

1 The northernmost discovery of a Miocene proboscidean bone in Europe

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27 **ABSTRACT**

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29 We discuss a proboscidean bone fragment discovered in southern Finland, including the
30 morphological analysis of the bone, as well as pollen and diatom analyses from sediment
31 contained in the marrow cavity. Preliminary analysis of the bone suggested petrification and
32 thus an apparently old age, while the microfossil assemblages include numerous unequivocally
33 pre-Quaternary pollen, spore, and diatom types. A Miocene age for the bone is determined
34 based on the presence of the diatom genus *Alveolophora*, indicating a minimum age of 5 Ma,
35 and based on the earliest appearance of proboscideans outside Africa, setting a maximum age of
36 19 Ma. Based on morphology, the bone is determined as a partial humerus of the left foreleg of
37 a large proboscidean. The bone is tentatively assigned to cf. *Deinotherium* sp., which is
38 consistent with the diatom-based minimum age. The pollen assemblage is rich in spores of
39 shoreline pteridophytes, while the diatom assemblage is also consistent with a shoreline
40 freshwater environment, suggesting that the bone was deposited post-mortem near the shore of a
41 lake or a stream. Miocene sediments do not currently exist in southern Finland or in the near
42 vicinity. This implies that the bone has been transported over a considerable distance. Due to the
43 discovery of the bone in early-Holocene Baltic Sea clay, the final transport phase and deposition
44 must have taken place via iceberg rafting. This was likely preceded by one or more phases of
45 glacial and/or glacio-fluvial transport. While we are unable to conclusively ascertain the region of
46 origin, the alkaline composition of the contained sediment and diatoms point towards the
47 Russian Plain region in the east. This specimen represents the oldest mammalian bone
48 discovered in Finland and the northernmost discovery of a Miocene proboscidean bone in
49 Europe.

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51 **Keywords:** Finland, *Deinotherium*, Neogene, pollen, diatoms, environmental reconstruction

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54 **INTRODUCTION**

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56 **Discovery of the bone**

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58 In about 1960, a 25-cm-long bone fragment was found during autumn gardening at a lake-shore
59 “summer house” situated in the municipality of Suomusjärvi, southern Finland (Fig. 1a–b). The
60 finder, young biology student Marja Sorsa, discovered the bone fragment in sandy clay at a
61 depth of about 50–60 cm. The piece, first thought to be a remnant of a ploughing ox or a piece
62 of a mammoth, was stored in a cardboard box in a garden shelter. The bone was later removed
63 from its original finding site into a city garage storage and forgotten until finally in 2006, the
64 finder (M.S.) presented the bone to professor Mikael Fortelius at the meeting of the Finnish
65 Academy of Science and Letters. The bone was identified as a partial humerus of the left foreleg
66 of a proboscidean. Due to its big size and structure, the original hypothesis was that the bone
67 belongs to a proboscidean of Quaternary age, as all fossil mammal specimens previously
68 discovered in Finland have been of late Quaternary or Holocene age, including the ten finds of
69 woolly mammoth (e.g. Ukkonen et al., 2011) the oldest of which is dated to ca. 120 ka
70 (Ukkonen et al., 2010). However, the Suomusjärvi bone raised special interest as it was partly
71 eroded and heavy, possibly indicating a petrification and thus a greater age. As the then
72 available information was too sparse for inferring the age of the bone, we performed
73 sedimentological and microfossil analyses (pollen, diatoms) in order to estimate the age and the
74 depositional environment of the bone. In addition, the morphology and structure of the bone
75 were thoroughly investigated.

76

77 [Figure 1]

78

79 **Geological setting**

80

81 Finland is situated at the centre of the area covered by the Scandinavian Ice Sheet during the
82 Late Pleistocene, and thus in the vicinity of large periglacial centres of terrestrial mammals in
83 Europe and Siberia (Ukkonen, 2001). The Finnish geological setting is mainly composed of
84 Precambrian bedrock (with some small bits of Palaeozoic), stripped clean of younger layers by
85 repeated glacial erosion during the Pleistocene, with the crystalline Precambrian bedrock
86 typically only overlain by glacial deposits of the last glaciation. As the repeated glaciations have
87 generated a landscape consisting of bedrock that is up to 3.2 Ga old and a sediment layer less
88 than 20 ka old, practically no fossil bearing deposits have survived (Ukkonen, 2001). For
89 example, deposits of the Neogene or the Palaeogene do not exist in southern Finland. In
90 contrast, isolated remains of sediments representing these periods have been preserved in
91 northern Finland, where Pleistocene glacial erosion has been weaker due to the location closer
92 to the Fennoscandian ice divide. These deposits include the Palaeogene marine clay at
93 Akanvaara, as well as a Neogene freshwater diatomite in Naruskajärvi (Hirvas and Tynni, 1976;
94 Tynni, 1982; Rasmussen et al., 2008).

95

96 The site of bone discovery is situated in the west of Lake Enäjärvi, in the municipality of
97 Suomusjärvi, in southern Finland (60°17'47"N 23°38'28"E) (Fig. 1a). Today the site is located
98 60 m above the present sea level. The bone was found in clay sediment covered by a thin
99 agricultural soil, at a depth of about 50 cm. The depth and character of the clay layer was
100 confirmed in a later excavation in 2006 (Fig. 1c). The area was released from the late
101 Weichselian ice sheet at the onset of the Holocene around 11,500 years ago (Saarnisto and
102 Saarinen, 2001), and the site of discovery is located between the Salpausselkä II and III ice-
103 marginal formations. In the Baltic Sea history, this timing corresponds with the Yoldia Sea
104 stage, which started when the Baltic Ice Lake was drained to ocean level through channels in
105 central Sweden and water level dropped around 25 m in the Baltic basin ca. 11,700 years ago
106 (e.g. Björck, 1995). During the Yoldia Sea stage, clayish sediments and ice-rafted material from
107 icebergs accumulated at the site within the water depth of around 60 m at this time.

108

109 **Outline of this study**

110

111 Examination of the bone revealed hard-packed brownish silty sediment preserved in the bone
112 marrow cavity (Fig. 1b,d). As microfossils such as pollen and diatoms often contain useful
113 chronological and environmental indicators, the preservation of the sediment thus presents an
114 opportunity to provide further constrains on the history of the bone, both in terms of its age and
115 its geographic origin, as well as the systematic determination of the animal.

116

117 Here we present the results of a multidisciplinary investigation into the origin of the
118 Suomusjärvi bone, including (A) the analysis of the bone fragment itself, (B) pollen and diatom
119 analyses for the sediment contained within the bone, and (C) consideration of the geological
120 context and processes in the setting in which the bone was found. In assessing the results we
121 especially focus on the following four questions:

122

- 123 1. Is it possible to provide a species or genus level identification for the animal based on
124 bone morphology and size?
- 125 2. Is it possible to narrow down the age of the bone based on the species identification
126 together with the microfossil assemblages?
- 127 3. Is it possible to reconstruct the living environment of the animal based on the
128 microfossil assemblages?
- 129 4. If yes, does the environmental reconstruction help confirm the geographical origin of
130 the bone?

131

132 **METHODS**

133

134 **Analysis of the bone**

135

136 The specimen from Suomusjärvi is confirmed to be a fragment of a left humerus diaphysis of a
137 proboscidean. We describe the specimen systematically and compare it with other published
138 proboscidean humeri from the Neogene of Europe. The preservation of the specimen is
139 discussed. Linear osteometric measurements were taken on 1 mm precision with a digital
140 caliper, and minimum circumference was measured with a flexible measuring tape. The
141 measurements were taken following Göhlich (1998) and Huttunen and Göhlich (2002).
142 Minimum depth of the diaphysis was measured from the location of minimum width in the
143 bone. The specimen was weighed at 1 g precision using a digital scale.

