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1 **Evolution and extinction of the giant rhinoceros *Elasmotherium***
2 ***sibiricum* sheds light on late Quaternary megafaunal extinctions**

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23
24 **Understanding extinction events requires an unbiased record of the chronology and ecology of**
25 **victims and survivors. The rhinoceros *Elasmotherium sibiricum*, known as the ‘Siberian unicorn’,**
26 **was believed to have gone extinct around 200 ka, well before the Late Quaternary megafaunal**
27 **extinction event. However, no absolute dating, genetic analysis, or quantitative ecological**
28 **assessment of this species has been undertaken. Here we show, by AMS radiocarbon dating of 23**
29 **individuals, including cross-validation by compound specific analysis, that *E. sibiricum* survived in**
30 **Eastern Europe and Central Asia until at least 39 ka BP, corroborating a wave of megafaunal**
31 **turnover prior to the Last Glacial Maximum in Eurasia, in addition to the better-known Late-glacial**
32 **event. Stable isotope data indicate a dry steppe niche for *E. sibiricum* and, together with**
33 **morphology, a highly specialised diet that likely contributed to its extinction. We further**
34 **demonstrate, with DNA sequence data, a very deep phylogenetic split between the subfamilies**
35 **Elasmotheriinae and Rhinocerotinae that includes all the living rhinos, settling a debate based on**
36 **fossil evidence and confirming that the two lineages had diverged by the Eocene. As the last**
37 **surviving member of the Elasmotheriinae, the demise of the ‘Siberian unicorn’ marked the**
38 **extinction of this subfamily.**

39

40 The rhinoceros family (Rhinocerotidae) was formerly much more diverse than it is today, with some
41 250 named species¹ of which only five survive. During the Miocene (ca. 23-5 Ma), rhinos were a
42 dominant part of the large mammal fauna in Africa, Eurasia, and North America. Phylogenetic
43 analysis of fossil species has resolved two main lineages: the Rhinocerotinae, which includes all living
44 species and the recently-extinct woolly rhinoceros (*Coelodonta antiquitatis*), and the extinct
45 Elasmotheriinae². Based on morphological diagnoses of early remains, the two subfamilies are
46 thought to have diverged very early in rhinoceros evolution, by at latest 35 Ma^{2,3}. The
47 Elasmotheriinae subsequently gave rise to some 20 genera, of which only *Elasmotherium* survived
48 the Miocene, with *E. sibiricum* its last surviving member, although some authors have separated
49 *Elasmotherium* from other members of the group and place it within Rhinocerotinae^{4,5}. A
50 spectacular megafaunal species of Eurasia, at ca. 3.5 tonnes, *E. sibiricum* was the largest Quaternary
51 rhinoceros. *E. sibiricum* was also remarkable in its anatomy: relatively slender limbs indicating
52 adaptation for running, despite its mass⁶; absence of incisors and canines; and – uniquely among
53 rhinos – continuously-growing cheek-teeth with distinctive, highly convoluted enamel plates. The
54 presence of a massive single horn in *Elasmotherium* has been inferred from the bony protuberance
55 on the frontal bone of the skull which implies a horn base much larger than in any other rhino, living
56 or extinct; hence the informal name ‘Siberian unicorn’ (Fig. 1). The known geographical ranges of
57 both *E. sibiricum* and related (in some cases possibly synonymous) *Elasmotherium* species were very
58 limited, with most confirmed records from Kazakhstan, western and central Russia, Ukraine,
59 Azerbaijan, Uzbekistan, as well as isolated finds (referred to *E. caucasicum*) from Mongolia and
60 China^{2,7,8} (Fig. 2). *E. sibiricum* was thought to have become extinct by 200,000 years ago, although
61 recent, unconfirmed reports suggested that it might have persisted into the Late Pleistocene^{7,9}. Its
62 ecological niche has been a matter of speculation, from grazing on dry steppes to foraging for roots
63 in damp riverine environments⁷.

