

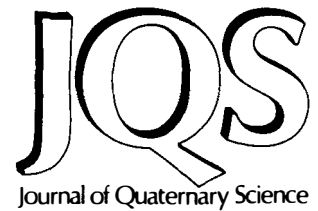
A pre-Ipswichian cold stage mammalian fauna from the Balderton Sand and Gravel, Lincolnshire, England

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ABSTRACT: The Balderton Sand and Gravel has yielded one of very few mammalian faunas dated to the penultimate Cold Stage in Britain. The assemblage is dominated by mammoth and woolly rhinoceros, with subordinate horse, red deer, bison, straight-tusked elephant, musk ox, reindeer, wolf, lion, brown bear and cf. narrow-nosed rhinoceros. This fauna indicates cold stage conditions, probably including one or more interstadial episodes. The presence of straight-tusked elephant and cf. narrow-nosed rhinoceros supports its pre-Devensian age, and provides corroboration for the occurrence of these taxa in the British Wolstonian. An attempt is made to analyse the fossil collection by preservation type and adhering sediment: the occurrence of individual species appears to be largely uncorrelated with lithology. The Balderton assemblage corresponds well to other British mammal faunas assigned to a cold interval between the Hoxnian and Ipswichian Interglacials.



KEYWORDS: Pleistocene mammals, penultimate cold stage, biostratigraphy, palaeoecology.

Introduction

Cold stages covered the majority of time during the British Middle and Upper Pleistocene, yet their mammalian faunas are much less well known than those of the relatively short interglacials. Only for the Last Cold Stage (Devensian) are a considerable number of dated mammalian assemblages known; sampling of the preceding cold stages is extremely poor (Stuart, 1982).

This paper reports an extensive collection of mammalian fossils from fluvial sand and gravel deposits underlying the Balderton Terrace between Newark and Lincoln. This deposit, the Balderton Sand and Gravel (Brandon and Sumbler, 1988), marks a former course of the River Trent, and has been exposed by numerous commercial aggregate workings in recent years. Brandon and Sumbler (1988, 1991) present several lines of evidence for a post-Hoxnian, pre-Ipswichian age for the Balderton Sand and Gravel, probably within the second part of this interval and corresponding to Oxygen Isotope Stage 6. This evidence includes (i) the height of the Balderton Sand and Gravel river long profile, lying above that of the hippo-bearing Ipswichian Fulbeck Terrace deposits, and below the probably Anglian Eagle Moor Terrace deposits; (ii) indications of a significant pre-Flandrian temperate episode post-dating the Balderton Sand and Gravel; (iii) electron spin

resonance dates in the range 130–190 ka BP (Grün, in Brandon and Sumbler, 1991); (iv) the occurrence of an unworn Acheulean artefact in the deposit. This age determination is supported by evidence from the mammalian fauna, presented below. The term 'Wolstonian' is here used for the interval between the Hoxnian and Ipswichian interglacials, in the chronological sense of Gibbard and Turner (1988), and does not necessarily imply correlation with the Wolston Series of the Midlands (Shotton, 1953).

Fossils have been collected from six localities, numbered 1–6; pits at each locality are labelled a, b, c, etc. Full details of localities and stratigraphy are given by Brandon and Sumbler (1991), where the same numbering scheme is used. Although at least eight of the working pits have yielded remains, the majority come from Locality 2, where they have been hand-picked from conveyor belts by quarry workers, notably Mr N. Sexton. The abundance of fossils from this site does not necessarily indicate unusually fossiliferous deposits; it probably relates more to the working methods and diligence of quarry staff. All fossil material collected during this study will be conserved at the University Museum of Zoology, Cambridge, and the British Geological Survey, Keyworth.

In addition to specimens from extant workings, several were collected in 1983–1984 by employees at the now disused Thorpe-on-the-Hill Quarry [SK 915 666], near to present Locality 3 and here named Pit 3d. Two mammoth

molars and a ?bison bone from former pits at Balderton, collected between 1938 and 1957, are listed in the catalogue of the Newark Afton Gate Museum. Finally, a lower molar and scapula of mammoth from an excavation for a pylon at Coddington [SK8373 5605] are housed in the Natural History Museum, Woollaton Hall, Nottingham.

As might be expected in a high-energy fluvial deposit, the fossils are predominantly large and durable types. They are generally well preserved and unrolled, suggesting minimal transportation before burial. In a few cases, matching fossils suggest that partly articulated skeletons may be present in the deposit. Thus, three mammoth molars (dP4s) collected (*ex situ*) on the same day from Pit 2a are undoubtedly from one animal (Fig. 1); similarly, left and right mammoth upper third molars from Pit 2a pertain to a single individual. Suspected associations of limb bones include a perfectly matching metatarsal and astragalus of horse from Pit 2a (Fig. 2), and a tibia and ulna of juvenile rhinoceros, of similar ontogenetic age and identical preservation, found in the same part of Pit 4e. Finally, two fragments of a single bone shaft coming from a silt channel at Pit 6b have unusual, polished ends (Fig. 3). This is not thought to be the result of human activity (R. M. Jacobi, pers. comm.; J. J. Wymer, pers. comm.), but may suggest abrasion of some description during a phase of subaerial exposure.

