

**Title: Prehistory of the British Isles: A tale of coming and going**

**Titre: La préhistoire des îles britanniques: Une histoire de va-et-vient**

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**Abstract:**

It is now recognized that Britain has not always been geographically isolated from Europe and, for most of the last one million years, formed an extension of the northwest European landmass. During most of this time, Britain was accessible to migrating humans and animals, although climatic conditions varied greatly from Mediterranean-like through to glaciations and extreme cold, making Britain a difficult place to settle for any length of time. The oldest evidence for humans in Britain dates to between about 850,000 and 1 million years ago. Recovered lithic artefacts suggest that hominin species occupied and deserted the British Isles at least nine times. In this article, we review the prehistory of the British Isles and present the main sites and time periods.

Il est bien connu que les îles britanniques n'ont pas toujours été des îles et que pendant la plus grande partie du dernier million d'années, elles faisaient partie d'une péninsule s'étendant à partir du (ou à l'extrémité) nord-ouest de l'Europe. Cette région était alors accessible aux humains et aux animaux venant du continent. Les conditions climatiques ont varié entre celles trouvées aujourd'hui en Méditerranée et les conditions désertiques des régions polaires, rendant la Grande-Bretagne un endroit difficile à habiter. La plus ancienne preuve de présence humaine en Grande-Bretagne date entre 850000 et 1 million d'années. Les industries lithiques suggèrent que les espèces d'hominines se sont depuis installées puis ont déserté les îles britanniques au moins neuf fois. Dans cet article, nous proposons une revue des connaissances sur la préhistoire des îles britanniques, à partir des principaux sites et périodes correspondantes.

### ***Introduction***

When did the first humans arrive in what is now known as the British Isles? It is well known that the British Isles were not always islands and for most of the last one million years, they formed part of a peninsula extending from northwest Europe, potentially accessible by migrating humans and animals. Britain was not a straightforward place to settle, however, with the local climate oscillating between temperatures similar to those found in the modern Mediterranean through to polar desert conditions. Humans were able to migrate into the territory temporarily but were repeatedly pushed out by successive ice ages. The process of colonisation was repeated at least 9 times, but when the last British ice sheets began to melt around 12,000 years ago, a new wave of migrants was able to settle more permanently. Lithic artefacts of varying industries and ages have been found across most of Britain for its 1-million-year-long human history, but human fossil remains are few. In this paper, we provide an overview of the presence of humans in the British Isles and present their tale of coming and going.

### ***The first explorers (1 million to 450,000 years ago)***

Layers dating back to the late early Pleistocene (between 1 and 0.78My ago) from Happisburgh (pronounced ‘Hays-bruh’) have yielded flint artefacts, butchered animal bones and even human footprints [1, 2]. The lithic artefacts of a Lower Palaeolithic industry were found in river deposits, and are the oldest known stone tools in northwest Europe.

### ***Connected lands***

From the early Pleistocene, Britain was connected to mainland Europe by a land-bridge that enabled humans and fauna to migrate in and out (Figure 1A). Until about 130,000 years ago, this narrow chalk isthmus, separating the north (North Sea) and southwest (English Channel)

57 marine embayments, kept Britain connected to varying extents even when sea-levels were  
58 high during the warm interglacial periods [3]; the eventual complete breaching of this chalk  
59 barrier was crucial in forming the island and the Dover Strait. During glacial periods much of  
60 the earth's water would have been trapped in the ice caps and when, during the later  
61 Pleistocene, the bed of the North Sea was exposed, a large land area known as Doggerland,  
62 created by geological uplift and sedimentation from rivers, also provided a route into the  
63 British Isles and fauna, including hominins, would have entered this way. The flooding of the  
64 shallow shelf areas of the English Channel and the North Sea are the consequence of the  
65 current high interglacial sea levels.

66

#### 67 **The main sites and their evidence**

68 The site with the oldest evidence for humans in the British Isles is at **Happisburgh**, Norfolk,  
69 now located on the eastern English coast (Figures 2 and 3) [1]. During the Early Pleistocene  
70 Happisburgh formed part of a large river estuary, close to the confluence of the now extinct  
71 Bytham and the palaeo-Thames (currently flowing further south through London) [4]. The  
72 Happisburgh sites, now numbering more than five localities, are situated on and near the  
73 present-day beach. The cliffs there are composed of till deposited by glaciers with laminae of  
74 undisturbed bedding surfaces beneath. The sediments at the base of the cliffs (Happisburgh  
75 site 3) were excavated between 2005 and 2010, and around 80 lithic artefacts were  
76 discovered dating broadly to between 850,000 and 950,000 years ago [5]; a borehole through  
77 the cliffs to the underlying estuarine sediments was taken in May 2013. Results show that  
78 these sediments are predominantly estuarine sands and silts forming the infill of channels  
79 with intermittent gravel deposits. The gravel deposits, up to 20cm in thickness, within these  
80 sands and silts have yielded flint flakes and cores. In addition, a rich assemblage of flora and

81 fauna has allowed their attribution to the latter part of an interglacial during the late Early  
82 Pleistocene, perhaps Marine Isotope Stage (MIS) 21 or 25.