64 **Results**

65 Direct dating of unambiguously identified remains is an essential prerequisite for determining the
66 extinction chronology of late Quaternary megafauna¹⁰. Of a total of 25 *Elasmotherium sibiricum*
67 bone samples analysed in the present study, 23 contained sufficient collagen for radiocarbon dating
68 (Supplementary Table 1, Fig. 3). All samples were first dated by Accelerator Mass Spectrometry
69 (AMS) either at the Groningen Centre for Isotope Research (CIO), Netherlands (lab code GrA) or at
70 the Oxford Radiocarbon Accelerator Unit (ORAU), UK (lab code OxA) using the routine procedures
71 (See Methods). All nine samples yielding dates younger than 35,000 radiocarbon years were then
72 cross-dated by the other laboratory (Supplementary Table 1), and the results were compared using a
73 chi-squared test (Supplementary Table 8). In five of nine cases, the pairs of dates were not
74 statistically distinguishable. For the other four paired samples, however, there was a discrepancy
75 between the dates obtained in the two laboratories. In two cases the dates obtained in Oxford were
76 older than those obtained in Groningen, in the other two cases the opposite was the case. These
77 differences are likely due to contamination which could not be totally removed using standard
78 methods of collagen purification. For two samples (IPAE 897/123 and ZIN 36330), the difference
79 between the dates obtained by the two laboratories was ~10,000 years. It was therefore decided to
80 undertake further dating of all nine samples using the single amino acid radiocarbon method
81 developed at the ORAU¹¹. This method involves the separation of the underivatized amino acids
82 from hydrolysed bone collagen using preparative High Performance Liquid Chromatography (Prep-

83 HPLC), isolating the amino acid hydroxyproline for AMS measurement. This pretreatment approach
84 (coded 'HYP') is the most efficient available technique to remove contaminants including, but not
85 limited to, conservation materials (with the exception of collagen-based glue). All of the
86 chronometric data from ORAU is reported in Supplementary Table 7. Chi-squared tests showed that
87 in four of the cases, the dates obtained on ultrafiltered collagen and hydroxyproline are not
88 statistically distinguishable (Supplementary Table 8), indicating that all the contaminant had been
89 removed by the AF/AF* treatment (see Methods). In the other five cases, the dates obtained on
90 hydroxyproline are older than those obtained on collagen both in Groningen and Oxford. For these
91 five samples, we suspect that some contaminant had remained in the collagen (possibly crosslinked
92 to it) but was removed by hydrolysing the collagen and isolating hydroxyproline. Similar
93 observations have been made on a range of contaminated Palaeolithic bone samples (see, for
94 example, refs. ¹²⁻¹⁶). Ages obtained on hydroxyproline were therefore retained over those obtained
95 from bulk collagen on these nine samples. In the final dataset of conventional radiocarbon ages
96 (CRA), 19 are finite dates and 5 are beyond the radiocarbon limit. The five youngest ages are all
97 corroborated by HYP. The 19 finite dates were then calibrated against the IntCal13 dataset¹⁷ using
98 OxCal version 4.3¹⁸ (Supplementary Fig. 2), and were incorporated within a single Phase model in
99 OxCal v.4.3 (Supplementary Table 9). We used a General outlier model (prior probability set at
100 0.05)¹⁹ to explore the degree to which likelihoods were outlying. Using IntCal13, the calibrated
101 95.4% confidence intervals for the finite ages range in an overlapping series from 50-44.76 to 38.97-
102 36.52 cal ka BP (Fig. 3, Supplementary Fig. 2). The end boundary in the model provides an estimate
103 of the last appearance of *Elasmotherium* at 38.48-35.06 cal ka BP (at 95.4% probability). Our data
104 demonstrate the late Quaternary extinction of *E. sibiricum*, and imply an extinction before the Last
105 Glacial Maximum. With 23 dates this conclusion is provisional, but it is supported by the lack of any
106 known remains in dated post-LGM contexts^{20,21}.