144

145 **Sedimentological analysis**

146

147 The composition of the fine fraction sediment preserved in the bone was carried out by the Field
148 Emission Scanning Electron Microscope (SEM) method in the Research Laboratory of the
149 Geological Survey of Finland.

150

151 **Pollen analysis**

152

153 A pollen sample was prepared from ca. 1 cm³ of sediment using KOH and HF treatments
154 (Moore et al., 1991). The entire residue was mounted in silicone oil on six slides and analysed
155 using a light microscope. The pollen were identified using literature on modern European
156 (Moore et al., 1991; Reille, 1992) and Asian (Wang et al., 1997) pollen types, supplemented
157 with literature on European Neogene palynology (Shatilova and Stuchlik, 1996; Grímsson and
158 Zetter, 2011; Grímsson et al., 2011).

159

160 **Diatom analysis**

161

162 The diatom sample of ca. 1 cm³ was prepared using standard methods (Battarbee, 1986). A
163 Nikon microscope with 1000x magnification was used for the identification of diatoms. One
164 hundred valves were counted in the sample. The taxonomy is based on the following sources:
165 Mölder and Tynni (1967–1973), Tynni (1975–1980), Ross et al. (1979), Krammer and Lange-
166 Bertalot (1986–1991), and Usoltseva et al. (2013).

167

168 **RESULTS**

169

170 **Bone**

171

172 *Systematic description and comparison*

173

174 Order Proboscidea Illiger, 1811

175 cf. *Deinotherium* Kaup, 1829 sp.

176

177 Material – humerus (sin.), partial diaphysis

178

179 *Description*

180

181 The specimen from Suomusjärvi is a fragment of the diaphysis (shaft) of a left humerus,
182 belonging to a large-sized proboscidean (Fig. 2). It is fully re-mineralised and heavy for its size,
183 with a mass of 3045 g. The specimen is approximately from the middle of the shaft, preserving
184 the narrowest part of the bone. Measurements of the specimen are shown in Table 1. Despite the
185 fragmentary nature of the specimen, the middle part of the shaft is relatively well preserved in
186 the caudal and lateral surfaces. The cranial surface is more eroded, especially in the proximal
187 part of the specimen, but less so in the distal part which represents the narrowest part of the
188 diaphysis. In the distal end of the specimen, the proximal-most edge of the crista

189 supracondylaris lateralis is partly preserved. The proximal part of the specimen shows a slightly
190 cracked and eroded proximal edge of crista humeri. The crista humeri overall is not prominent
191 and the sulcus musculus brachialis is shallow, making the cross-section of the narrowest part of
192 the shaft rounded rather than triangular in shape. This is likely to approximately represent the
193 original morphology of the bone, because despite the slight fragmenting and erosion of the
194 surface of the specimen, there does not appear to be major distortion to the middle of the shaft.
195 Because the epiphyses are not preserved, it is impossible to estimate how fused they were,
196 making it impossible to estimate the age or growth stage of the individual animal.

197

198 [Figure 2]

199 [Table 1]

200

201 *Comparison and discussion*

202

203 The lack of a prominent crista humeri and the subsequently shallow sulcus musculus brachialis,
204 as well as the relatively rounded cross-section of the Suomusjärvi proboscidean humerus
205 diaphysis, are features characteristic for the genus *Deinotherium* Kaup, 1829 (see Huttunen,
206 2004; Kovachev and Nikolov, 2006) (Figs 2–3). However, the fragmentary nature of the
207 specimen raises some concern about the preservation of these features. In contrast to the
208 Suomusjärvi specimen, gomphotheres (Gomphotheriidae) and mammutids (Mammutidae)
209 typically exhibit strong crista humeri which sometimes result in an almost triangular rather than
210 rounded cross-section of the middle of the humerus shaft (e.g. Göhlich, 2010; Tsoukala and
211 Mol, 2014). Also the earlier, on average smaller-sized deinotheres genus *Prodeinotherium* differs
212 from *Deinotherium* in having a strong crista humeri and deep sulcus musculus brachialis
213 (Huttunen, 2004). The reduced crista humeri of *Deinotherium* compared to other proboscidean
214 taxa is visually shown in Fig. 4. In elephantimorphan proboscideans (Mammutidae,
215 Gomphotheriidae and Elephantidae, sensu Shoshani and Tassy, 2005) the middle part of the

216 humerus shaft tends to be relatively deep in relation to its width, although there is considerable
217 variation, whereas in deinotheres the mid-shaft is craniocaudally somewhat flattened. This is
218 demonstrated by significantly higher average width/depth ratios in deinothere humeri than in the
219 humeri of mammutids, gomphotheres and elephants (Fig. 5). In this respect also, the
220 Suomusjärvi specimen is closer to the average of deinotheres than to the mammutids,
221 gomphotheres and elephants (Fig. 5), although this characteristic does not definitely exclude the
222 other taxa. We tentatively assign this specimen to cf. *Deinotherium* sp.

223

224 [Figure 3]

225 [Figure 4]

226 [Figure 5]

227

228 Measurements of the Suomusjärvi specimen fit with those reported for some specimens of
229 *Deinotherium*, but are relatively small for that genus (Table 1). In particular, the Suomusjärvi
230 specimen is close in size to the *Deinotherium giganteum* specimen from Munich described by
231 Stromer (1938). Another example of a comparable medium-sized *Deinotherium* is the partial
232 skeleton from the late Middle Miocene locality of Gratkorn, Austria, identified as *Deinotherium*
233 *levius* or early *D. giganteum*, although this skeleton lacks humeri almost entirely (Aiglstorfer et
234 al., 2014). Erosion of the Suomusjärvi specimen could have had some (but probably not major)
235 effect on its measurements. It is also worth noting that because the epiphyses of the bone are
236 lacking, we cannot estimate the age or growth stage of the individual, which makes it
237 impossible to estimate whether it was a juvenile or a fully grown animal. This is particularly
238 relevant in the case of proboscideans which continue to grow throughout their life. Other
239 reported specimens of European *Deinotherium*, of presumably younger geological age, are
240 notably larger in size and have variably been assigned to the species *D. giganteum* (e.g.
241 Bachmayer and Zapfe, 1976; Huttunen, 2002; Christiansen, 2004), *D. gigantissimum*
242 (Stefanescu, 1894; Markov, 2008), *D. thraceiensis* (Kovachev and Nikolov, 2006), or *D.*

243 *proavum* (e.g. Pickford and Pourabrishami, 2013).

244

245 **Sediment properties**

246

247 The mineral composition of the clayish fine fraction preserved in the bone differs from that of
248 clay sediments in Finland, including the finding site. The sediment in the marrow cavity appears
249 to originate from more alkaline bedrock compared to the Fennoscandian Shield region in which
250 the bone was found. Such sediments are common further east, e.g. in today's Russia.

251

252 **Pollen content**

253

254 The pollen density in the sediment was extremely low, with only 147 palynomorphs counted
255 from the entire residue remaining from ca. 1 cm³ of sediment. The condition of the
256 palynomorphs was often (but not exclusively) poor, and only 98 palynomorphs could be
257 identified, with 49 left unidentified as degraded and/or broken (37 grains), obscured (9) or
258 unidentified (3). The identified palynomorphs (Table 2) are a combination of various Pre-
259 Quaternary types, exotic to modern Europe, and types closely resembling modern and Late-
260 Quaternary North European pollen.