Identification and taxonomy

Of specimens collected from the recent excavations up to March 1990, 268 were identifiable to species level. These form the basis of the faunal list presented in Table 1. Additionally, 42 specimens of elephantid (sp. indet.) and 151 unidentifiable fragments, have been found.

The mammalian faunal assemblage recovered from the Balderton Sand and Gravel is dominated by large herbivorous

mammals. Wet sieving to 1 mm of bulk samples from several of the organic and silty channel fills failed to produce any identifiable small mammal material.

Carnivora

Canis lupus L., wolf

This species is represented by a single specimen, the distal end of a right femur (Fig. 4).

Ursus sp. (cf. *U. arctos* L.), bear

A partial humerus shaft is identifiable as bear, and is indistinguishable in size and form from brown bear, *U. arctos* (Fig. 5). The possibility that the specimen represents cave bear, *U. spelaeus*, cannot be ruled out, although remains of this species are generally of somewhat larger size.

Panthera leo (L.), lion

A single specimen, the shaft of a right tibia, is identifiable as lion (Fig. 6). As in most British Pleistocene lion fossils, the specimen is considerably larger than modern African comparative material. The minimum circumference of the shaft is 10.7 cm, comparing well with a range of 9.9–12.2 cm for five specimens from Sandford Hill and Bleadon Caves, Somerset (probably Last Cold Stage), and markedly larger than a range of 7.6–8.3 cm for three modern *P. leo* (comparative measurements given by Dawkins and Sanford, 1872). Of pre-Last Cold Stage material, several fossils of lion from the Crayford brickearth are also of very large size (Dawkins and Sanford, 1872), as are remains from the

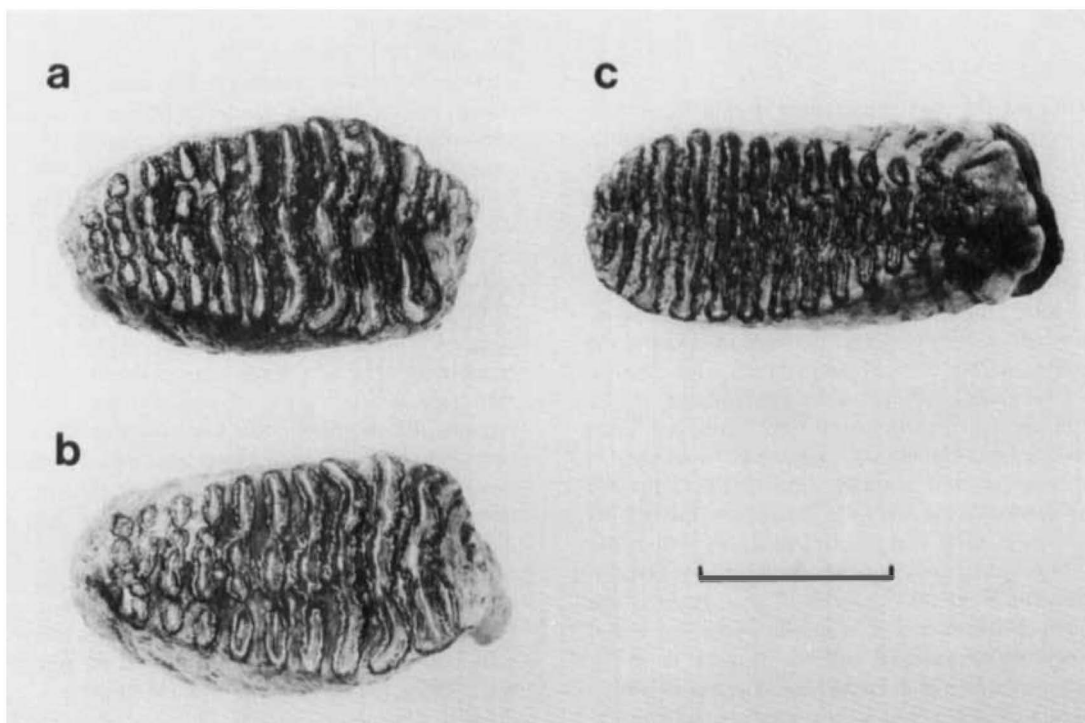


Figure 1 Associated last milk molars of mammoth, *M. primigenius*, from Pit 2a. (a) right upper 6A/75, (b) left upper 6A/76, (c) right lower 6A/77. Scale bar 5 cm.

