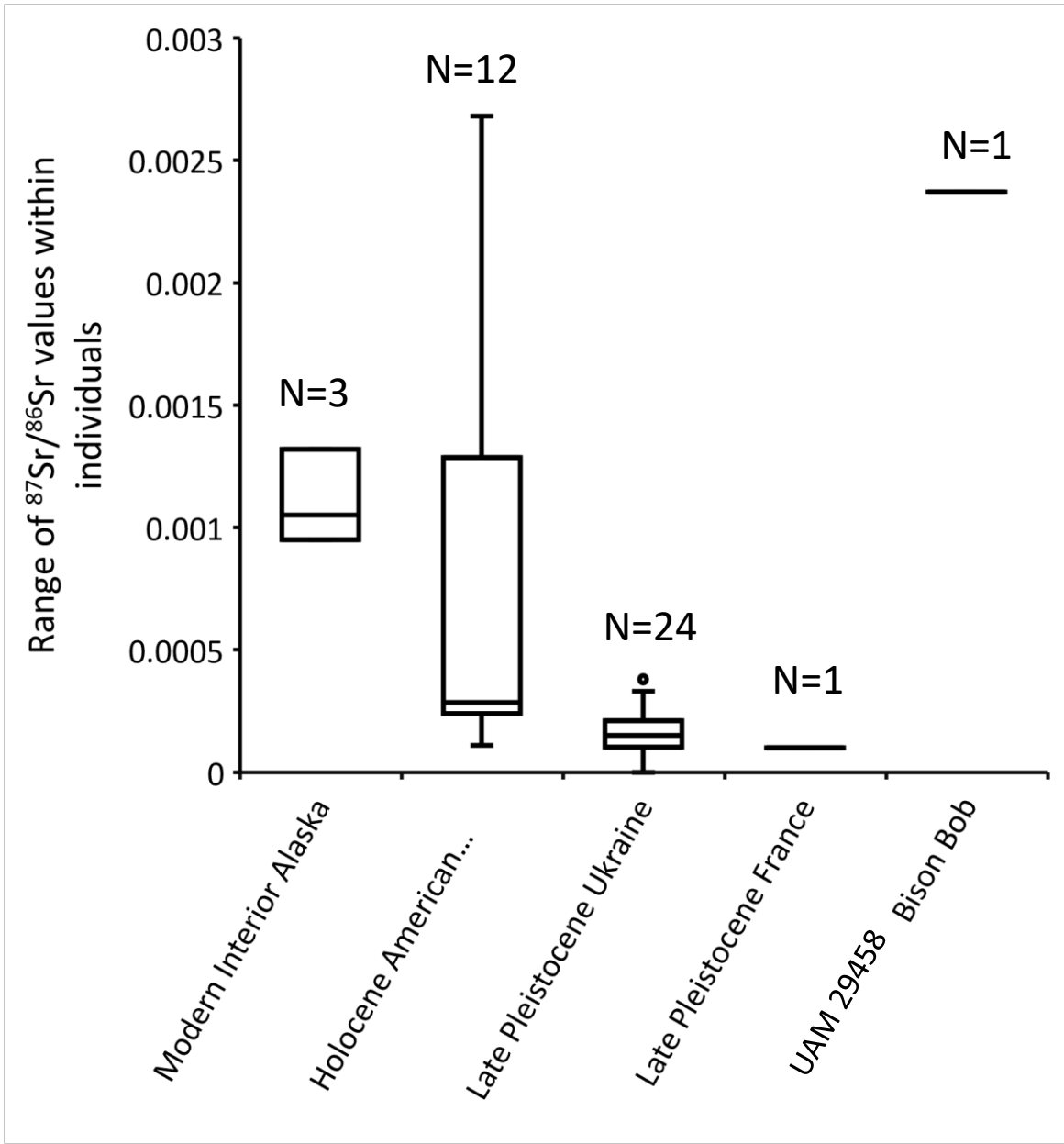
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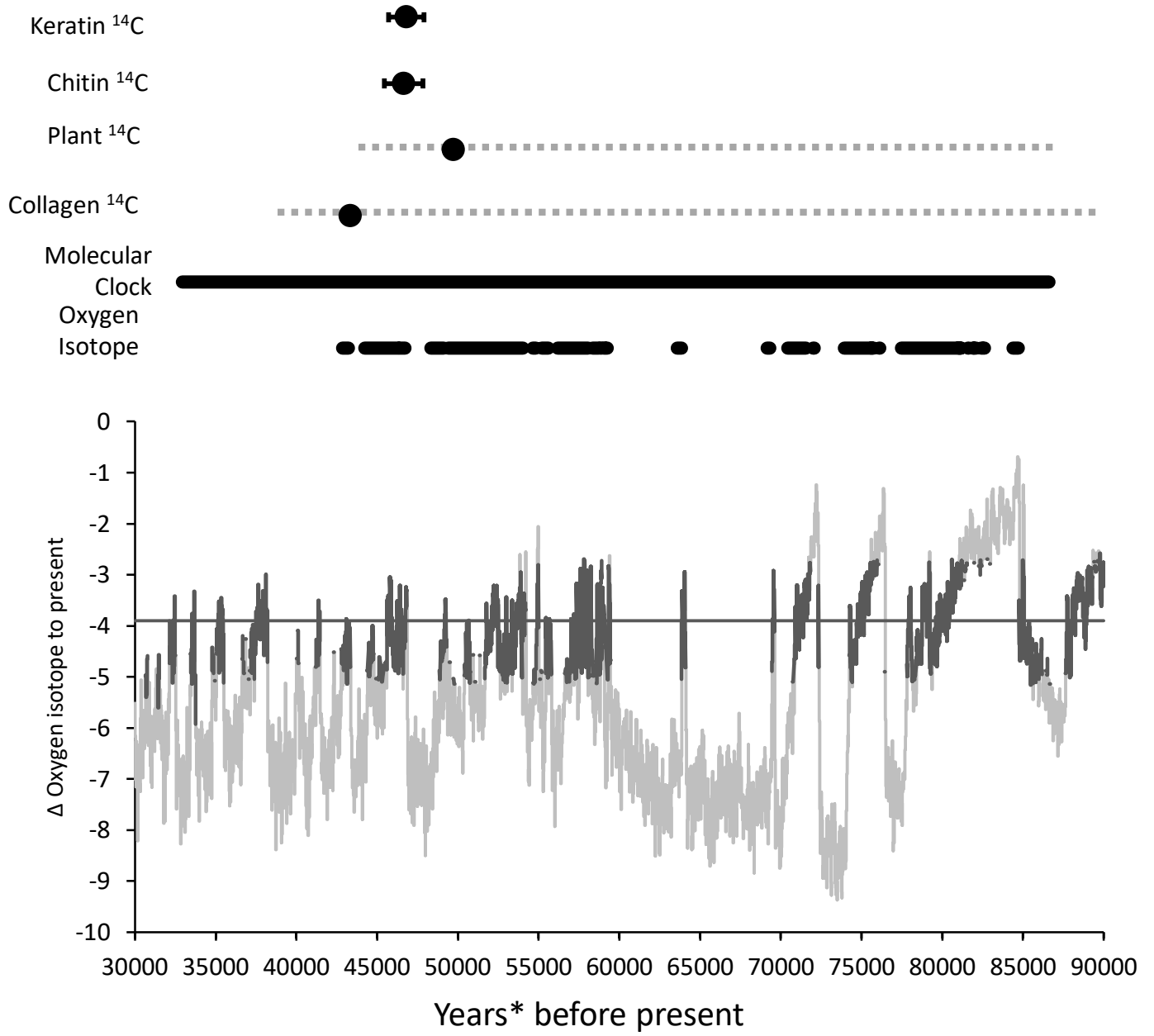
# Supplemental materials
## S1

# Supplemental materials

## S4



**A**

Regression — No clusters = 35 — Randomised data sets

Root-to-tip distance vs Dates

$r = 0.5$

Time of MRCA = 174334 yrs BP

$p$-value = 0.01

min $p$-value = 0.001

**B**

Regression — No clusters = 34 — Randomised data sets

Root-to-tip distance vs Dates

$r = 0.44$

Time of MRCA = 213001 yrs BP

$p$-value = 0.025

min $p$-value = 0.001