261

262 [Table 2]

263

264 The most commonly occurring palynomorph, at 26.5 % abundance, is a large, tuberculate type
265 of trilete spore (Fig. 6a–c). Well-preserved specimens of this type match excellently the
266 description of the fossil species *Pteridacidites variabilis* Stuchlik & Shatilova, 1996, with ca.
267 50–55 µm equatorial diameter, sides from polar view either straight or slightly convex but never
268 concave, tuberculate exine with the tubercles on the proximal face concentrated around the
269 laesura to form a ridge-like shape (Fig. 6a) while tubercles on the distal side coalesce to form

270 sinuous shapes (Fig. 6c) (but never a reticulum as seen in some other *Pteridacidites* fossil
271 species; Shatilova and Stuchlik, 1996), and the width of the equatorial collar 4–7 µm with the
272 collar sometimes but not always narrowing at the angles (Shatilova and Stuchlik, 1996). Little
273 variability is seen in size, shape or ornamentation between individual spores, and the examples
274 shown in Fig. 6a–c are representative. Shatilova and Stuchlik (1996) regard *Pteridacidites*
275 *variabilis* as the probable closest ancestor of the modern *Pteris cretica* L. (Cretan brake fern).
276 The spores here designated as *Pteridacidites variabilis* also very closely resemble those of
277 modern *Pteris cretica* (Reille, 1992; Shatilova and Stuchlik, 1996).

278

279 [Fig. 6]

280

281 The second-most commonly occurring type, at 15.3 % abundance, is a small (equatorial
282 diameter ca. 20–22 µm), echinate trilete spore (Fig. 6d). These are comparable with the spores
283 of modern *Selaginella* species (but not the much larger spores of *S. selaginoides* type which
284 occur in late-Quaternary sediments of northern Europe). Consequently, they are here placed
285 within *Echinatisporis*, a fossil genus used for *Selaginella*-type spores (e.g. Grímsson et al.,
286 2011).

287

288 Monolete, bean-shaped spores resembling the modern *Dryopteris*-type occur at 12.2 %. In
289 addition, the sample includes smaller numbers of other, large trilete spores of types not
290 encountered in late-Quaternary sediments of northern Europe (an example in Fig. 6e).

291

292 A final clearly pre-Quaternary feature is the occurrence of pollen grains of Cupressaceae (but
293 representing types other than *Juniperus* which also occurs in the North-European Quaternary).
294 These are small (diameter 22–28 µm) and round inaperturate grains, either fractured (Fig. 6f) or
295 collapsed (Fig. 6g) in the thin-walled germination area. Numerous Cupressaceae tree species
296 were elements in Palaeogene and Neogene forests of Europe, up to the Pliocene (Grímsson and

297 Zetter, 2011). It is not possible to identify these specimens to genus level, as critical diagnostic
298 features such as the papilla are not preserved or visible (Grímsson and Zetter, 2011).

299

300 The remaining palynomorphs (Table 2) represent types which occur in both Neogene and
301 Quaternary sediments of Europe (*Pinus*, Poaceae, *Betula*, *Artemisia*, Chenopodiaceae, *Alnus*,
302 *Equisetum*, and *Juniperus*).

303

304 **Diatom content**

305

306 The investigated sediment sample was abundant in diatoms. They were very well preserved and
307 in good condition, and the diatom assemblage was uniform suggesting a consistent
308 sedimentation environment. This indicates that the analyzed sediment sample is not redeposited.

309 The results of the diatom analysis are presented in Table 3 and micrographs of the most
310 commonly occurring types in Fig. 7. The diatom assemblage was unilateral, i.e. a few diatom

311 species dominate the flora. The most common diatom species were the (mero)planktonic
312 *Alveolophora* sp. and *Aulacoseira granulata* (Ehrenberg) Simonsen (1979), covering about 90

313 % of the total diatom sum. Other species identified at species level were the planktonic species
314 *Cyclotella stelligera* Cleve & Grunow, and the benthic species *Cocconeis pediculus* Ehrenberg

315 and *Nitzschia amphibia* Grunow. Excluding *Alveolophora* sp., the other identified species are still
316 common today in freshwater environments and favour alkaline waters. For example,

317 *Aulacoseira granulata* is a freshwater, meroplanktonic species which prefers alkaline, eutrophic
318 waters. The species is found also in Miocene deposits and remains common today.

319

320 [Table 3]

321 [Figure 7]

322

323 The *Alveolophora* genus is currently understood to be entirely extinct as it existed only from the

324 Late Eocene until the end of the Miocene (Kozyrenko et al., 2008). One finding of *Alveolophora*
325 species is dated to the Early Pliocene (Kozyrenko et al., 2008). *Alveolophora* is primarily
326 reported from fossil localities in Asia, including the Russian Far East (Khursevich, 1994;
327 Kozyrenko et al., 2008) and Lake Baikal (Khursevich and Fedenya, 2006). Recently, three new
328 species of this extinct diatom genus have been described from Miocene sediments in western
329 North America (Usoltseva et al., 2013). Previous studies indicate that all found species of
330 *Alveolophora* are freshwater ones and that the distributions of the species belonging to this
331 genus are regional rather than global. The *Alveolophora* sp. found in our sediment sample could
332 not be identified to species level suggesting that it is a new, previously unknown species of this
333 extinct genus.

334

335 **DISCUSSION**

336

337 **Chronological constraints**

338

339 The most common diatom species *Alveolophora* sp. of the sediment existed from the late
340 Eocene to the late Miocene, between ca. 32 and 5 Ma. As the genus became extinct at the end of
341 the Miocene, this limits the minimum age of the bone at about 5 Ma. The pollen and spore
342 content appears to rule out the pre-Miocene, as fossil spores bearing similarities to *Pteris* are
343 only documented in the European fossil record starting in the Miocene (Shatilova and Stuchlik,
344 1996). However, this inference is uncertain as few Palaeogene and Neogene deposits survive in
345 northernmost Europe, and thus the data on the regional vegetation is scarce.

346

347 However, a more robust estimate of the maximum age can be done based on the expansion of
348 proboscids from Africa. Proboscideans only arrived in Europe in the Early Miocene, ca. 19–17
349 Ma ago (Göhlich, 1999). The genus *Deinotherium* arrived in Europe in the Middle Miocene,
350 somewhere between 16 and 13 Ma, and became extinct in the Pliocene, somewhere between 5

351 and 2 Ma (Göhlich, 1999; see also the NOW database: Fortelius, 2015). The probable affinity of
352 the Suomusjärvi specimen with this genus, together with the information from the diatoms and
353 pollen, would place the age of the find within this time frame, probably in the Late Miocene (ca.
354 11–5 Ma). However, the comparably small size of the specimen for the genus *Deinotherium*
355 could even point at a late Middle Miocene (ca. 16–11 Ma) age, because the size is close to the
356 late Middle Miocene specimens of *Deinotherium* from Austria and Germany, and there was a
357 progressive size increase in European *Deinotherium* through time (see Aiglstorfer et al., 2014).
358 This is, however, highly speculative, especially because the age or growth stage of the
359 individual animal cannot be reliably estimated. Furthermore, the nutritional and general health
360 status of the individual cannot be assessed.

361

362 In summary, a Quaternary age can be conclusively rejected based on the presence of numerous
363 unequivocally pre-Quaternary pollen, spore and diatom types. Further constraints are provided
364 by the presence of the diatom *Alveolophora* sp. which suggests a *minimum age* of 5 Ma, while a
365 *maximum age* of 19 Ma is derived from the earliest appearance of proboscideans outside Africa.
366 There is nothing in the pollen, spores, or diatoms to contradict this age bracket of 19–5 Ma.

