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

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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 species<sup>1</sup> 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 Elasmotheriinae<sup>2</sup>. 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<sup>2,3</sup>. 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<sup>4,5</sup>. 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 mass<sup>6</sup>; 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<sup>2,7,8</sup> (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<sup>7,9</sup>. Its  
62 ecological niche has been a matter of speculation, from grazing on dry steppes to foraging for roots  
63 in damp riverine environments<sup>7</sup>.

## 64 **Results**

65 Direct dating of unambiguously identified remains is an essential prerequisite for determining the  
66 extinction chronology of late Quaternary megafauna<sup>10</sup>. 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 ORAU<sup>11</sup>. 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. <sup>12-16</sup>). 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 dataset<sup>17</sup> using  
98 OxCal version 4.3<sup>18</sup> (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)<sup>19</sup> 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<sup>20,21</sup>.

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<sup>22,23</sup>, 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<sup>23,24</sup>. 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  $-18.1 \pm 0.3$  ‰. The  $\delta^{15}\text{N}$  values (n=21) range from +6.5‰ to +12.8‰ with a mean of  $+9.4$   
137  $\pm 0.3$  ‰ (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. <sup>4,5</sup>) 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<sup>3,25</sup>, while the earliest certain representative  
156 of Rhinocerotinae is *Epiaceratherium naduongense*<sup>26</sup> 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<sup>2,3</sup>.

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<sup>7,8</sup>. 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 <sup>9</sup>, and <sup>2</sup>, 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, Kazakhstan<sup>27</sup>, 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 ultrafiltration<sup>28</sup>.

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. <sup>29</sup>). 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 ka<sup>30</sup>. 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)<sup>31,32</sup>. 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<sup>33,34</sup>. The latest dates for *E. sibiricum* are closely coincident with those for *Homo*  
185 *neanderthalensis* and the east Beringian stilt-legged horse *Haringtonhippus francisci*<sup>32,35,36</sup>. This was  
186 followed by apparent peripheral range reduction in *C. antiquitatis*<sup>32,37</sup>, and major genetic turnover in  
187 several species including mammoth and bison<sup>32</sup>. The latest records of Eurasian spotted hyaena *C.*  
188 *crocuta* and cave bear *U. spelaeus* are at ca. 31 ka and 28-27 ka, respectively<sup>38-41</sup>, while

189 *Megaloceros giganteus* suffered major range collapse, recovering only in the Late-glacial (GI-1)<sup>42</sup>.  
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<sup>20,43</sup>, 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 3<sup>32</sup>. 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 Atlantic<sup>44</sup>. Plant, insect and lithostratigraphic proxies from across northern Eurasia  
199 corroborate a sustained shift to cold tundra-steppe beginning around 35 ka <sup>14</sup>C BP (equivalent to 40-  
200 38 ka), with the breakup of grass/herb-dominated vegetation cover<sup>45</sup>. 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 adaptations<sup>7</sup>. 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 grazer<sup>46-49</sup>. 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<sup>50,51</sup>, 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 present<sup>52</sup>. 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 biotope<sup>53</sup>. 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*<sup>54</sup>, and/or to the pulling up and  
219 consumption of roots (as suggested for *E. sibiricum*<sup>7</sup>), since non-photosynthetic plant parts tend to  
220 be elevated in  $\delta^{13}\text{C}$  (ref. <sup>55</sup>).

221

222 Previous stable isotope studies on mammalian herbivore species from Europe have illustrated  
223 change in ecological niches during the pre-LGM<sup>56</sup> and the Late glacial<sup>57</sup>. 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 flexibility<sup>54</sup>. 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 size<sup>58</sup>,  
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 ka<sup>59</sup>. 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 <sup>51</sup>; ref.<sup>2</sup>, 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. <sup>60</sup> 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 CO<sub>2</sub> 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 CO<sub>2</sub> using an Elemental Analyser  
254 (Isocube) connected to an Isotope Ratio Mass Spectrometer (Isoprime), providing stable isotope ratios <sup>13</sup>C/<sup>12</sup>C  
255 and <sup>15</sup>N/<sup>14</sup>N. For <sup>14</sup>C, the CO<sub>2</sub> was cryogenically trapped using an automatic collection device. The routine

256 graphitization procedure at the CIO has been operational for over 20 years<sup>61,62</sup>, with only minor, mainly  
257 mechanical, adjustments. The <sup>14</sup>C/<sup>12</sup>C ratio in the graphite was measured by Accelerator Mass Spectrometry<sup>63</sup>.  
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.<sup>64</sup>. 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 ORAU<sup>11</sup>. 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 <sup>14</sup>C ages were calibrated against the Northern Hemisphere calibration (IntCal13) dataset<sup>17</sup>. Here we used a  
273 single 'Phase' model in OxCal 4.3 (ref. <sup>18</sup>) 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<sup>35,65</sup>, archaeological phases of  
285 occupation and ceramic development<sup>66,67</sup>, and palaeoearthquakes<sup>68</sup>, providing robust age estimates for the  
286 start and end of phases, often with fewer <sup>14</sup>C 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 life<sup>69</sup>, 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 CO<sub>2</sub> concentrations, nitrogen  
293 cycling and nutrient availability<sup>70-72</sup>. 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 CO<sub>2</sub> by Isotope Ratio Mass Spectrometry (IRMS).  
295 Published comparative data comprised woolly rhinoceros (*Coelodonta antiquitatis*)<sup>43</sup>, Merck's rhinoceros  
296 (*Stephanorhinus kirchbergensis*) and indeterminate *Stephanorhinus* specimens (*S. kirchbergensis* &/or narrow-  
297 nosed rhinoceros *S. hemitoechus*)<sup>73</sup>, and saiga antelope (*Saiga tatarica*)<sup>54</sup>. 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 method<sup>74</sup>. Sequencing libraries were then  
301 created from the DNA extracts following the protocol of ref. <sup>75</sup>. We enriched each of the sequencing libraries  
302 for mammalian mitochondrial DNA using a previously published set of RNA probes<sup>76</sup> 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 BEAST<sup>77</sup> and RAxML<sup>78</sup>. Additional details can be found in the Supplementary Information.

### 307 **Code availability**

308 The code used to calibrate the <sup>14</sup>C 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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## 542 Figure Captions

543 Figure 1: (A) Artist's impression of *Elasmotherium* in life (from ref<sup>79</sup>). (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*<sup>7,8</sup>. 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 <sup>43,80,81</sup>).

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  $2\sigma$  uncertainty<sup>82</sup>; for the start of S5 (GS-5.1), this is 1008 years<sup>29</sup>.  
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*<sup>43</sup>), Middle  
568 Pleistocene Merck's rhinoceros (*Stephanorhinus kirchbergensis*<sup>73</sup>) and/or narrow-nosed rhinoceros  
569 (*Stephanorhinus hemitoechus*<sup>73</sup>) and Late Pleistocene saiga antelope (*Saiga tatarica*<sup>54</sup>). *Coelodonta*  
570 and *Saiga* data are restricted to the spatio-temporal extent of our *E. sibiricum* samples.

571

**A**



**B**