83

84 In May 2013, a footprint surface was discovered near Happisburgh site 3 and found to be in  
85 the same complex of channel fills as the archaeological layers. The exposure of the laminated  
86 silts through coastal erosion is frequent at Happisburgh and usually takes the form of flat or  
87 gently undulating surfaces. The exposed surface, approximately 12m<sup>2</sup>, showed very different  
88 characteristics with a series of hollows from circular to elongate, and the visual similarity to  
89 other coastal footprint surfaces in Britain (e.g. Formby, Sefton Coast) prompted analyses of  
90 these hollows [6]. The surface was located in the intertidal zone and subsequently eroded by  
91 tidal action over a period of two weeks, until the footprints were completely destroyed. The  
92 footprints may well have been left by *Homo antecessor*, the only hominin species so far  
93 known in Europe at that time [1]

94

95 Although no human fossils have been found at **Pakefield** (Suffolk), flint artefacts dating back  
96 approximately 700,000 years were, until the more recent Happisburgh discoveries, the  
97 earliest evidence for human presence in Britain (Figure 4) [7]. The presence of  
98 hippopotamus, elephant, lion, and deer remains, as well as analyses of sediments and pollen,  
99 suggest the climate of the British Isles was warmer than at the earlier Happisburgh 3 site,  
100 with summers as warm as those in the Mediterranean today [8, 9]. At **West Runton**, on the  
101 North Norfolk coast, an almost complete skeleton of a mammoth was found in 1990, the  
102 largest and oldest steppe mammoth skeleton found in Britain, dating to about 700,000 years  
103 ago, but no evidence of human occupation was found at the site [10]. Climatic conditions at  
104 West Runton were similar to those today. However, from soon after this time climatic  
105 oscillations became more extreme and Britain was regularly plunged into severe ‘Ice Ages’,

106 experiencing the effects of the ice caps reaching the lower latitudes and the chilling of the  
107 North Atlantic.

108

109 Archaeological excavations at **Boxgrove, in Sussex, England**, uncovered a land surface with  
110 freshwater pools where animals gathered, dating from about 500,000 years ago (Figure 5).  
111 Besides the butchered bones of a range of herbivores such as rhinoceros, horse and deer,  
112 large numbers of Acheulian handaxes were discovered [11, 12]. These tools are more  
113 sophisticated than those found at Happisburgh and Pakefield, and the earliest British human  
114 fossils, a tibia and two teeth, were uncovered here alongside the butchered animal bones and  
115 the handaxes [13]. Around 475,000 years ago we see the onset of the most severe cold stage  
116 of the Middle and Late Pleistocene, known as the Anglian (or Elsterian), with ice sheets  
117 extending far into southern Britain, making it uninhabitable.

## 118 **Hominins**

119 There are no *Homo antecessor* fossils currently known from Britain, but the footprint surface  
120 associated with Happisburgh 3, with a range of juvenile to adult hominin foot sizes, may be  
121 evidence of that species. Using foot length to stature ratios, the hominins who left the prints  
122 were estimated to have been between 0.93m and 1.73m in height, which suggests that the  
123 group consisted of individuals of different ages. The estimated adult statures of the hominins  
124 from Happisburgh fall within the range derived from the fossil evidence of *Homo antecessor*,  
125 the only known species in western Europe of a similar age and known only from fossils found  
126 at the site of Gran Dolina, Atapuerca, Spain and dated to about 860,000-780,000 years ago.  
127 The species is believed to have evolved from *Homo erectus* but had unique features that  
128 distinguish it from other *Homo* species [14-17]. A number of lithic artefacts similar in  
129 typology to those found at Gran Dolina were found at Happisburgh.

130  
131 Animal remains at these early Pleistocene sites suggest that the climate was largely warm but  
132 this changed after about 650,000 years ago. At times, conditions throughout Europe became  
133 harsh and cold and Britain became uninhabitable. It is unclear whether *Homo antecessor* gave  
134 rise to *Homo heidelbergensis*, and subsequently to Neanderthals, or whether they were an  
135 evolutionary dead-end.