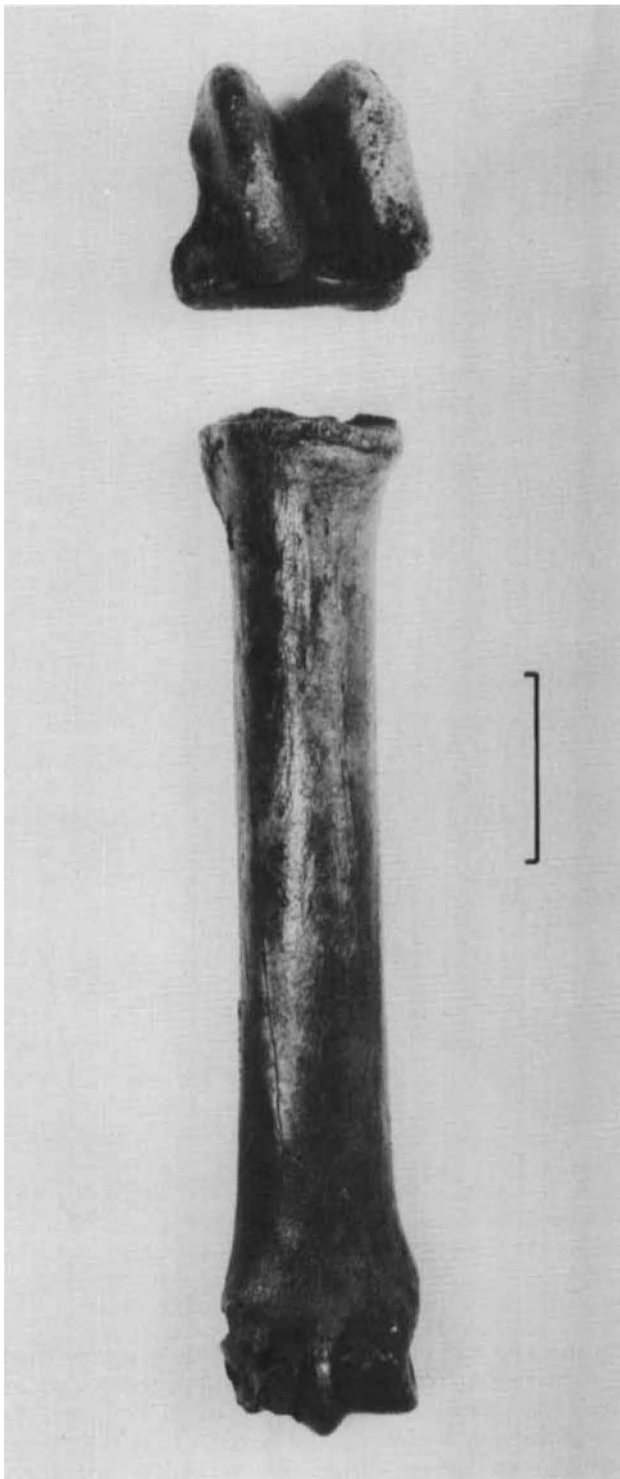


Figure 2 Right astragalus 6A/95 and metatarsal 6A/94 of horse, *E. caballus*, from Pit 2a, in anterior view. Probably associated. Scale bar 5 cm.

Marsworth Lower Channel (Green *et al.*, 1984; G. R. Coope pers. comm.).

European Pleistocene lions have sometimes been referred to a separate species, *Panthera* (or *Felis*) *spelaea*, but as Dawkins and Sanford (1872, p. 150) showed, they are indistinguishable skeletally, apart from larger size, from the modern species, to which they are now referred (e.g. Kurtén, 1968).

Proboscidea

Mammuthus primigenius (Blum.), woolly mammoth

Of the 163 specimens definitely identifiable as mammoth, 160 are partial or complete cheek teeth. The majority are permanent molars (M1–M3, sometimes termed M4–M6), although a few last milk molars (dP4, sometimes termed M3) also occur. The teeth are identified as *M. primigenius* on the basis of their wide crowns; their narrow, closely packed lamellae, divided into subequal annuli at their apex; and their thin, relatively unconvoluted enamel (Figs 1 and 7). Three tusk fragments are referred to mammoth (rather than to straight-tusked elephant) on the basis of their marked curvature (Fig. 8).

In addition, there are 42 fragments of indeterminate elephantid tusks and limb bones. Since identifiable mammoth teeth outnumber those of straight-tusked elephant (the only other elephantid species present) by 163:9 (ca. 18:1), it is likely that the majority of these fossils are mammoth.

Woolly mammoth (*M. primigenius*), of which the typical form existed in the Devensian (ca. 115–10 ka BP), is believed to have evolved from a precursor, *M. trogontherii*, which is best known from the early Middle Pleistocene (ca. 500–600 ka BP) at sites such as Süssenborn and Mosbach, Germany, and the Cromer Forest-bed Formation in Britain. In the dentition, *M. trogontherii* is characterised by larger teeth, thicker enamel, and lower lamellar frequency than *M. primigenius* (Aguirre, 1969; Maglio, 1973). In Table 2, a comparison of dental measurement of third molars from the Balderton Sand and Gravel, with classic samples of the two species, shows that the Balderton mammoth is morphologically very close dentally to fully evolved *M. primigenius* of the Last Cold Stage. This corresponds to growing evidence that, in northwest Europe at least, *Mammuthus* had completed its evolution by the penultimate cold stage (Lister, 1989; in preparation).