107 Six bone samples were subjected to ancient DNA analysis and all yielded usable DNA data, although
108 molecular preservation varied markedly (Supplementary Table 2). We were able to reconstruct a
109 high-quality mitochondrial genome sequence for the best-preserved specimen – IPAE915/2804
110 (GenBank accession: MH937513) – with a mean read-depth of 116.1x, which covered 99.3% of the
111 modern white rhinoceros reference (*Ceratotherium simum*, NC_001808). It is notable that
112 IPAE915/2804, from Tobolsk (latitude ~58°), is the most northerly of our samples (Fig. 2), possibly
113 accounting for its better DNA preservation. Despite poorer preservation in the other samples – as
114 low as 0.8x depth for 2388/1 – all sequences were very similar to IPAE915/2804 (≥99.7% identical at
115 unambiguously called nucleotide sites).

116 Phylogenetic analyses including the IPAE915/2804 consensus sequence strongly suggest that
117 *Elasmotherium* is sister-taxon to Rhinocerotinae (Fig. 4; Maximum Likelihood Bootstrap, MLB = 99%,
118 Bayesian Posterior Probability, BPP = 1.0). Relationships among perissodactyls were otherwise
119 concordant with the results of past molecular studies^{22,23}, although the position of the root of
120 Rhinocerotinae remains poorly resolved.

121

122 Our molecular dating analyses suggest that the divergence between *Elasmotherium* and the
123 Rhinocerotinae occurred around 47.3 Ma (95% Highest Posterior Density, HPD = 41.9 – 53.2 Ma).
124 The primary divergence within crown Rhinocerotinae (the split between *Diceros*+*Ceratotherium* and
125 the remaining taxa) occurred 30.8 Ma (95% HPD = 26.5 – 35.3 Ma), while the divergence of
126 Rhinoceroidea from Tapiroidea occurred 57.5 Ma (95% HPD = 52.6 – 62.8 Ma). Highest Posterior

127 Densities (HPDs) for node ages estimated in the present study overlapped with those of comparable
128 nodes in previously published studies^{23,24}. However, our mean age estimates for nodes deeper in the
129 tree (i.e. crown ages of Perissodactyla and Ceratomorpha) were slightly older than those in
130 previously published studies, as our conservative node age constraints allowed for the possibility
131 that perissodactyl diversification began during the Palaeocene (see Supplementary Information).

132

133 For stable isotope analysis, C:N ratios of all samples were within acceptable range (Supplementary
134 Table 6), with the exception of sample IPAE 420-111 which is just outside the range and is excluded
135 from further discussion. The *Elasmotherium* $\delta^{13}\text{C}$ values (n=22) range from -21.5‰ to -16.3‰ with a
136 mean of -18.1 ± 0.3 ‰. The $\delta^{15}\text{N}$ values (n=21) range from +6.5‰ to +12.8‰ with a mean of $+9.4$
137 ± 0.3 ‰ (Fig. 5; Supplementary Table 6). The range of stable isotope values might partly be due to
138 geographic or temporal variation, although no trend through time or a correlation with latitude is
139 observed in the data (Supplementary Fig. 1). However, the *Elasmotherium* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values
140 clearly differ from those of other fossil Rhinocerotidae from Eurasia (Fig. 5). The majority of *E.*
141 *sibiricum* individuals are relatively higher in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than narrow-nosed and/or Merck's
142 rhinoceros (*Stephanorhinus hemitoechus/kirchbergensis*) from the Middle Pleistocene of
143 Schöningen, Germany. Most of our samples are also enriched in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than woolly
144 rhinoceros (*Coelodonta antiquitatis*) from within the temporal and geographical range of the
145 *Elasmotherium* material. Conversely, *E. sibiricum* overlaps strongly with a sample of saiga antelope
146 (*Saiga tatarica*) from the same spatio-temporal range (Fig. 5).