367

368 **Palaeobiogeographic significance of the Suomusjärvi proboscidean specimen**

369

370 The proboscidean humerus specimen from Suomusjärvi, Finland, latitude 60°22'N, is the
371 northernmost Miocene proboscidean fossil found anywhere in the world so far. Even accounting
372 for all the possible transport directions of the specimen, it could not have been drifted from very
373 much further south, and indeed it is more likely to originate from even further north than where
374 it was found (see the discussion below). In Eurasia, the previously northernmost proboscidean
375 finds come from localities up to ca. 52°N (e.g. Ermak and Bestobe, Kazakhstan, and
376 Rothenstein, Germany), and the northernmost finds of *Deinotherium* from Germany (49–50°N),
377 e.g from N-Ebing Inn, Wissberg and Gau-Weinheim (NOW database: Fortelius, 2015). In North

378 America the northernmost finds of the Miocene proboscideans *Zygodon* and
379 *Gomphotherium* come from Wood Mountain, Saskatchewan, Canada, 49°37'N (Madden and
380 Storer, 1985). The ca. 50°N northern limit in the distribution of Miocene proboscidean finds has
381 most likely been a bias caused by a lack of mammal bearing fossil localities further north, and
382 there is no ecological or climatic reason to expect that proboscideans could not have occurred
383 further north. In fact, the Miocene palaeobotanic records from Denmark and Iceland show a
384 mixture of temperate and subtropical vegetation indicating subtropical climate in Northern
385 Europe, substantially warmer than at present (Larsson et al., 2006; Grímsson et al., 2007),
386 which is supported by the pollen and diatoms associated with the Suomusjärvi specimen (see
387 discussion below). Humid, heavily wooded conditions prevailed throughout the Late Miocene in
388 the proboscidean localities from Germany (Franzen et al., 2003; Costeur et al., 2013), although
389 the habitats of *Deinotherium* further north could have been different. Most likely representing
390 the genus *Deinotherium*, the Suomusjärvi proboscidean would have been a large woodland
391 browser feeding primarily on leaves from trees (see e.g. Calandra et al., 2008). This would fit
392 well with the suggested environmental interpretations.

393

394 **Interpretation based on the microfossil content and environmental reconstruction**

395

396 A remarkable feature of the palynoflora is that 54 % of the count consists of spores of just three
397 types (*Pteridacidities variabilis*, *Echinatisporis* sp., and *Dryopteris*-type), presumably
398 representing pteridophyte species of *Pteris*, *Selaginella*, and the various pteridophyte taxa
399 producing monolete spores commonly lumped together as the *Dryopteris*-type (e.g. Moore et
400 al., 1991). In the Neogene, all three genera (*Pteris*, *Selaginella*, *Dryopteris*) are regarded to have
401 occurred as components in the shoreline vegetation of lakes or streams (Shatilova and Stuchlik,
402 1996; Grímsson et al., 2011). As these spores occur at anomalous frequencies compared with
403 other European Miocene deposits (Fig. 8), in which pteridophyte spores occur only at very low
404 numbers (e.g. Jiménez-Moreno et al., 2005; Larsson et al., 2006; Grímsson et al., 2011), and as

405 just a few spore types dominate the palynoflora, the likeliest explanation is that the bone was
406 first deposited very close to the shore of a lake or a stream. This caused the observed over-
407 representation of the shoreline pteridophytes which happened to occur at the site of deposition,
408 while comparatively few pollen from the regional terrestrial vegetation are seen.

409

410 [Figure 8]

411

412 Although all the pollen and spore types found do occur in the European Miocene, we consider it
413 probable that some Quaternary admixture has taken place during the later transport of the bone.
414 Admixture of Quaternary pollen is suggested especially by the relatively large proportions of
415 Chenopodiaceae and *Artemisia* (Table 1). These taxa are key components in the tundra–steppe
416 vegetation of the cold stages of the Quaternary, while in the European Miocene palynoflora,
417 although present, they do not typically occur at such percentages (e.g. Stuchlik and Shatilova,
418 1987; Jiménez-Moreno et al., 2005; Larsson et al., 2006). We note that while the unequivocally
419 pre-Quaternary spore and pollen types were generally in good condition (see examples in Fig.
420 6), the pollen and spore types consistent with a Quaternary age were often much worse
421 preserved, being superficially similar to the reworked pollen commonly seen in Quaternary
422 glacial sediments of Fennoscandia. The observed palynoflora might best be explained as a
423 Neogene local shoreline assemblage (with some Cupressaceae from the surrounding terrestrial
424 vegetation included) later mixed with a smaller fraction of reworked late-Quaternary pollen
425 (*Alnus*, *Betula*, *Juniperus*, *Pinus*, *Artemisia*, Chenopodiaceae, Poaceae, *Equisetum*) during the
426 transport of the bone.

427

428 *Pteris cretica* today has a wide distribution in subtropical and tropical climates, including the
429 Mediterranean and Black Sea regions, Madagascar, South and East Asia, Central America and
430 the Caribbean, and Florida (Shatilova and Stuchlik, 1996). The presence of its probable close
431 ancestor *Pteridacidites variabilis* thus suggests at least a subtropical climate at the time of bone

432 deposition. We note that other *Pteris* species also have a mainly subtropical and tropical
433 distributions (Shatilova and Stuchlik, 1996), while the *Pteris* species constituting the *Pteris*
434 *cretica* complex in North America occur in the tropics (Martínez and Morbelli, 2009), and thus
435 the inference of at least subtropical conditions is likely robust to the species-level identification
436 of our *Pteris*-type spores. Results on Miocene vegetation in Austria (Grímsson and Zetter, 2011;
437 Grímsson et al., 2011), Germany (Uhl et al., 2006), Denmark (Larsson et al., 2006), and Iceland
438 (Grímsson et al., 2007), showing a mixture of temperate and subtropical vegetation elements
439 and a generally subtropical climate, preclude full-tropical conditions in northern Europe, and
440 thus the final climatic inference becomes subtropical.

441

442 Diatoms indicate freshwater, alkaline and eutrophic sedimentation environment, i.e. the bone
443 was stratified in a river or small lake of relatively high nutrient content. This sedimentation
444 environment might indicate a relatively warm climate. Thus the diatom results are consistent
445 with the pollen-based inference both in terms of depositional environment and climate.

446

447 Miocene proboscidean assemblages from Europe are typically associated with sediments
448 indicating riparian environments or the presence of substantial waterbodies. This probably
449 indicates a preference of these animals to seek waterbodies in order to get a regular access to
450 drinking water and to wallow in water, similarly to modern elephants. Major Early and Middle
451 Miocene proboscidean localities, such as German Molasse Basin localities and Sansan from
452 France, indicate the presence of riparian, lacustrine and wetland environments (Calandra et al.,
453 2010; Costeur et al., 2012). The early Late Miocene (Vallesian) locality of Eppelsheim in
454 Germany, the type locality of the abundant and wide-spread European Late Miocene deinothere
455 species *Deinotherium giganteum*, consists of fluvial deposits of the Dinotheriensande Formation
456 deposited by the ancient Rhine River (Franzen et al., 2003). The same locality has yielded
457 remains of the gomphotheriid proboscidean *Tetralophodon longirostris*. Pollen records from
458 Eppelsheim indicate a floodplain environment surrounded by subtropical forests (Franzen et al.,

459 2003; Kaiser, 2004). The later Late Miocene (Turolian) locality of Dorn-Dürkheim 1 from
460 Germany has provided fossils of *Deinotherium* and gomphotheres (Franzen et al., 2013). The
461 environment of Dorn-Dürkheim 1 was suggested by Costeur et al. (2013) to have comprised
462 both forest and patches of open vegetation based on the diverse mammal community. Moreover,
463 e.g. the abundant and diverse record of fossil beavers suggests the presence of substantial
464 waterbodies and river channels in the palaeoenvironment of Dorn-Dürkheim 1 (Costeur et al.,
465 2013). The inferred riparian environment of the Suomusjärvi proboscidean are consistent with
466 these observations.