Palaeoloxodon antiquus (Falc. and Caut.), straight-tusked elephant

Nine partial molar teeth are identifiable as straight-tusked elephant. This is based on their narrow crowns; their broad, fusiform lamellae, divided into a long median and small lateral annuli at their apex; and their thick, convoluted enamel (Fig. 9). The teeth are well preserved, little rolled, and have the same range of coloration and sediment type as mammoth teeth from the same localities. There is no evidence that they have been reworked from an older deposit.

Perissodactyla

Equus caballus L. (= *E. ferus* Boddaert), horse

There are 15 specimens, comprising 14 partial and complete limb bones and one molar fragment (Fig. 2). The remains indicate a horse of large body size, and although the Balderton sample is small, it is interesting that the lengths of two metatarsals are above the range of several British and French Last Cold Stage samples, but within the range of pre-Devensian (Ipswichian and Wolstonian/Saalian) material (Prat, 1976; Egginton, 1982; Eisenmann, 1988; see Table 3).



Figure 3 Two fragments of longbone shaft, probably from the same bone, showing unusual polish at one end (the edge at the top of the picture). Specimens 5/1 and 5/2, from a silt channel about 2 m above the base of the Balderton Sand and Gravel [SK 9353 6768] at Pit 6b. Scale bar 5 cm.

Coelodonta antiquitatis (Blum.), woolly rhinoceros

Fifty specimens, comprising 39 partial postcranial bones, nine molars and two skull fragments, are referred to this species (Figs 10 and 11b). By comparison with known material from the Natural History Museum (NHM) collections, all of the teeth, the skull fragments, and about half of the postcranial bones can be identified with certainty as *C. antiquitatis* rather than *Dicerorhinus* spp., the other rhinoceros genus of the European Middle and Upper Pleistocene. Since there is only one specimen identifiable as *Dicerorhinus* from the Balderton Sand and Gravel (see below), the remaining rhinoceros postcranial bones, while not strictly identifiable as *C. antiquitatis*, are placed here.

Dicerorhinus cf. *hemitoechus* (Falc.), cf. narrow-nosed rhinoceros

A single proximal radius fragment (Fig 11a) of a rhinoceros does not correspond to *C. antiquitatis*, but is entirely

conformable with material of *Dicerorhinus*, e.g. from Ilford, Essex (NHM collection). The distinguishing features are the small size (proximal radius width of 93 mm), and the morphology of the anterior and posterior faces. Of the two *Dicerorhinus* species of the British Middle and Upper Pleistocene, the Balderton specimen is tentatively referred to *D. hemitoechus* (Falc.) rather than to *D. kirchbergensis* (Jäger) on the basis of its size. Guérin (1980) gives proximal radius widths of 88.5–105 mm ($n = 24$) for *D. hemitoechus*, and 102–119 mm ($n = 18$) for *D. kirchbergensis*. The specimen, from Pit 2a, shows signs of slight transport, but no more than many other bones from the Balderton Sand and Gravel. There is no reason to think it is reworked, although this cannot be ruled out entirely.

Artiodactyla

Rangifer tarandus (L.), reindeer

Only five specimens of reindeer have been recovered. Of these, two are small fragments of antler beam, two are antler

Table 1 Mammalian faunal list from the Balderton Sand and Gravel, arranged by order of overall abundance of species. For each species, the number of identifiable specimens from each pit or group of pits is given, and expressed in brackets as a percentage of the total identifiable fossils from that pit or group of pits. The numbering of the localities (1–5) and pits (a, b, etc) follows Brandon and Sumbler (1991); 3d is the disused Thorpe-on-the-Hill Quarry (see text). No identifiable fossils were available from pits 2c, 3a, 4b, c, 5b, 6a, b

Taxon	Localities and pits							Total
	1a	2a	2b	3b,c	3d	4a,e	5a	
<i>Mammuthus primigenius</i> (Blum.), mammoth	33 (67)	68 (64)	52 (68)	4 (57)	3 (75)	1 (5)	2 (100)	163 (61)
<i>Coelodonta antiquitatis</i> (Blum.), woolly rhinoceros	4 (8)	19 (18)	12 (16)	1 (14)	1 (25)	13 (59)		50 (19)
<i>Equus caballus</i> L., horse	2 (4)	8 (7)	3 (4)			2 (9)		15 (6)
<i>Cervus elaphus</i> L., red deer	2 (4)	5 (5)	3 (4)					10 (4)
<i>Palaeoloxodon antiquus</i> (Falc. & Caut.), st-t. elephant	5 (10)	1 (1)	3 (4)					9 (3)
<i>Bison/Bos</i> , bison or aurochs	1 (2)	3 (3)	2 (3)	1 (14)		1 (5)		8 (3)
<i>Rangifer tarandus</i> (L.), reindeer			1 (1)			4 (18)		5 (2)
<i>Ovibos moschatus</i> Zimmerman, musk ox		2 (2)	1 (1)	1 (14)				4 (1.5)
<i>Canis lupus</i> L., wolf	1 (2)							1 (0.4)
<i>Panthera leo</i> (L.), lion						1 (5)		1 (0.4)
<i>Ursus arctos</i> L., brown bear	1 (2)							1 (0.4)
<i>Dicerorhinus</i> cf. <i>hemitoechus</i> (Falc.), narrow-nosed rhino		1 (1)						1 (0.4)
Total	49(100)	107(100)	77(100)	7(100)	4(100)	22(100)	2(100)	268(100)

bases (one shed, one unshed), and one (Fig. 12) is a substantial part of the skull and fully grown left antler of a mature male.