136  
137 *Homo heidelbergensis* is the earliest human species for which we have fossil evidence in  
138 Britain, from around 500,000 years ago at Boxgrove. Two lower incisors were found close to  
139 one another and probably belong to the same adult individual. The morphology of the teeth is  
140 similar to that of other middle Pleistocene hominins making their assignment to *Homo*  
141 *heidelbergensis* possible. The tibia most likely originated from a different individual because  
142 it was discovered in a different stratigraphic context from the two teeth [18]. The tibia reveals  
143 a mosaic morphology relative to other archaic *Homo* tibiae. The external diaphyseal  
144 robusticity and mediolaterally thickened cortical bone distribution are characteristic of Late  
145 Pliocene to Late Pleistocene archaic *Homo*. The estimated cold-adapted body proportions  
146 would have promoted body heat conservation in a hominin practicing minimal cultural  
147 buffering during the late interglacial cool temperate climate [19]. From the Boxgrove tibia it  
148 has been shown that *Homo heidelbergensis* was taller than the later, cold-adapted,  
149 Neanderthals [20]. Although no other British sites have yielded *Homo heidelbergensis*  
150 fossils, some have yielded similar lithic artefacts to those found at Boxgrove, Brandon and  
151 Waverley Wood for example [11, 21]. The tools associated with *Homo heidelbergensis* were  
152 more varied than those of *Homo antecessor* and included bifacial handaxes, cleavers and  
153 scrapers; they were probably skilled hunters of large animals, such as rhinoceros, bear, horse

154 and deer [11].

155

156 *The colonisers (450,000 – 40,000 years ago)*

157

158 **Connected or disconnected?**

159 Britain's history of connectivity to mainland Europe is complex. However, in broad terms  
160 around 450,000 years ago (MIS 12), ice stretched right across the North Sea, from Britain to  
161 Scandinavia, and at the end of this glacial stage there was an initial breaching of the chalk  
162 ridge (Figure 1B). This initial erosion of the land bridge was probably characterised by  
163 waterfalls and channels that would have emptied proglacial lakes in the southern North Sea  
164 basin [3]. During the following glacial periods Britain would have been too cold to inhabit  
165 and Neanderthals would have been pushed out of the British Isles to return during the  
166 interglacials. From around 180,000 years ago there was a steady decline in global  
167 temperature which must have forced the Neanderthals out of Britain, and at about 160,000  
168 years ago (MIS 6) it is unlikely that any humans were still present; however, the climate then  
169 recovered rapidly at around 130,000 years ago. This led to sea levels rising and the  
170 submerging of the land surface between Britain and the continent, making Britain an island.  
171 Some mammals, depending on the distances of their glacial refugia, were fast to migrate and  
172 managed to reach Britain before it became an island. Others, such as elephants and  
173 hippopotamus, may have swum across, but Neanderthals (without boats) are not thought to  
174 have returned until around 60,000 years ago [22].

175 **Coming and going: Ice ages and deserted lands**

176 Just over 400,000 years ago a rapid improvement of the climate after the Anglian glaciation  
177 made Britain habitable again. **Swanscombe** is the only British site, to date, where a very



178 early Neanderthal fossil [23] has been discovered and it is possible that Neanderthals evolved  
179 from *Homo heidelbergensis* around this time (Figure 6). The climate worsened again by  
180 about 375,000 years ago, driving these early Neanderthals out again. Neanderthals returned to  
181 Britain after the ice had retreated around 330,000 years ago, bringing with them new  
182 technologies. The Neanderthals are mostly known from sites across Britain with Mousterian  
183 artefacts, an industry which incorporates Levallois technique<sup>1</sup>. **Baker's Hole** (Ebbsfleet,  
184 Kent) is one of the foremost sites that shows the Levallois industry [24].

185  
186 The oldest human fossils in Wales found so far come from **Pontnewydd Cave**, which has  
187 been dated to about 225,000 years ago [25, 26], and comprise teeth of early Neanderthal  
188 adults and children (Figure 7). The Mousterian industry was also found at **Crayford**, Kent  
189 [27, 28]. Additionally, more than 250,000 lithic artefacts were found on the other side of the  
190 Channel at the site of **La Cotte** and although this site is now on the island of Jersey, the  
191 island was connected to mainland France during periods of Neanderthal occupation.  
192 Generations of Neanderthals most likely returned to the site over a period totalling more than  
193 150,000 years [29-32]. Although for a long time it was believed Neanderthals did not return  
194 to Britain until about 60,000 years ago, a recent discovery from Dartford (Kent), dated at  
195 about 100,000 years ago, may hint that small Neanderthal groups possibly made rare visits  
196 into Britain from their more permanent camps in France or Belgium [33, 34]. It is possible  
197 they followed herds of mammoths, rhinoceros, horse and deer into Britain, but further  
198 analyses and evidence are needed to support this claim.