467

468 **Constraints on transport direction**

469

470 The discovery of an apparently Miocene-age bone from the southern Finland presents a
471 considerable conundrum, as no Miocene bones are known from the Nordic countries. To date,
472 the northernmost findings are from ca. 50°N (Fig. 8). As even deposits of Miocene age are not
473 known from either southern Finland or the near vicinity (Rasmussen et al., 2008), the
474 implication is that the bone must have been transported over considerable distance to the site of
475 discovery.

476

477 One possibility for bone origin is glacial transport from the North, during one or more of the
478 latest Quaternary glaciations. The site of discovery lies south of the Fennoscandian ice divide,
479 and in the general direction of glacial erratic drift from the ice divide (e.g. Donner, 1989). As
480 noted, sparse terrestrial Miocene sediments have been discovered in the northern Finland ice-
481 divide region (Hirvas and Tynni, 1976; Tynni, 1982), presenting a possible source region.
482 However, as the bone was found in clay representing an early-Holocene stage of the Baltic Sea
483 (Yoldia Sea), the final transport and deposition must have been through iceberg rafting. Given
484 the prevailing currents in the Baltic Sea, this transport phase likely had a westward direction.
485 However, considering the great distance to closest known Miocene deposits (Fig. 8), this early-

486 Holocene iceberg rafting was likely preceded by other transport phases, including one or more
487 phases of glacial and/or glacio-fluvial transport during the late Quaternary. Considering the
488 likelihood of multiple phases and modes of transport, but with the exact number of transport
489 phases and modes unknown, we are unable to estimate the likely region of origin with any
490 confidence.

491

492 We note, however, that both the alkaline composition of the bone-cavity sediment and the
493 diatom flora suggest an origin in a region of alkaline bedrock. This points towards an origin in
494 the east, in the Russian Plain region, instead of the acidic bedrock region of the Fennoscandian
495 Shield. The maximum transport distance is set by the maximum extent of Quaternary
496 glaciations in northern Europe (e.g. Svendsen et al., 2004), as all credible transport mechanisms
497 require the presence of an ice sheet. Together, these considerations suggest a possible origin in
498 the northern part of European Russia.

499

500 The pollen, spores and diatoms found within the bone include some environmental indicators,
501 but we are unable to better pinpoint the origin of the bone with these, especially as only sparse
502 Miocene sediments survive in northern Europe to serve as points of comparison and Miocene
503 environments and species compositions in northern Europe are thus poorly resolved. As noted,
504 the presence of *Pteridacidites variabilis* suggests a subtropical climate during bone deposition.
505 Climate reconstructions from other European sites suggest humid-subtropical-type climates (~
506 Köppen classification Cfa) to have prevailed widely in central and northern Europe, from
507 Austria to Iceland (Uhl et al., 2006; Grímsson et al., 2007, 2011; Grímsson and Zetter, 2011)
508 during the Miocene, with further indications of subtropical trees such as palms and *Engelhardia*
509 also thriving in Denmark (Larson et al., 2006). Taken together, these evidence suggests a weak
510 latitudinal temperature gradient in Europe. Thus, while the pollen and spore content in the
511 Suomusjärvi bone are consistent with these palaeoclimatic reconstructions from other central
512 and northern European sites, the bone cannot confidently be said to originate from any specific

513 region.

514

515 The diatoms within the bone's marrow cavity do not support transport from northern Finland as
516 this kind of diatom assemblage has not been previously discovered from Finland. Of course, this
517 can be due to the very sparse Miocene deposits found in Finland and thus the transport from the
518 north cannot be ruled out. Sediment properties and the presence of *Alveolophora* sp. might
519 suggest transport from the east (Russia) as there this species is rather common in the Miocene
520 sediments, although most of the findings originate as far away as the Russian Far East.
521 However, the lack of *Alveolophora* findings from the W–NW European Russia can be due to
522 the regionally restricted occurrence of the species of this diatom genus and/or the several
523 glaciations which have eroded the area.

524

525 CONCLUSIONS

526

527 We return here to the four questions presented in the Introduction:

528

529 1. The specimen from Suomusjärvi was identified as a partial diaphysis of the left
530 humerus of a large proboscidean. Based on a few key morphological features and size
531 of the specimen, it most likely represents the genus *Deinotherium*, and it is described
532 here as cf. *Deinotherium* sp. Coming from the latitude of ca. 60°N, and possibly
533 originating from even further north, this is the northernmost Miocene proboscidean
534 fossil found anywhere in the world. The previously northernmost finds, including those
535 of European *Deinotherium*, come from localities ca. 50°N.

536 2. A minimum age of 5 Ma for the bone is set based on the presence of an unidentified
537 diatom species belonging to the genus *Alveolophora*, while a maximum age of 19 Ma is
538 set by the earliest arrival of proboscideans to Europe. Together, these evidence confirm
539 a Miocene age for the specimen. If the identification of the bone as *Deinotherium* sp. is

540 correct, the maximum age is further reduced to 13.5 Ma based on the first appearance of
541 this genus in Europe.

542 3. The pollen and diatom assemblages suggest that the bone was deposited close to the
543 shore of a lake or a stream. The pollen assemblage suggests at least a subtropical
544 climate, which is consistent with the inferences of a subtropical climate from other
545 Miocene sites in central and northern Europe.

546 4. The geographical origin (i.e. transport direction) of the bone remains poorly resolved.
547 The discovery of the bone in early-Holocene Palaeo-Baltic clay suggests iceberg rafting
548 as the final transport mode, however this was likely preceded by one or more phases of
549 glacial and/or glacio-fluvial transport. The alkaline composition of the bone-cavity
550 sediment and the generally alkaline diatom flora suggest a possible origin in the east, in
551 the Russian Plain. However, the microfossils found cannot conclusively ascertain the
552 region of origin as few Miocene deposits survive for comparison in northern Europe.

553

554 **ACKNOWLEDGEMENTS**

555

556 JSS acknowledges funding from the Academy of Finland program on long-term environmental
557 changes (project no. 278692) and the Finnish Cultural Foundation. JS was working at the
558 Natural History Museum of London during this collaboration, funded by Osk. Huttunen
559 Foundation, Finland. MU acknowledges funding from the project no. VI.50.1.3 (0345-2014-
560 0001). The Suomusjärvi bone has been donated to and is on permanent display at the Finnish
561 Museum of Natural History in Helsinki, Finland. The *Elephas recki* humerus from Olduvai
562 shown in Fig. 3 is stored in the Natural History Museum, London, UK. The *Mammuthus*
563 *primigenius* humerus from Lampertheim, Germany, shown in Fig. 4 is stored in the Staatliches
564 Museum für Naturkunde, Stuttgart. We thank Reinhard Ziegler from Staatliches Museum für
565 Naturkunde, Stuttgart, for granting a permission to use the photo of a mammoth humerus in Fig.
566 4e, and Spyridoula Pappa from the Natural History Museum of London for the permission to

567 use the photo of *Elephas recki* humerus in Fig. 3.

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809 **Table 1.** Measurements of the Suomusjärvi specimen and some European deinothere humerus
 810 specimens. Min. diaph. width = smallest latero-medial diameter of diaphysis. Min. diaph. depth
 811 = smallest cranio-caudal diameter of diaphysis. Min. diaph. circ. = smallest circumference of
 812 diaphysis.