Cervus elaphus L., red deer

There are ten specimens of this species: five portions of skull with antler base attached, two bases of shed antlers (Fig. 13), one portion of antler beam, and two partial limb bones. The remains indicate a red deer considerably larger than those in Britain today, typical of Middle and Upper Pleistocene material, including both Wolstonian and Devensian fossils (Lister, in preparation). The five unshed antler bases have developed a burr, implying death between September and March (cf. Taylor Page, 1971). The two shed antlers imply that red deer were in the area in February–March.

cf. *Bison priscus* Bojanus, large bovid cf. bison

Eight partial or complete limb bones of large bovid have been recovered. The distinction between Pleistocene *Bos primigenius* Bojanus and *Bison priscus* is notoriously difficult but has been the subject of a recent detailed investigation by Gee (1991). The Balderton material has kindly been examined by H. E. Gee, who regards six of the specimens as indeterminate, but two as tentatively referable to *B. priscus*. These are a complete metatarsal (Fig. 14a and b), showing characteristic anterior confluence of the proximal facets (Coxon *et al.*, 1980), and an astragalus (Fig. 14c), which in anterior view is tall and slender, with a roughly emarginated lateral edge, which are features of *B. priscus*. All of the Balderton specimens are of an exceptionally large size for *B.*

Table 2 Lamellar frequency (the number of enamel lamellae in a 10 cm length of tooth) and enamel thickness (averaged over the occlusal surface) in third upper molars of mammoths. Samples: *Mammuthus primigenius*, Předmostí, Czechoslovakia, mid-Last Cold Stage (cf. Musil, 1968); *Mammuthus trogontherii*, Mosbach, Germany, early Middle Pleistocene. All data original

	Third upper molars							
	Lamellar frequency				Enamel thickness			
	<i>n</i>	Mean	Range	SD	<i>n</i>	Mean (mm)	Range (mm)	SD
Předmostí	43	9.45	7.61–11.80	1.03	40	1.56	1.2–2.0	0.20
Balderton	19	9.72	7.67–12.17	1.25	18	1.81	1.4–2.2	0.20
Mosbach	18	6.99	5.83–8.74	0.66	19	2.35	1.8–3.0	0.32

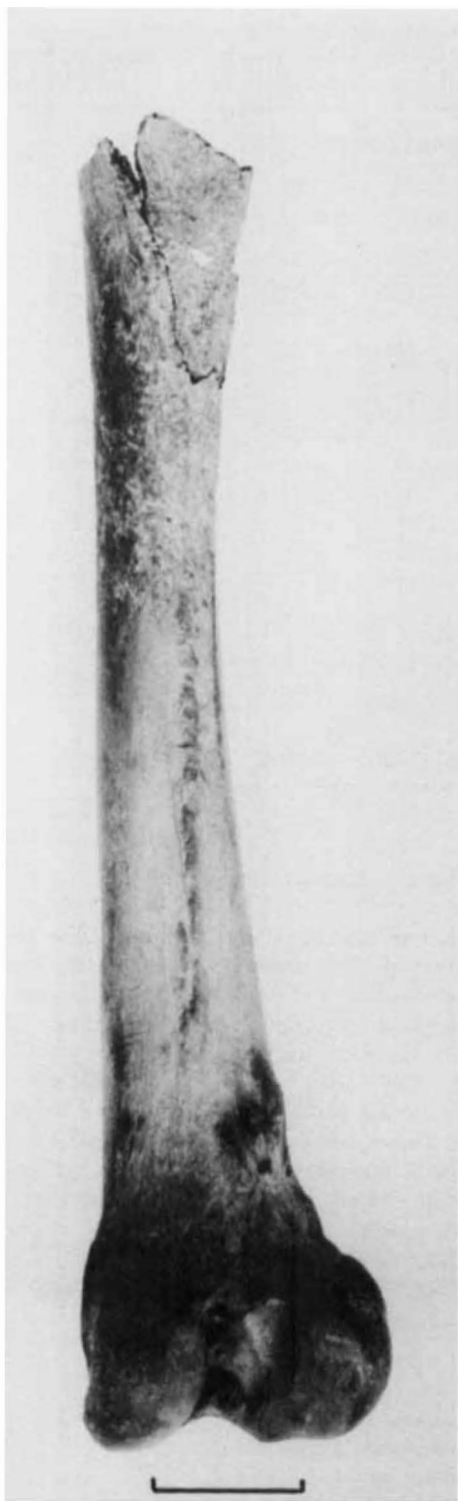


Figure 4 Distal end of right femur of wolf, *C. lupus*, 7A/69, found *in situ* in shelly silt channel at base of Balderton Sand and Gravel [SK 8662 5895] at Pit 1a, in posterior view. Scale bar 2 cm.

priscus, above the range of Early to Middle Devensian samples from Isleworth, Tattershall Castle and Wretton, and at the upper end of variation of the larger bison from the Ipswichian and the Middle Devensian of Windy Knoll and Kent's Cavern (Gee, 1991; see Table 4). Comparative measurements of other British Wolstonian bison are not available.