147

148 Discussion

149 Our results have implications for both the phylogenetic position and extinction of the last
150 elasmotheriine rhinoceros, and for the pattern and causality of Late Quaternary megafaunal
151 turnover. The deep division between *Elasmotherium sibiricum* and the extant rhinoceroses in our
152 molecular phylogeny (Fig. 4) is strongly supportive of an ancient split between Elasmotheriinae
153 (including *Elasmotherium*, contra refs. ^{4,5}) and Rhinocerotinae, in keeping with recent
154 palaeontological evidence: the earliest fossil species referred to Elasmotheriinae are *Subhyracodon*
155 *occidentalis* and *Penetrigonias dakotensis* at ca. 38 Ma^{3,25}, while the earliest certain representative
156 of Rhinocerotinae is *Epiaceratherium naduongense*²⁶ at ca. 39-35 Ma. Our early- to mid-Eocene
157 estimate of ~47.4 Ma for the divergence between Elasmotheriinae and Rhinocerotinae pre-dates
158 their first fossil appearances by 8-9 Ma, with this lag likely explained by the incompleteness of
159 taxonomic samples included in morphology-based phylogenetic analyses of Rhinocerotidae,
160 especially regarding stem Eocene taxa^{2,3}.

161 Previously, the loss of *E. sibiricum* has been regarded as part of the 'background extinction' of large
162 mammals that proceeded through the Early and Middle Pleistocene. The species was considered
163 typical of the Singhil and Khazar faunistic complexes of Russia, broadly early and late Middle
164 Pleistocene, respectively, with its youngest occurrences attributed to the late Middle Pleistocene, ca.
165 200 ka^{7,8}. However, most of the remains, from locations in the Volga region, were found on river
166 banks, with likely mixing of bones from different geological horizons. On the basis of locally
167 associated faunas, a possible Late Pleistocene age for some of the remains had been suggested (refs.
168 ⁹, and ², p.42, but except for Smelovskaya II these specimens were also recovered *ex situ* and all
169 radiocarbon dates on associated fauna are infinite (Supplementary Information). A radiocarbon

170 measurement of $26,038 \pm 356$ BP (UBA-30522) was obtained from a partial skull of *E. sibiricum* from
171 Kozhamzhar, Kazakhstan²⁷, but the context otherwise appeared Middle Pleistocene, and the
172 laboratory indicated that the date was unreliable as collagen yield was only 0.3% after
173 ultrafiltration²⁸.

174 Our results therefore provide reliably dated Late Pleistocene occurrences of *E. sibiricum* ranging
175 from close to the older limit of radiocarbon dating to just before the onset of Greenland Stadial 8
176 (ca. 36-35 cal ka BP: ref. ²⁹). This places its extinction firmly within the Late Quaternary extinction
177 event, during which approximately 40% of northern Eurasian mammal species with body weights
178 >45 kg (megafauna) died out in the interval ca. 50-4 ka³⁰. Many of these species became extinct in
179 the Late-glacial (GI-1 & GS-1) and Holocene (MIS 1), starting from ca. 15 cal ka BP. The latest dates
180 for *E. sibiricum* around 39-35 ka, however, form an important addition to the growing evidence for
181 turnover in the northern Eurasian large mammal fauna before or early in the Last Glacial Maximum
182 (LGM)^{31,32}. The LGM has been variously defined, including the minimum in $\delta^{18}\text{O}$ in Greenland ice ca.
183 30-25 ka (Fig. 3), or the minimum sea level and maximum expansion of northern hemisphere ice
184 sheets ca. 21 ka^{33,34}. The latest dates for *E. sibiricum* are closely coincident with those for *Homo*
185 *neanderthalensis* and the east Beringian stilt-legged horse *Haringtonhippus francisci*^{32,35,36}. This was
186 followed by apparent peripheral range reduction in *C. antiquitatis*^{32,37}, and major genetic turnover in
187 several species including mammoth and bison³². The latest records of Eurasian spotted hyaena *C.*
188 *crocuta* and cave bear *U. spelaeus* are at ca. 31 ka and 28-27 ka, respectively³⁸⁻⁴¹, while

189 *Megaloceros giganteus* suffered major range collapse, recovering only in the Late-glacial (GI-1)⁴².
190 The available dates for *E. sibiricum* strongly corroborate this pre-LGM phase of faunal turnover.
191 There are many fossil localities within the sampled geographical area that have produced later dates
192 for other megafauna^{20,43}, so the absence of *Elasmotherium* is unlikely to be due to lack of suitable
193 assemblages.