813

Measurement (mm)	cf. <i>Deinotherium</i> sp., Suomusjärvi	<i>Deinotherium giganteum</i> , Munich (Stromer, 1938)	<i>Deinotherium giganteum</i> , Kettlasbrunn (measurements by J. Saarinen)	<i>Deinotherium thraceiense</i> , Ezerovo (Kovachev and Nikolov, 2006)	<i>Prodeinotherium bavaricum</i> , Franzenbad (Huttunen, 2004, J. Saarinen)	<i>Prodeinotherium bavaricum</i> , Untertzolling (Huttunen and Göhlich, 2002)
Min. diaph. width	114	115	170	190 sin., 195 dext.	104	132
Min. diaph. depth	99	-	154	-	95	-
Min. diaph. circ.	359	-	545	-	350	420

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832 **Table 2.** Pollen analysis results.

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Type	Count	% of total
<i>Pteridacidites variabilis</i>	26	26.5
<i>Echinatisporis</i> sp.	15	15.3
<i>Dryopteris</i> -type	12	12.2
<i>Pinus</i>	12	12.2
Poaceae	10	10.2
<i>Betula</i>	6	6.1
Indet. trilete spores	6	6.1
<i>Artemisia</i>	3	3.1
Chenopodiaceae	3	3.1
Indet. Cupressaceae (Neogene non- <i>Juniperus</i> types)	2	2.0
<i>Alnus</i>	1	1.0
<i>Equisetum</i>	1	1.0
<i>Juniperus</i>	1	1.0
Total count	98	100.0

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859 **Table 3.** Diatom analysis results.

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Diatom species	Count	% of total
<i>Alveolophora</i> sp	65.5	54.6
<i>Aulacoseira granulata</i>	42.5	35.4
<i>Cocconeis pediculus</i>	3	2.5
<i>Cyclotella stelligera</i>	2	1.7
<i>Gomphonema</i> sp.	2	1.7
<i>Nitzschia amphibia</i>	2	1.7
<i>Nitzschia</i> sp1	2	1.7
<i>Nitzschia</i> sp2	1	0.8
Total count	120	100

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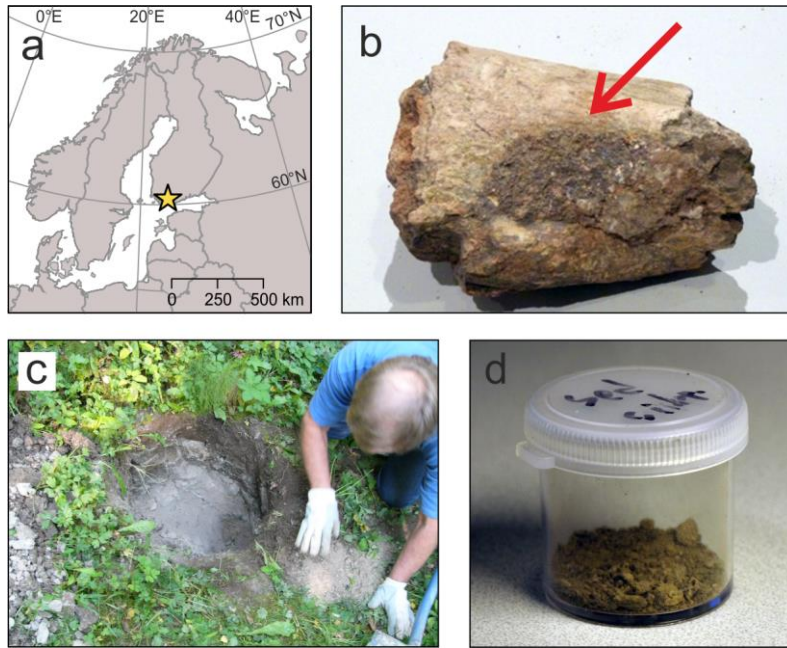
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883 **Figure 1.** (a) Site of bone discovery. (b) Photograph of the bone (the brownish sediment
884 indicated with a red arrow) (Photo: Laura Hiisivuori, the Finnish Museum of Natural History).
885 (c) An excavation in 2006 at the site of discovery, showing the Yoldia Sea clay layer (light
886 grey) in which the bone was found (Photo: Veikko Sorsa, University of Helsinki). (d) Some of
887 the sediment sample on which the diatom and pollen analyses were performed.

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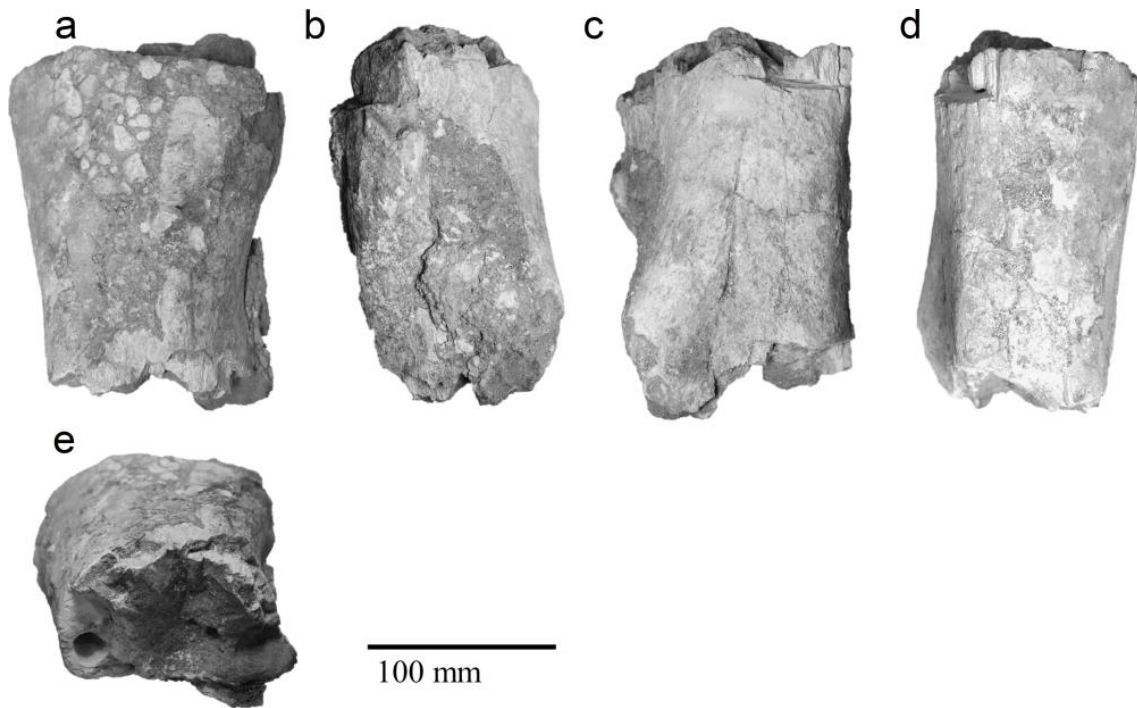
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901 **Figure 2.** The Suomusjärvi proboscidean fossil (left humerus diaphysis) in (a) cranial, (b) left

902 lateral, (c) caudal, (d) right lateral and (e) craniodistal view.