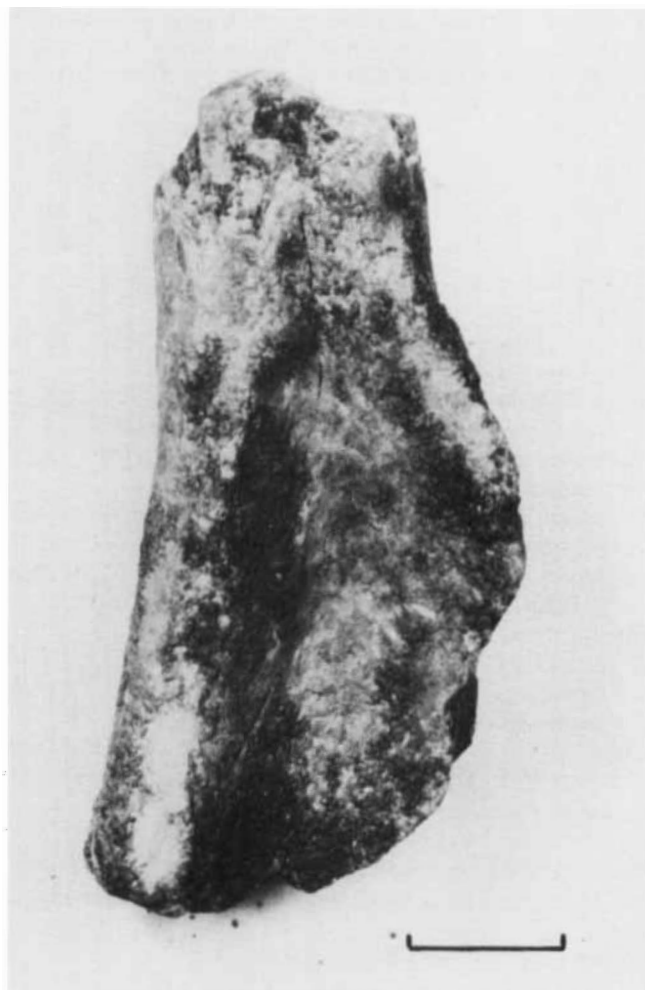


Figure 5 Distal shaft fragment of bear humerus, *Ursus* sp., 7A/24, from Pit 1a, in posterior view. Scale bar 2 cm.

Ovibos moschatus Zimmerman, musk ox

This species is represented by four specimens: the proximal half of a right metatarsal (Fig 15a), an axis (second cervical) vertebra (Fig. 15b), and the shafts of a radius and a tibia. The material indicates an animal substantially larger than living musk oxen: data on the two measurable specimens, the axis and metatarsal, are compared with modern reference material in Table 5. Musk oxen of similarly large size are already known from both Devensian and pre-Devensian deposits in Europe. For example, two large metatarsals dredged from the southern North Sea to the west of the Brown Bank, described by Bosscha Erdbrink (1986) and believed to be of early Devensian age, are of similar size to the Balderton specimen (Table 5), and the musk ox skull and teeth from Crayford, of either late Ipswichian (Stuart, 1976) or Wolstonian (Currant, 1986) age, are of particularly large size (Dawkins, 1872; Davies, 1879). On the other hand, an adult skull from the Taplow Gravels at Maidenhead, now regarded as late Wolstonian (Gibbard, 1986), is no larger than modern specimens (Owen, 1856). The difference between the Maidenhead specimen, and those from Crayford and Balderton, is probably too large to be accounted for by sexual dimorphism, so there may have been complex patterns of size variation within Wolstonian musk oxen that, with our limited material, cannot be explored properly.