194 The inferred timing of these events falls during a period of pronounced climate and environmental
195 change, the series of Greenland Stadials and Interstadials that characterised Marine Isotope Stage
196 3³². The start of the dated faunal events, including the last appearance of *E. sibiricum*, are
197 approximately coincident with GS-8 and Heinrich stadial 4, a major episode of ice rafting into the
198 North Atlantic⁴⁴. Plant, insect and lithostratigraphic proxies from across northern Eurasia
199 corroborate a sustained shift to cold tundra-steppe beginning around 35 ka ¹⁴C BP (equivalent to 40-
200 38 ka), with the breakup of grass/herb-dominated vegetation cover⁴⁵. These changes are a potential
201 contributor to the turnover and extinction of large mammals in the interval preceding the LGM, but
202 further data are required to examine their regional effects in areas such as the central Asian range of
203 *E. sibiricum*.

204 The extinction of *Elasmotherium* may also have been linked to its high degree of specialisation,
205 including extreme dietary adaptations⁷. Among other rhinoceros species, morphological and tooth-
206 wear data show that *S. kirchbergensis* and *S. hemitoechus* were browse- and graze-dominated
207 mixed-feeders, respectively, while *C. antiquitatis* was a grazer⁴⁶⁻⁴⁹. In *E. sibiricum* the obtuse angle
208 between the plane of the occiput and the palate indicates that the head was carried lower even than
209 in the woolly rhinoceros and the living white rhino^{50,51}, an extreme adaptation to feeding close to the
210 ground. The hypsodont, rootless, permanently-growing cheek teeth, with highly convoluted enamel,
211 imply hypergrazing adaptation and/or the consumption of substantial quantities of dust or grit. Our

212 stable isotope analyses of *E. sibiricum* also show values clearly differing from those of other
213 rhinoceros species (Fig. 5). Pollen, plant macrofossil and faunal data suggest that during MIS 3, the
214 areas inhabited by *E. sibiricum* included open steppe habitats in the southern Trans-Urals, while in
215 other areas forest-steppe landscapes with extensive grassy areas were present⁵². High $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
216 values, seen in *E. sibiricum*, are typical for mammals inhabiting a dry steppe or desert biotope⁵³. The
217 $\delta^{13}\text{C}$ values of *E. sibiricum* may also have been influenced by the consumption of Chenopodiaceae
218 (C4 photosynthesisers), as in modern saiga antelope *Saiga tatarica*⁵⁴, and/or to the pulling up and
219 consumption of roots (as suggested for *E. sibiricum*⁷), since non-photosynthetic plant parts tend to
220 be elevated in $\delta^{13}\text{C}$ (ref. ⁵⁵).

221

222 Previous stable isotope studies on mammalian herbivore species from Europe have illustrated
223 change in ecological niches during the pre-LGM⁵⁶ and the Late glacial⁵⁷. Both *C. antiquitatis* and *S.*
224 *tatarica* survived the extinction of *E. sibiricum*, the former with an isotopic signature implying a
225 dietary niche consistently different from that of *E. sibiricum*, the latter with a shift in its range of
226 isotopic values. While *Saiga* samples from pre-LGM central Asia show $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values
227 overlapping strongly with contemporary *Elasmotherium* (Fig. 5), samples from later periods (LGM to
228 Late-glacial Interstadial, GI-1), and those from other regions, include lower $\delta^{15}\text{N}$ values (down to +2.8
229 ‰), indicating dietary flexibility⁵⁴. The implication is that both *Coelodonta* and *Saiga* could cope with
230 the environmental change that began around 38 ka but *E. sibiricum* could not. Added to this, the
231 persistently restricted geographical range of *Elasmotherium*, also likely linked to its specialized
232 habitat, as well as low population size and slow reproductive rate associated with large body size⁵⁸,
233 would have predisposed it to extinction in the face of environmental change, while the ecologically
234 similar, but much smaller species (*S. tatarica*) survived. The extinction of *E. sibiricum* could in theory
235 have been exacerbated by human hunting pressure, given the replacement of *H. neanderthalensis*
236 by *H. sapiens* in Eurasia ca. 45-40 ka⁵⁹. There is currently no record of the species' remains from any
237 archaeological site, and the very few suggested depictions of *Elasmotherium* in Palaeolithic art (ref.
238 ⁵¹; ref.², p. 46-7) are unconvincing.