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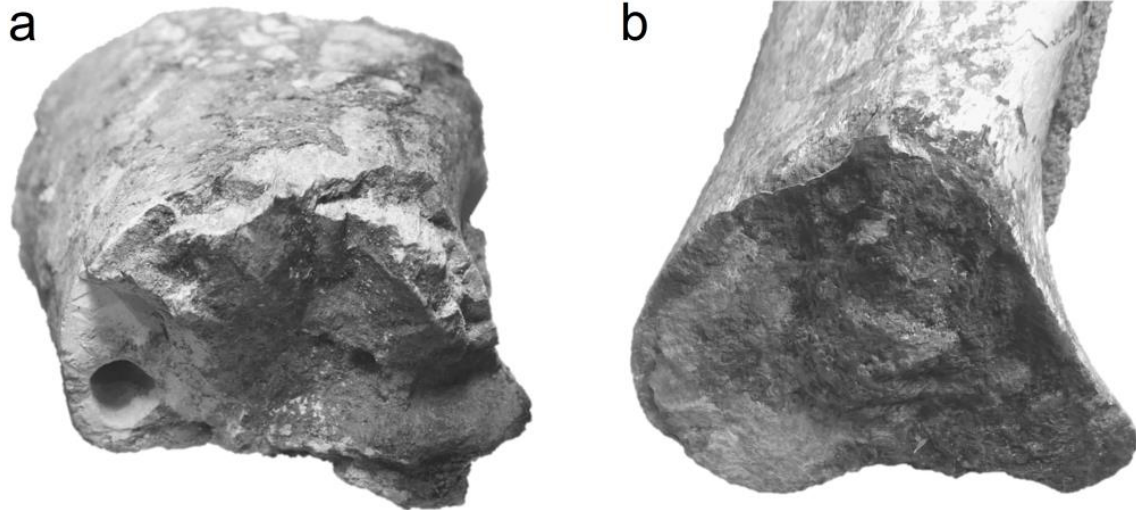
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918 **Figure 3.** Visual comparison of the cross-sections of (a) the Suomusjärvi specimen and (b) a
919 fossil elephant (*Elephas recki*) humerus (NHM M 14691) from Olduvai, Tanzania. Note the
920 lack of prominent crista humeri in the Suomusjärvi humerus resulting in a rounded rather than
921 triangular cross-section at the mid-shaft of the bone. The elephantid humerus figure has been
922 reversed for comparison. The photos are not in the same scale. The *E. recki* specimen from
923 Olduvai is stored at the Natural History Museum of London.

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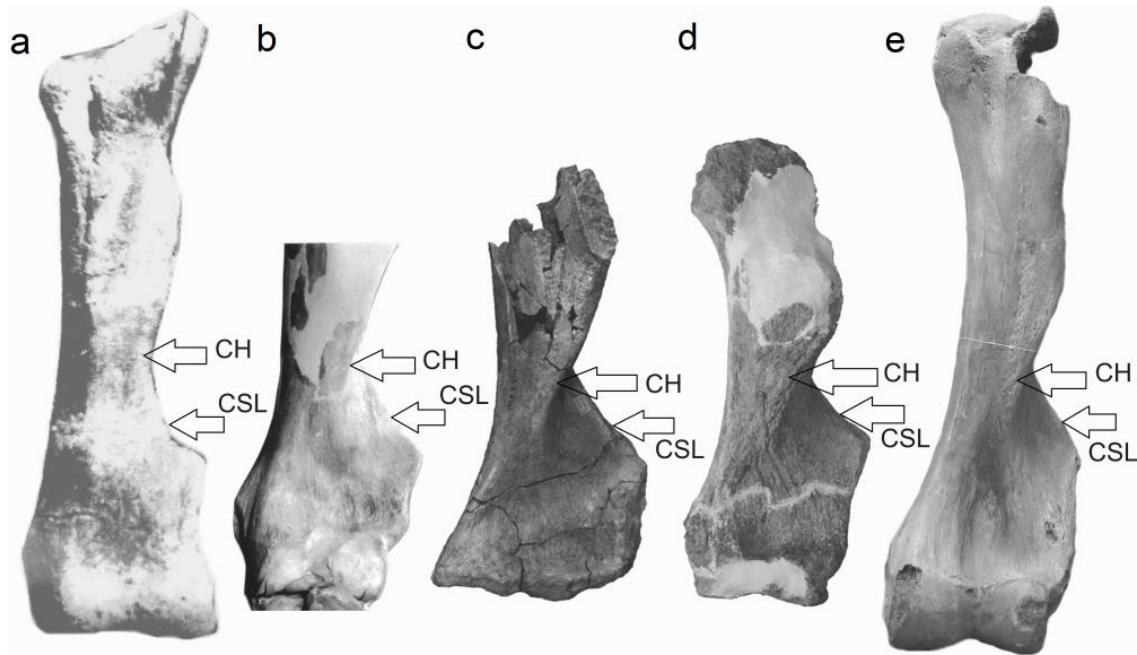
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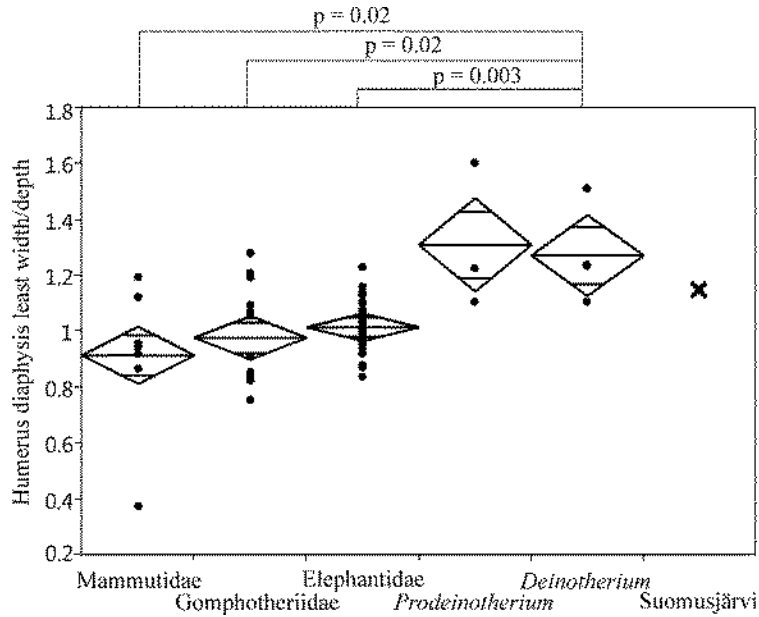
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937 **Figure 4.** Examples of the humeri of *Deinotherium* (a), *Prodeinotherium* (b), *Gomphotherium*
938 (c), *Mammuthus* (d) and *Mammuthus* (e), with arrows pointing at the crista humeri (CH) and the
939 crista supracondylaris lateralis (CSL). Photos c, d and e are reversed in order to show the
940 features as they appear in the Suomusjärvi specimen. The photos are not to the same scale. Note
941 the strongly reduced and inconspicuous crista humeri of *Deinotherium* compared to the other
942 taxa. a. *Deinotherium thraceiensis* (Deinotheriidae) from Ezerovo, Bulgaria (Kovachev and
943 Nikolov, 2006), b. *Prodeinotherium bavaricum* (Deinotheriidae) from Franzensbad, Czech
944 Republic (Huttunen, 2004), c. *Gomphotherium subtapiroideum* (Gomphotheriidae) from
945 Sandelzhausen, Germany (Göhlich, 2010), d. *Mammuthus americanum* (Mammutidae) from
946 Hidalgo, Mexico (Bravo-Cuevas et al., 2015) and e. *Mammuthus primigenius* (Elephantidae)
947 (SMNS 6316.2.6.82.2) from Lampertheim, Germany (J. Saarinen, specimen stored in
948 Staatliches Museum für Naturkunde, Stuttgart). Photos are reproduced with permissions from
949 the journals (a, b, d) or publishers (c).

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955 **Figure 5.** Minimum width / minimum depth of the narrowest part of humerus diaphysis for
 956 proboscidean groups. Mean values are indicated by mean diamonds in which the middle line
 957 shows the mean and the upper and lower lines represent 95% confidence limits. The deinotheres
 958 have on average larger width in relation to depth than the other families (significant differences
 959 in mean width/depth between *Deinotherium* and Elephantidae, Gomphotheriidae and
 960 Mammutidae are indicated as p-values in the figure), and the Suomensjärvi specimen fits closer
 961 to the average of deinotheres than to the average of the other proboscideans in this respect. The
 962 data for this comparison is gathered from literature (Göhlich, 1998, 2010; Huttunen and
 963 Göhlich, 2002; Christiansen, 2004; Kovachev and Nikolov, 2006; Ferretti, 2010, Tsoukala and
 964 Mol, 2014; Bravo-Cuevas et al., 2015) and from specimens measured by J. Saarinen.