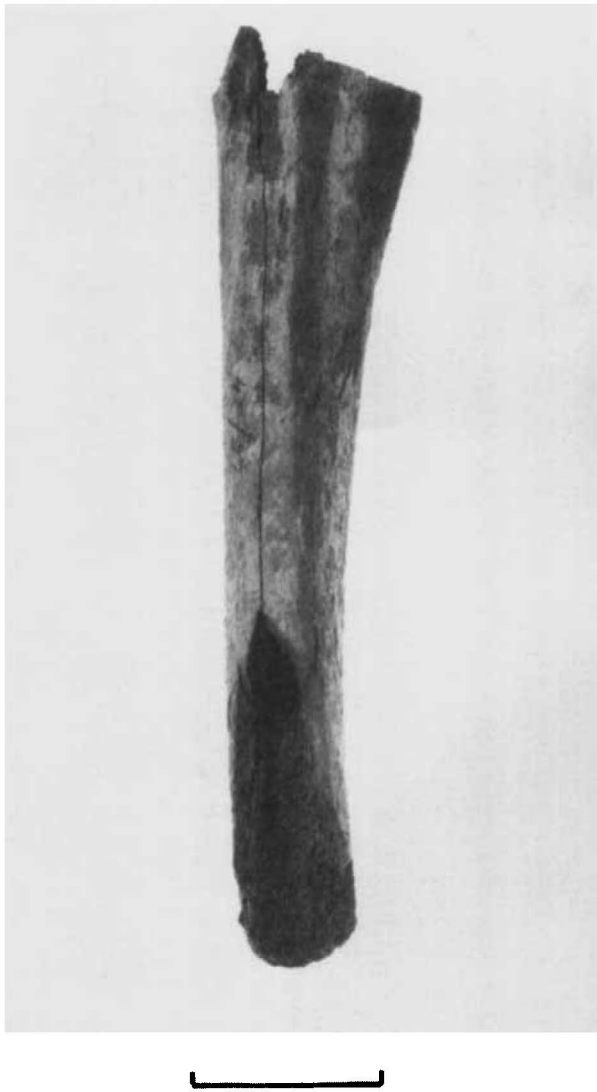


Figure 6 Right tibia shaft of lion, *P. leo*, 4E/37, from Pit 4e, in postero-lateral view. Scale bar 5 cm.

Various species names have been applied to the fossil musk oxen (Reynolds, 1934; Kennard, 1944, p. 135), but here the simple policy of referring the Balderton material to the living species has been adopted.

Preservation and adhering sediments

Collections of Pleistocene fossil bones are frequently made from working sand and gravel pits in the British Isles. Almost always, the fossils are collected from conveyor belts or from piles of sorted aggregate, so that their precise provenance in relation to often complex stratigraphy is unknown. This is the case with the Balderton assemblage, where all but two of the specimens were collected *ex situ*. An attempt has been made to deduce possible stratigraphical associations by looking at the distribution of species between pits, and the nature of the adhering sediments and preservation types of bones. The overall percentage representation of each species is given in Table 1 (right-hand column). Considering pits individually, only 1a, 2a and 2b have provided a sufficiently large number of fossils for meaningful comparisons of species distributions. The proportion of mammoth at each of the three pits is remarkably similar (67, 64 and 68%, respectively). Possibly significant differences are a rather lower percentage of woolly rhino, and a higher percentage of straight-tusked elephant, in Pit 1a compared with 2a and 2b. Locality 4 is unusual in showing a relatively high proportion of woolly rhinoceros, a low proportion of mammoth, and the majority of the sparse reindeer from the Balderton Sand and Gravel. This might reflect a taphonomic difference or a chronological one, although the total identifiable sample from locality 4 (22 specimens) is still too small to allow any firm conclusions to be drawn.

As described by Brandon and Sumbler (1991), the lithology of the Balderton Sand and Gravel includes grey clayey and

Table 3 Dimensions of two horse metatarsals from the Balderton Sand and Gravel, and comparison of their lengths with British and French samples from the Devensian/Weichselian and Ipswichian-Wolstonian/Saalian

Sample	Length (mm)	Proximal width (mm)	Distal width (mm)	<i>n</i>	Reference
Balderton 6A/94	286	56	58	1	This paper
Balderton 4E/4	281	57	57	1	This paper
<i>French Saalian and British Wolstonian or Ipswichian</i>					
Achenheim, Loess anciens	294–304 ^b			9	Prat, 1976, fig. 2
Chatillon-St.-Jean	282–291 ^b			16	Prat, 1976, fig. 2
Crayford	276–291 ^a			8	Egginton, 1982
Stoke Tunnel	280–285 ^a			2	Egginton, 1982
Brundon	272–297 ^a			8	Egginton, 1982
<i>French Weichselian and British Devensian (last cold) stage</i>					
Solutré	244–277 ^a			49	Nobis, 1971
Pair-non-Pair	266–271 ^b			19	Prat, 1976, fig. 2
Kent's Cavern	261–279 ^a			6	Egginton, 1982
Pin Hole	247–271 ^a			6	Egginton, 1982
Ponders End	255–277 ^a			2	Egginton, 1982

^a Sample measurement ranges.