199

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<sup>1</sup> A method of stone reduction, involving the striking of flakes from a prepared core which provided much greater control over the size and shape of the final flakes which would then be employed as scrapers, knives and points.

200 Neanderthals were back in full force around 60,000 years ago. The site of **Lynford Quarry**,  
201 Norfolk has extensive evidence for classic Neanderthal Mousterian tools associated with the  
202 remains of at least eleven woolly mammoths [35, 36]. Although no butchery marks were  
203 found on the recovered mammal bones, none of the large meat-bearing bones were found,  
204 indicating they may have been transported away from the kill site.

205

## 206 **Hominins**

207 The oldest fossil evidence for Neanderthals in the British Isles is the partial skull from  
208 Swanscombe. The three cranial bones were discovered between 1935 and 1955; the  
209 articulated bones form the back of the skull of what is believed to be an early Neanderthal  
210 female and were found alongside a number of flint handaxes [37]. Despite its chronological  
211 association with the Middle Pleistocene, the occipital bone carries Neanderthal features: a  
212 weak occipital torus with bilateral projection, a central suprainiac depression and a strongly  
213 convex occipital plane. This makes the Swanscombe hominin one of the earliest primitive  
214 Neanderthals and supports an ancient root for the Neanderthal clade. The early emergence of  
215 these Neanderthal features in Swanscombe, while other roughly contemporary fossil  
216 hominins from Italy, Hungary and Germany display less derived Neanderthal morphology,  
217 suggests a more complex pattern of human evolution than has generally been assumed [20,  
218 37]. Neanderthals fossils were also found in **Pontnewydd Cave**, North Wales. The nineteen  
219 hominin teeth were associated with bifacial and Levallois artefacts and belonged to both  
220 juveniles and adults. The teeth are taurodont and the overall dental morphology shows clear  
221 affinities with Neanderthals and the pre-Neanderthal Middle Pleistocene teeth from the Sima  
222 de los Huesos, Atapuerca, Spain.

223 *The founding people (40,000 – 10,000 years ago)*

224

225 **An island established**

226 Neanderthals had returned to the British Isles by about 60,000 years ago, and although MIS 3  
227 climate was variable and complex, conditions did not improve permanently until the end of  
228 the glacial period (MIS 2), which reached its cold peak around 20,000 years ago, the Last  
229 Glacial Maximum (Figure 1C). During the early part of the current interglacial, the Holocene,  
230 Doggerland, the exposed land area in the present-day North Sea region, gradually  
231 disappeared as the ice melted and sea levels slowly rose to those of today (Figure 1D). Well  
232 before this time (around 40,000 years ago) we see the demise of the Neanderthals and the  
233 arrival of *Homo sapiens* in Europe [38]. The role of modern humans in the physical  
234 extinction of the Neanderthals is the subject of much debate [38], but genetic data show that  
235 Neanderthal DNA entered the modern human gene pool through interbreeding events. At  
236 present, no evidence of overlap exists for the occupation of Britain by Neanderthals and  
237 modern humans; any interbreeding probably happened more centrally within the Neanderthal  
238 range rather than at its geographical limits.

239 **Still coming and going**

240

241 The oldest modern human fossil in Britain, a fragment of maxilla, was found at **Kent's**  
242 **Cavern** (Figure 9) and dates back to at least 40,000 years [39]. The “Red Lady of **Paviland**”  
243 (actually the skeleton of a young man initially wrongly identified as a female) was discovered  
244 at **Goat's Hole**, South Wales, in 1823. The skeleton was coated in red ochre and the body had  
245 been buried wearing jewellery made from mammoth tusks; recent dating to about 33,000  
246 years makes this discovery the oldest ceremonial burial in western Europe [40]. During the