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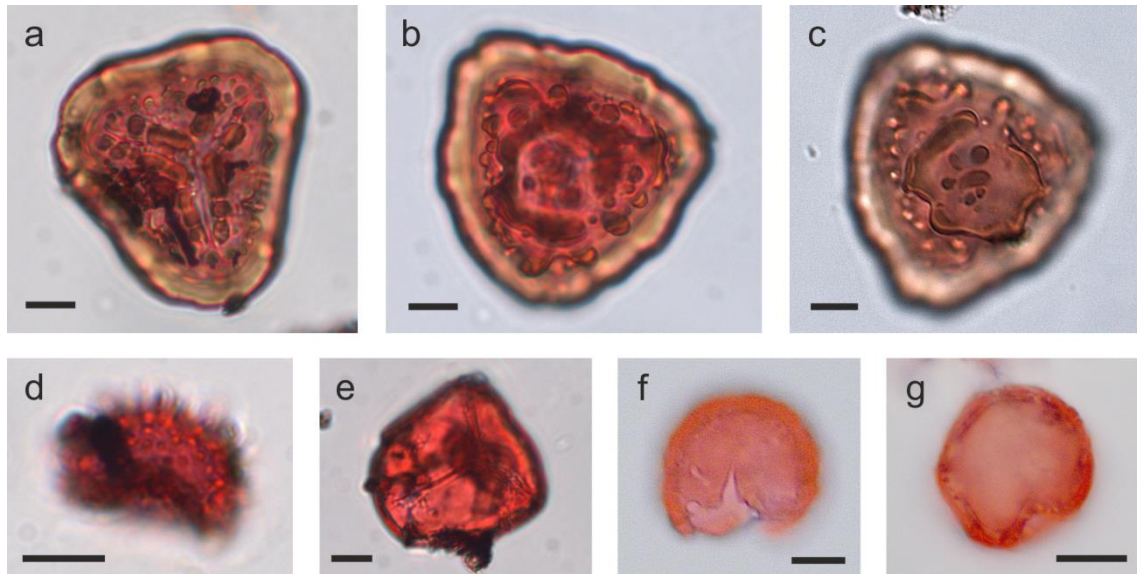
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973 **Figure 6.** Micrographs of Miocene palynomorphs found in the Suomusjärvi bone: **(a)**

974 *Pteridacidites variabilis*, specimen 1, proximal view, 400× magnification; **(b)** *Pteridacidites*

975 *variabilis*, specimen 2, distal view, 400×; **(c)** *Pteridacidites variabilis*, specimen 3, distal view

976 on surface ornamentation, 400×; **(d)** *Echinatisporis* sp., 600×; **(e)** indet. trilete spore, 400×; **(f)**

977 indet. Cupressaceae, specimen 1, 400×; **(g)** indet. Cupressaceae, specimen 2, 1000× in oil

978 immersion. Scale bars = 10 μm.

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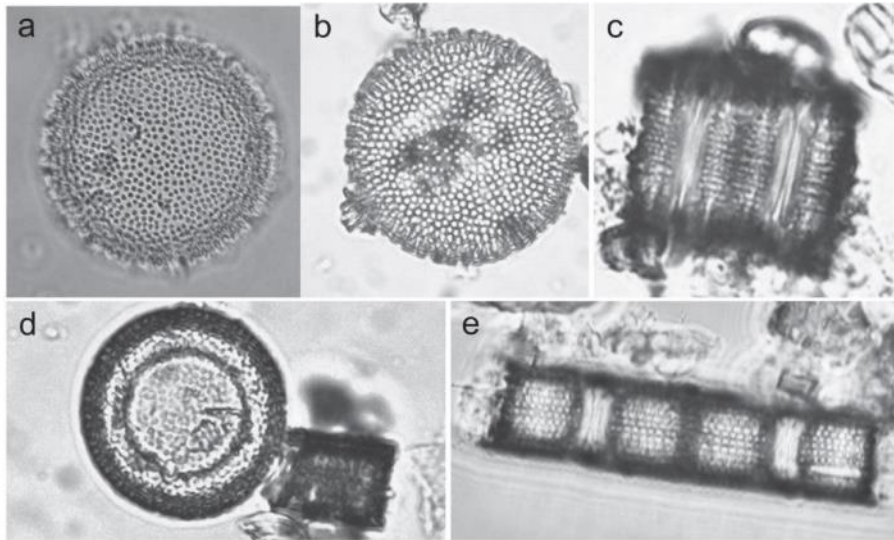
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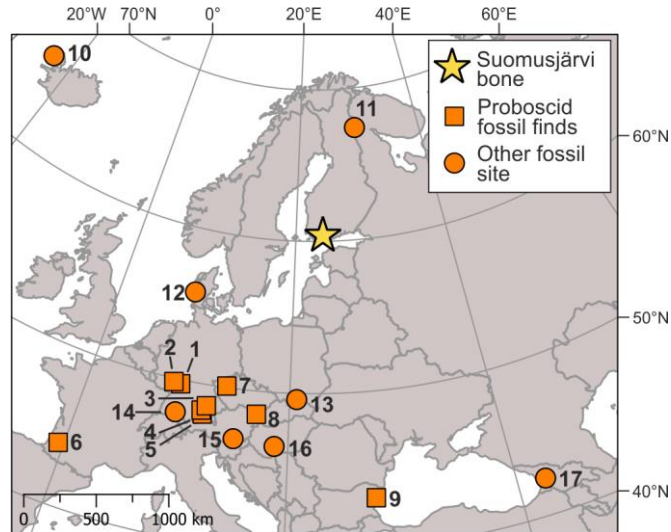
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Figure 7. The most common diatom species in the sample: (a, b, d) *Alveolophora* sp. (valve view); (c) *Alveolophora* sp. (mantle view); (e) *Aulacoseira granulata* (mantle view).



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1011 **Figure 8.** Map showing the site of bone discovery and locations of Neogene/Miocene proboscis
 1012 and other fossil sites referenced in the text. Names and references for the numbered sites: **1**,
 1013 Eppelsheim (Fortelius, 2015); **2**, Dorn-Dürkheim 1 (Fortelius, 2015); **3**, Sandelzhausen
 1014 (Fortelius, 2015); **4**, Unterzolling (Fortelius, 2015); **5**, Munich (Fortelius, 2015); **6**, Sansan
 1015 (Fortelius, 2015); **7**, Franzensbad (Fortelius, 2015); **8**, Kettlasbrunn (Fortelius, 2015); **9**,
 1016 Ezerovo (Fortelius, 2015); **10**, Iceland (Grímsson et al., 2007); **11**, Naruskajärvi (Hirvas and
 1017 Tynni, 1976; Tynni, 1982); **12**, Sønder Vium (Larsson et al., 2006); **13**, Nowy Sącz and Nowy
 1018 Targ-Orawa Basins (Stuchlik and Shatilova, 1987); **14**, Bohlinger Schlucht (Uhl et al., 2006);
 1019 **15**, Lavanttal Basin (Grímsson and Zetter, 2011; Grímsson et al., 2011); **16**, Pannonian Basin
 1020 (Jiménez-Moreno et al., 2005); **17**, Western Georgia (Stuchlik and Shatilova, 1987; Shatilova
 1021 and Stuchlik, 1996).