239 **Materials and Methods**

240 We sampled a total of 25 specimens of *E. sibiricum* from the collections of the Museum of the Institute of Plant
241 and Animal Ecology UB RAS (Ekaterinburg), Sverdlovsk Regional History Museum (Ekaterinburg), Zoological
242 Institute RAS (St Petersburg) and the Natural History Museum (London). Specimens were readily identified
243 from the highly characteristic features of the skull, mandible, postcranial bones, and the hypsodont, rootless
244 cheek teeth with their distinctive convoluted enamel. Sample provenances are detailed in the Supplementary
245 Information.

246 At the Groningen Centre for Isotope Research (CIO), samples underwent standard chemical cleaning and
247 collagen extraction following an improved version of the Longin method, as described in ref. ⁶⁰ and in the
248 Supplementary Information. In short, bone samples are decalcified over at least 24 hrs using weak HCl (4%
249 w/vol). When CO₂ release has ceased and the fragments are soft and pliable they are rinsed thoroughly with
250 distilled water (DW). The extract is exposed to NaOH (1%, >30 min) to eliminate humic acids, rinsed to
251 neutrality and again treated with HCl (4% w/vol, 15 min). The raw collagen fraction is denatured to gelatin in
252 acidified DW (pH 3) at 90 °C for 18 hrs. Dissolved gelatin is filtered through a 100 µm mesh to eliminate any
253 remaining foreign particulates, and dried. The collagen is combusted to CO₂ using an Elemental Analyser
254 (Isocube) connected to an Isotope Ratio Mass Spectrometer (Isoprime), providing stable isotope ratios ¹³C/¹²C
255 and ¹⁵N/¹⁴N. For ¹⁴C, the CO₂ was cryogenically trapped using an automatic collection device. The routine

256 graphitization procedure at the CIO has been operational for over 20 years^{61,62}, with only minor, mainly
257 mechanical, adjustments. The ¹⁴C/¹²C ratio in the graphite was measured by Accelerator Mass Spectrometry⁶³.
258 At the Oxford Radiocarbon Accelerator Unit (ORAU), samples were dated using two different methods. First,
259 samples were pre-treated following the routine procedure at the ORAU comprising decalcification in acid, a
260 base wash, re-acidification, gelatinisation and ultrafiltration (coded 'AF'), as described in ref.⁶⁴. Samples that
261 had been preserved with glues, or samples for which we did not have complete knowledge of post-excavation
262 history, were also washed with organic solvents (acetone, methanol and chloroform) prior to AF treatment
263 (coded 'AF*'). Samples were also re-dated using the single amino acid radiocarbon dating method optimised at
264 ORAU¹¹. This method involves separation of the underivatized amino acids using preparative High Performance
265 Liquid Chromatography after hydrolysis of the bone collagen samples. Using this method, the amino acid
266 hydroxyproline was isolated and then combusted, graphitised and dated by AMS. The sample C/M 12836 was
267 prepared in duplicate as part of an internal control at the ORAU. In both laboratories the quality of the
268 collagen (or hydroxyproline) extracted was monitored by measuring carbon and nitrogen contents (%C and
269 %N) and the atomic ratio of carbon to nitrogen (C:N) that is acceptable in the range 2.9–3.5 in the case of
270 collagen or ~5.0 in the case of hydroxyproline.