247 Last Glacial Maximum much of Scotland and upland Wales would have been under an ice  
248 sheet that was up to one kilometre thick in places, and cold winds and dry air would have  
249 prevailed across Britain. This severe environment seems to have been too difficult to deal  
250 with, even for the resourceful first modern humans, and Britain was deserted once more,  
251 probably by around 28,000 years ago [41].  
252  
253 Around 15,000 years ago the climate started to improve and the ice gradually retreated  
254 making Britain, once again, a welcome place for large game and the hunters who followed  
255 them [42]. **Gough's Cave** in Cheddar Gorge was one of the first settlements for Magdalenian  
256 modern humans after the peak of the last glacial stage [43]. Not only did these humans bring  
257 with them finely decorated bone tools, such as batons and needles, they also made cups out of  
258 human skulls [44, 45]. For a long time, it was believed that one of the main differences  
259 between early British and mainland European modern human sites was the absence of  
260 figurative art such as figurines and cave paintings or engravings. In 2004 however, an  
261 engraving at least 13,000 years old of a bison, similar in style to those found in European  
262 caves, was found at **Church Hole** in the English midlands [46]. Shortly after 13,000 years  
263 ago another brief cold period hit Europe, but by about 11,700 years ago the current  
264 interglacial had started and temperatures soon returned to essentially what they are today [47,  
265 48]. Prehistoric hunter-gatherers coming from Europe had to deal with new challenges. The  
266 animals they were used to hunting on the European Steppe, such as reindeer and horse, were  
267 replaced by forest dwelling taxa such as deer and wild boar. Around 6,000 years ago new  
268 ideas of agriculture and animal husbandry arrived from Europe leading to the decline of the  
269 hunter-gathering way of life and the beginning of the Neolithic [49, 50]. As well as the  
270 adoption of agriculture, technological advances, and a more sedentary way of life, these

271 farming communities also implemented the construction of the first monuments in the  
272 landscape, such as Stonehenge 4,600 years ago [49].

### 273 **Conclusion**

274 This review has laid out how human occupation of the British Isles during the last one million  
275 years is a story of repeated migration. The changing environment, with temperatures  
276 decreasing and recovering during the glacials and interglacials, would have posed challenges  
277 to the humans and fauna that they would not have encountered in more southerly parts of  
278 Europe. Not only would the English Channel land area have been submerged or dissected by  
279 large rivers at times, making accessing Britain difficult or impossible, but also when the ice  
280 sheets were at their thickest the extreme cold would have made the area uninhabitable for  
281 long periods of time. The first hominins to venture into the British Isles, probably *Homo*  
282 *antecessor* and *Homo heidelbergensis*, would have been unable to survive these long cold  
283 periods. Even Neanderthals, a human species well adapted to living in the cold northwest  
284 European plains, seem to have been unable to survive in Britain during MIS 6. Modern  
285 humans, despite their controlled use of fire, building of shelters and advanced lithic  
286 technology, still needed several attempts before being able to settle because life at the  
287 western edge of the Old World was not easy. The prehistory of the British Isles is a tale of  
288 coming and going, of deserted lands and recurring migrations.

289

290

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298  
299

300 **REFERENCES**

301 1. Ashton N., Lewis S.G., De Groote I., et al. (2014) Hominin Footprints from Early Pleistocene  
302 Deposits at Happisburgh, UK. *PLoS ONE* 9(2), e88329. (doi:10.1371/journal.pone.0088329).  
303 2. Parfitt S., Ashton N., Lewis S., et al. (2010) Early Pleistocene human occupation at the edge  
304 of the boreal zone in northwest Europe. *Nature* 466(229-233).  
305 3. Gupta S., Collier J.S., Garcia Moreno D., et al. (2017) Two-stage opening of the Dover Strait  
306 and the origin of island Britain. *Nature Comms* 8.  
307 4. Lee J.R., Rose J., Hamblin R.J., et al. (2004) Dating the earliest lowland glaciation of eastern  
308 England: a pre-MIS 12 early Middle Pleistocene Happisburgh glaciation. *Quat Sci Rev* 23(14), 1551-  
309 1566.  
310 5. Parfitt S., Barendregt R., Breda M., et al. (2005) The earliest record of human activity in  
311 Northern Europe. *Nature* 438, 1008-1012.  
312 6. Huddart D., Roberts G., Gonzalez S. (1999) Holocene human and animal footprints and their  
313 relationships with coastal environmental change, Formby Point, NW England. *Quat Int* 55(1), 29-41.  
314 7. Parfitt S.A., Barendregt R.W., Breda M., et al. (2005) The earliest record of human activity in  
315 northern Europe. *Nature* 438(7070), 1008-1012.  
316 8. Ashton N., Lewis S.G. (2012) The environmental contexts of early human occupation of  
317 northwest Europe: The British Lower Palaeolithic record. *Quat Int* 271, 50-64.  
318 9. Stuart A., Lister A.M. (2001) The mammalian faunas of Pakefield/Kessingland and Corton,  
319 Suffolk, UK: evidence for a new temperate episode in the British early Middle Pleistocene. *Quat Sci*  
320 *Rev* 20(16), 1677-1692.  
321 10. Lister A.M., Stuart A.J. (2010) The West Runton mammoth (*Mammuthus trogontherii*) and  
322 its evolutionary significance. *Quat Int* 228(1), 180-209.  
323 11. Roberts M.B., Parfitt S.A. (1999) *Boxgrove: A Middle Pleistocene Hominid Site at Eartham*  
324 *Quarry, Boxgrove, West Sussex*, English Heritage.  
325 12. Stringer C.B. (1996) *The Boxgrove tibia: Britain's oldest hominid and its place in the Middle*  
326 *Pleistocene record*. Old Sarum, Trust for Wessex Archaeology.  
327 13. Roberts M.B., Stringer C.B., Parfitt S. (1994) A hominid tibia from Middle Pleistocene  
328 sediments at Boxgrove, UK. *Nature* 369(6478), 311.  
329 14. Fernandez-Jalvo Y., Carlos Diez J., Caceres I., et al. (1999) Human cannibalism in the Early  
330 Pleistocene of Europe (Gran Dolina, Sierra de Atapuerca, Burgos, Spain). *J Hum Evol* 37, 591-622.  
331 15. Lorenzo C., Arsuaga J.L., Carretero J.M. (1999) Hand and foot remains from the Gran Dolina  
332 Early Pleistocene site (Sierra de Atapuerca, Spain). *J Hum Evol* 37(3-4), 501-522.  
333 16. Carretero J.M., Lorenzo C., Arsuaga J.L. (1999) Axial and appendicular skeleton of *Homo*  
334 *antecessor*. *J Hum Evol* 37(3-4), 459-499.  
335 17. Arsuaga J.-L., Martínez I., Lorenzo C., et al. (1999) The human cranial remains from Gran  
336 Dolina lower Pleistocene site (Sierra de Atapuerca, Spain). *J Hum Evol* 37(3-4), 431-457.  
337 18. Hillson S., Parfitt S., Bello S., et al. (2010) Two hominin incisor teeth from the middle  
338 Pleistocene site of Boxgrove, Sussex, England. *J Hum Evol* 59(5), 493-503.  
339 19. Trinkaus E., Stringer C., Ruff C., et al. (1999) Diaphyseal cross-sectional geometry of the  
340 Boxgrove 1 Middle Pleistocene human tibia. *J Hum Evol* 37, 1-25.  
341 20. Buck L.T., Stringer C.B. (2014) *Homo heidelbergensis*. *Curr Biol* 24(6), R214-R215.  
342 21. Stout D., Apel J., Commander J., et al. (2014) Late Acheulean technology and cognition at  
343 Boxgrove, UK. *J Archaeol Sci* 41, 576-590.  
344 22. Ashton N. (2002) Absence of humans in Britain during the last interglacial (oxygen isotope  
345 stage 5e). *Publications du CERP* (8), 93-103.  
346 23. Stringer C., -J. H.J. (1999) New age estimates for the Swanscombe hominid, and their  
347 significance for human evolution. *J Hum Evol* 37, 873-877.  
348 24. Scott B., Ashton N., Penkman K.E., et al. (2010) The position and context of Middle  
349 Palaeolithic industries from the Ebbsfleet Valley, Kent, UK. *J Quat Sci*, 25(6), 931-944.  
350 25. Green H., Stringer C., Collcutt S., et al. (1981) Pontnewydd Cave in Wales—a new Middle  
351 Pleistocene hominid site.