271
272 The ¹⁴C ages were calibrated against the Northern Hemisphere calibration (IntCal13) dataset¹⁷. Here we used a
273 single 'Phase' model in OxCal 4.3 (ref. ¹⁸) coupled with a 'General' outlier model (probability = 0.05). Using
274 Bayes theorem, the algorithms employed sample possible solutions with a probability that is the product of
275 the prior and likelihood probabilities. Taking into account the deposition model and the actual age
276 measurements, the posterior probability densities quantify the most likely age distributions; the 'Outlier'
277 option was used to detect ages that fall outside the calibration model for each group, and if necessary, down-
278 weight their contribution to the final age estimates. The 'Phase' command is a grouping model which assumes
279 no geographic relationship between samples and that the ages represent a uniform distribution between a
280 start and end boundary. For the model a start and end boundary is included to bracket the *Elasmotherium*
281 'phase'. The posterior distributions allow us to determine probability distribution functions (PDF) for the
282 beginning and ending of the phase. Modelled ages are reported here at the 95% probability range in
283 thousands of calendar years BP (cal ka BP; relative to AD 1950). This method has been applied to a wide range
284 of contexts including studies on megafaunal and Neanderthal extinction^{35,65}, archaeological phases of
285 occupation and ceramic development^{66,67}, and palaeoearthquakes⁶⁸, providing robust age estimates for the
286 start and end of phases, often with fewer ¹⁴C measurements than those reported here. In OxCal, commands
287 or parameters are written in a CQL (Command Query Language).

288
289 The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in bone collagen of a herbivorous mammal reflect the isotopic composition of the
290 plant food and water the organism ingested during its life⁶⁹, and these are in turn related to climatic and local
291 environmental parameters. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of terrestrial C3 plants are mainly determined by (local)
292 environmental and biogeochemical factors, such as humidity, atmospheric CO₂ concentrations, nitrogen
293 cycling and nutrient availability^{70–72}. The stable carbon and nitrogen isotope concentrations ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
294 values) of *E. sibiricum* bone collagen were measured on CO₂ by Isotope Ratio Mass Spectrometry (IRMS).
295 Published comparative data comprised woolly rhinoceros (*Coelodonta antiquitatis*)⁴³, Merck's rhinoceros
296 (*Stephanorhinus kirchbergensis*) and indeterminate *Stephanorhinus* specimens (*S. kirchbergensis* &/or narrow-
297 nosed rhinoceros *S. hemitoechus*)⁷³, and saiga antelope (*Saiga tatarica*)⁵⁴. In the case of *C. antiquitatis* and *S.*
298 *tatarica* we plotted only samples from pre-LGM central Asia, for direct comparison with *E. sibiricum*.

299 Ancient DNA analyses were performed at the Australian Centre for Ancient DNA, University of Adelaide. DNA
300 was extracted from six *E. sibiricum* samples using a silica-based method⁷⁴. Sequencing libraries were then
301 created from the DNA extracts following the protocol of ref. ⁷⁵. We enriched each of the sequencing libraries
302 for mammalian mitochondrial DNA using a previously published set of RNA probes⁷⁶ and sequenced them on
303 an Illumina MiSeq. The resulting sequencing reads were mapped to the mitochondrial genome of the extant

304 white rhinoceros – *Ceratotherium simum* – and consensus sequences were generated for each sample using
305 Geneious (Biomatters; <http://www.geneious.com>). Phylogenetic analyses were performed on these data using
306 BEAST⁷⁷ and RAxML⁷⁸. Additional details can be found in the Supplementary Information.