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26. Compton T., Stringer C. (2015) The morphological affinities of the Middle Pleistocene hominin teeth from Pontnewydd Cave, Wales. *J Quat Sci*, 30(7), 713-730.
27. Roe D.A. (2014) *The lower and middle Palaeolithic periods in Britain*, Routledge.
28. Chandler R. (1916) The implements and cores of Crayford. *Proc Prehist Soc* 2(2), 240-248.
29. White M., Scott B., Ashton N. (2006) The Early Middle Palaeolithic in Britain: archaeology, settlement history and human behaviour. *J Quat Sci*, 21(5), 525-541.
30. Scott B., Bates M., Bates R., et al. (2014) A new view from La Cotte de St Brelade, Jersey. *Antiquity* 88(339), 13-29.
31. Bates M., Pope M., Shaw A., et al. (2013) Late Neanderthal occupation in North-West Europe: rediscovery, investigation and dating of a last glacial sediment sequence at the site of La Cotte de Saint Brelade, Jersey. *J Quat Sci*, 28(7), 647-652.
32. Callow P., Cornford J.M., McBurney C.B.M. (1986) *La Cotte de St. Brelade, 1961-1978: Excavations by C.B.M. McBurney*, Geo Books.
33. Wenban-Smith F.F., Bates M.R., Schwenninger J.L. (2010) Early Devensian (MIS 5d-5b) occupation at Dartford, southeast England. *J Quat Sci*, 25(8), 1193-1199.
34. White M.J., Pettitt P.B. (2011) The British Late Middle Palaeolithic: an interpretative synthesis of Neanderthal occupation at the northwestern edge of the Pleistocene world. *J World Prehist* 24(1), 25-97.
35. Boismier W., Schreve D.C., White M.J., et al. (2003) A Middle Palaeolithic site at Lynford Quarry, Mundford, Norfolk: interim statement. In *Proceedings of the Prehistoric Society* (pp. 315-324, Cambridge Univ Press.
36. Schreve D.C. (2006) The taphonomy of a Middle Devensian (MIS 3) vertebrate assemblage from Lynford, Norfolk, UK, and its implications for Middle Palaeolithic subsistence strategies. *J Quat Sci*, 21(5), 543-556.
37. Stringer C., Hublin J.-J. (1999) New age estimates for the Swanscombe hominid, and their significance for human evolution. *J Hum Evol* 37, 873-877.
38. Higham T., Douka K., Wood R., et al. (2014) The timing and spatiotemporal patterning of Neanderthal disappearance. *Nature* 512(7514), 306-309.
39. Higham T., Compton T., Stringer C., et al. (2011) The earliest evidence for anatomically modern humans in northwestern Europe. *Nature* 479(7374), 521-524.
40. Jacobi R., Higham T. (2008) The "Red Lady" ages gracefully: new ultrafiltration AMS determinations from Paviland. *J Hum Evol* 55(5), 898-907.
41. Jacobi R., Higham T. (2011) The British earlier Upper Palaeolithic: settlement and chronology. *The ancient human occupation of Britain*, 181-222.
42. Jacobi R., Higham T. (2009) The early Lateglacial re-colonization of Britain: new radiocarbon evidence from Gough's Cave, southwest England. *Quat Sci Rev* 28(19), 1895-1913.
43. Currant A., Jacobi R., Stringer C.B. (1989) Excavations at Gough's Cave, Somerset 1986 7. *Antiquity* 63, 131-136.
44. Bello S.M., Saladié P., Cáceres I., et al. (2015) Upper Palaeolithic ritualistic cannibalism at Gough's Cave (Somerset, UK): the human remains from head to toe. *J Hum Evol* 82, 170-189.
45. Bello S.M., Parfitt S.A., Stringer C.B. (2011) Earliest directly-dated human skull-cups. *PLoS One* 6(2), e17026.
46. Ripoll S., Muñiz F., Bahn P., et al. (2004) Palaeolithic Cave Engravings at Creswell Crags, England. In *Proceedings of the Prehistoric Society* (pp. 93-105, Cambridge Univ Press.
47. Woodward J. (2014) *The Ice Age: A Very Short Introduction*, OUP Oxford.
48. Shennan I., Horton B. (2002) Holocene land-and sea-level changes in Great Britain. *J Quat Sci*, 17(5-6), 511-526.
49. Bradley R. (2014) *The prehistoric settlement of Britain*, Routledge.
50. Cramp L.J.E., Jones J., Sheridan A., et al. (2014) Immediate replacement of fishing with dairying by the earliest farmers of the northeast Atlantic archipelagos. *Proc Roy Soc B* 281(1780). (doi:10.1098/rspb.2013.2372).
51. Stringer C. (2006) *Homo britannicus*. London, Allen Lane.
52. Penkman K.E., Preece R.C., Bridgland D.R., et al. (2011) A chronological framework for the British Quaternary based on Bithynia opercula. *Nature* 476(7361), 446-449.

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406 53. Debenham N.C., Atkinson T., Grun R., et al. (2012) Dating. In *Neanderthals in Wales:*  
407 *Pontnewydd and the Elwy Valley Caves* (eds. Aldhouse-Green S., Peterson R., Walker E.A.), pp. 283–  
408 319. Oxford, Oxbow Books.  
409 54. Pike A.W., Gilmour M., Pettitt P., et al. (2005) Verification of the age of the Palaeolithic cave  
410 art at Creswell Crags, UK. *J Archaeol Sci* 32(11), 1649-1655.  
411

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413 **Figure 1: Generalised reconstruction of the land surface and the extent of ice sheets of**  
414 **the British Isles. A: ~900,000 years BP; B: ~450,000 BP (MIS 12 – Elsterian Glaciation);**  
415 **C: ~20,000-30,000 years BP (MIS 2 - Last Glacial Maximum); D: ~10,000 years BP**  
416 **(MIS 1 – Early Holocene) (after [51]).**

417  
418 **Figure 2: Current distribution of the main Palaeolithic archaeological sites of the**  
419 **British Isles.**

420  
421 **Figure 3: Happisburgh, Norfolk. A: Site 3 excavation (courtesy of NHM, London). B:**  
422 **Artist’s reconstruction of the environment at Happisburgh ~900,000 years BP (courtesy**  
423 **of John Sibbick and the AHOB Project).**

424  
425 **Figure 4: Pakefield, Norfolk. A: Excavation at Pakefield with the Cromer Forest-bed**  
426 **deposits clearly visible at base of cliff. B: Flint artefacts recovered from the site**  
427 **(courtesy of NHM, London).**

428  
429 **Figure 5: Boxgrove, West Sussex. A: Reconstruction of butchering of a rhinoceros at the**  
430 **Boxgrove site (courtesy of John Sibbick). B: Excavations at Boxgrove. C: A rich**  
431 **assemblage of handaxes being excavated.**

432  
433 **Figure 6: Swanscombe, Kent. The partial cranium belonging to an early Neanderthal,**  
434 **probably female, and a selection of handaxes recovered at Swanscombe (courtesy of**  
435 **NHM, London).**

436

437 **Figure 7: Pontnewydd Cave, North Wales. A: Handaxes discovered at Pontnewydd**  
438 **Cave (courtesy of the National Museum of Wales). B: The cave entrance during**  
439 **excavations. C: A juvenile Neanderthal maxilla is part of the assemblage of 19 teeth**  
440 **discovered at the site (courtesy of the NHM, London).**

441

442 **Figure 8: The maxilla from Kent's Cavern, Devon, including three teeth of the earliest**  
443 **known modern human in Britain, discovered during excavations in 1927.**

444 **Table 1: Simplified table of the main Pleistocene sites in the text; dates given in most cases are approximate; at many sites, only the**  
 445 **relevant horizons and dates mentioned in the text are provided. BP = before present; AAR = amino acid racemization; OSL = optically**  
 446 **stimulated luminescence; TL = thermoluminescence; U-series = Uranium series; 14C = Ultra filtered radiocarbon; MIS = Marine**  
 447 **Isotope Stage.**  
 448

Site	Industry	Age	Dating method
Happisburgh 3	Lower Palaeolithic	950,000 – 850,000 BP Early Pleistocene; MIS 25 or 21	Palaeomagnetism, biostratigraphy
Pakefield	Lower Palaeolithic	750,000 – 680,000 BP; MIS 19 or 17	Lithostratigraphy, biostratigraphy, AAR, palaeomagnetism
West Runton	None	~700,000 BP; MIS 17	AAR, biostratigraphy
Boxgrove	Lower Palaeolithic	~500,000 BP; MIS 13	Lithostratigraphy, biostratigraphy
Swanscombe	Lower Palaeolithic	~400,000 BP; MIS 11	Lithostratigraphy, biostratigraphy AAR
Baker's Hole	Levallois	MIS 8/7	AAR, biostratigraphy
Pontnewydd Cave	Levallois	~225,000 BP; MIS 7a	U-series, ESR, TL, biostratigraphy
Crayford	Levallois	MIS 7a	AAR, biostratigraphy
La Cotte	Levallois	MIS 7 to 2	OSL, 14C, TL, biostratigraphy
Lynford Quarry	Middle Palaeolithic	~60,000BP; MIS 4/3	OSL (+14C)
Kent's Cavern	Middle & Upper Palaeolithic	Maxilla ~40,000 BP; MIS 3	14C, biostratigraphy
Paviland	Upper Palaeolithic	Burial ~ 34,000 BP; MIS 3	14C
Church Hole	Middle & Upper Palaeolithic	MIS 3 to 1	U-series, 14C
Gough's Cave	Late Upper Palaeolithic	14,700 BP; MIS 2	14C

449  
 450 **References:** HSB 3 [2]; Pakefield [7, 52]; West Runton [10, 52]; Boxgrove [11] ; Swanscombe [23, 52]; Baker's Hole [24, 52]; Pontnewydd  
 451 [53]; La Cotte [31, 32]; Lynford [36]; Kent's Cavern [39]; Paviland [40]; Church Hole [46, 54]; Gough's Cave [43].  
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