307 **Code availability**

308 The code used to calibrate the ¹⁴C ages in OxCal is given in the Supplementary Information.

309

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311

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322

323 **Author contributions**

324

325 PK, TvK, AJS, AL & AC conceived the project. PK, AT & EP provided samples & contextual information.
326 Ancient DNA work and phylogenetic analyses were performed by KJM and coordinated by AC.
327 Radiocarbon data was obtained and analyzed by TH, TD and DC at the ORAU, and by JvdP at
328 Groningen, while CT and TH undertook age modelling. Stable isotope analysis was performed and
329 interpreted by MK, while CT & AJS provided context on climate and extinctions, respectively. All
330 authors contributed to the interpretation of results and writing of the manuscript, which was co-
331 ordinated by AL.

332

333 **Additional Information**

334

335 **Supplementary information** accompanies this paper at [.....](#)

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339 **Data Availability:** The four mitochondrial genome consensus sequences with coverage $\geq 80\%$ and
340 mean read-depth $\geq 5\times$ are available on GenBank (MH937513-MH937516). All consensus sequences,
341 unmapped sequencing reads, and phylogenetic analysis files associated with our ancient DNA work
342 are available on figshare (<https://figshare.com/>) DOI: 10.25909/5ba34a40ba925. All the radiocarbon
343 data generated at the ORAU and at Groningen are archived internally at the respective laboratories
344 and are available upon request. ORAU Data is also available on the laboratory's website with link to
345 the paper.

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Figure Captions

543 Figure 1: (A) Artist's impression of *Elasmotherium* in life (from ref⁷⁹). (B) Mounted skeleton of *E.*
544 *sibiricum* from Gaevskaja Village near Stavropol, south-west Russia, on display in the Stavropol
545 Museum (length of skeleton approximately 410 cm, height 250 cm; photo by Dr. Igor Doronin).

546 Figure 2: Map of distribution and samples analysed. Dashed line: total range of specimens referred
547 to *E. sibiricum*^{7,8}. Red circles: samples producing radiocarbon and stable isotope data. Blue circles:
548 samples producing radiocarbon, stable isotope and DNA sequence data. Black circles: no collagen.
549 Note: there are fewer mapped points than actual samples analysed, because of multiple samples

550 from some localities. Map shows ice sheets (grey shading) and bathymetry for MIS 3 (from refs.
551 ^{43,80,81}).

552 Figure 3: Plot of calibrated ages for *E. sibiricum* (calibrated with IntCal13 in OxCal v4.3). Median ages
553 are represented as vertical black lines with 95.4% confidence limits as associated grey bars (HYP
554 dates in darker grey). The blue bar represents our estimate (95.4% posterior distribution) for the last
555 appearance of *Elasmotherium* as derived from our Phase model. The NGRIP $\delta^{18}\text{O}$ Greenland ice core
556 record is shown as a proxy for temperature (more positive values representing warmer
557 temperatures). The maximum counting error reported for the Greenland timescale (GICC05) is
558 considered to approximate the 2σ uncertainty⁸²; for the start of S5 (GS-5.1), this is 1008 years²⁹.
559 Greenland stadials (S1 to S8) and interstadials (I1 to I8) are indicated.

560 Figure 4: Maximum clade credibility tree of rhinoceroses and selected outgroup perissodactyls
561 resulting from our time-calibrated BEAST analyses. Scale is in millions of years before the present.
562 Node heights represent mean age estimates, while node bars represent 95% Highest Posterior
563 Densities (HPDs). Branch support values (BEAST posterior probability / maximum likelihood
564 bootstrap %) are presented in black text for nodes that received less than unequivocal support (i.e.
565 1.0 / 100).

566 Figure 5: Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) values of *Elasmotherium sibiricum* samples,
567 compared to those of Late Pleistocene woolly rhinoceros (*Coelodonta antiquitatis*⁴³), Middle
568 Pleistocene Merck's rhinoceros (*Stephanorhinus kirchbergensis*⁷³) and/or narrow-nosed rhinoceros
569 (*Stephanorhinus hemitoechus*⁷³) and Late Pleistocene saiga antelope (*Saiga tatarica*⁵⁴). *Coelodonta*
570 and *Saiga* data are restricted to the spatio-temporal extent of our *E. sibiricum* samples.

571

A



B