^b 95% confidence intervals of the mean

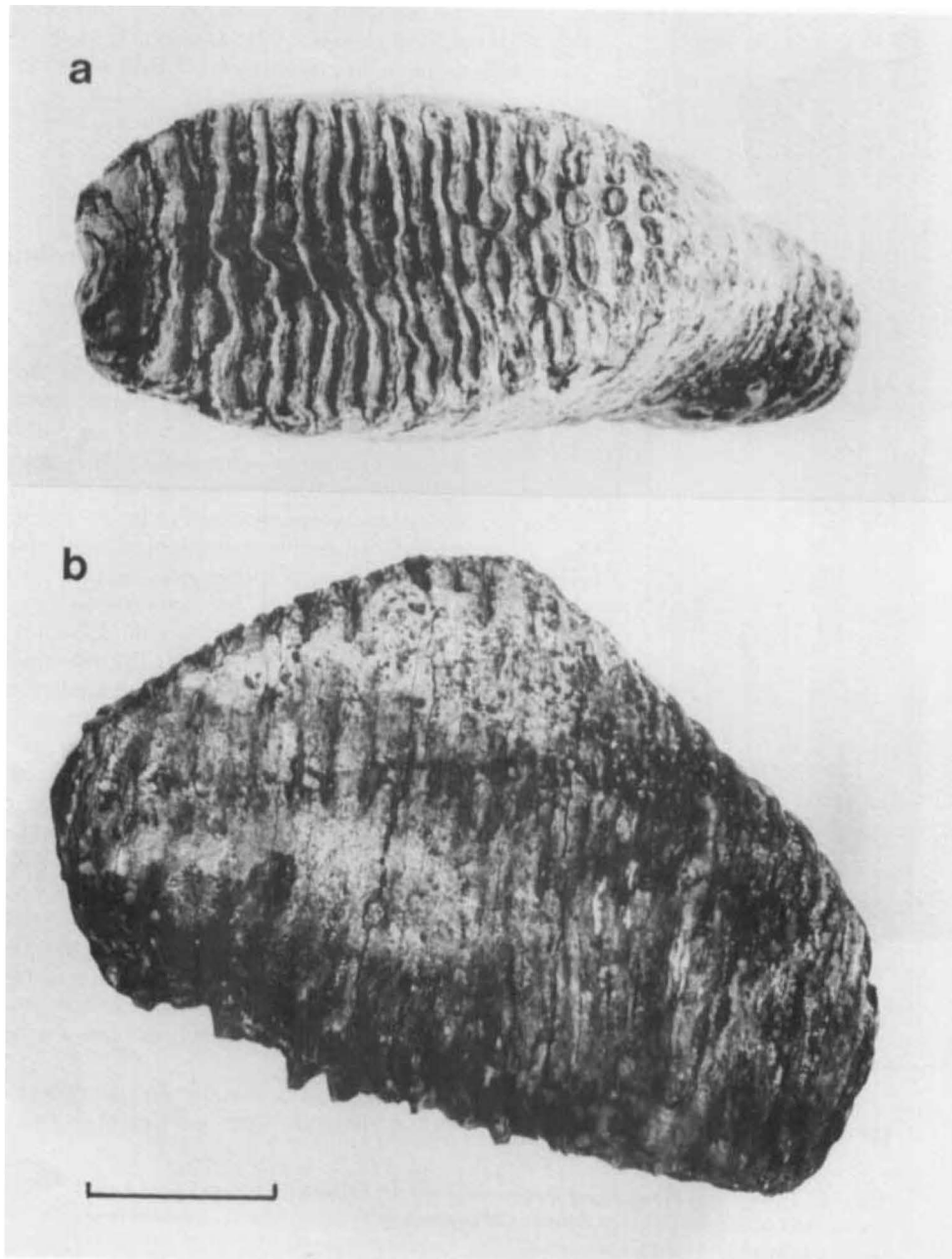


Figure 7 Left last upper molar of mammoth, *M. primigenius*, 6A/16, from Pit 2a. (a) Occlusal view, (b) lateral view. Scale bar 5 cm.

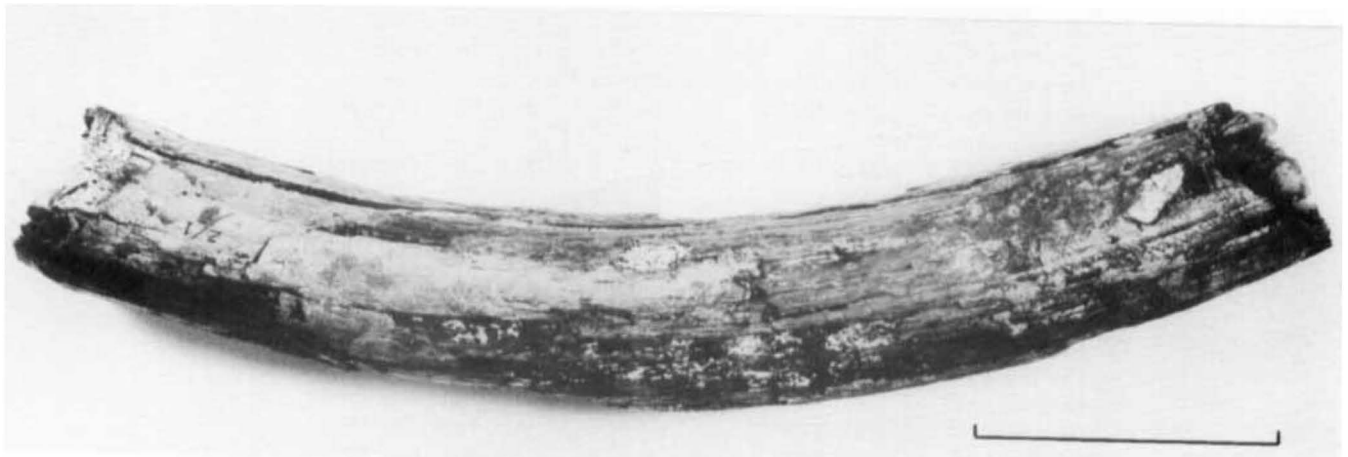


Figure 8 Portion of tusk of mammoth, *M. primigenius*, 2/1, from Pit 3d. Scale bar 10 cm.

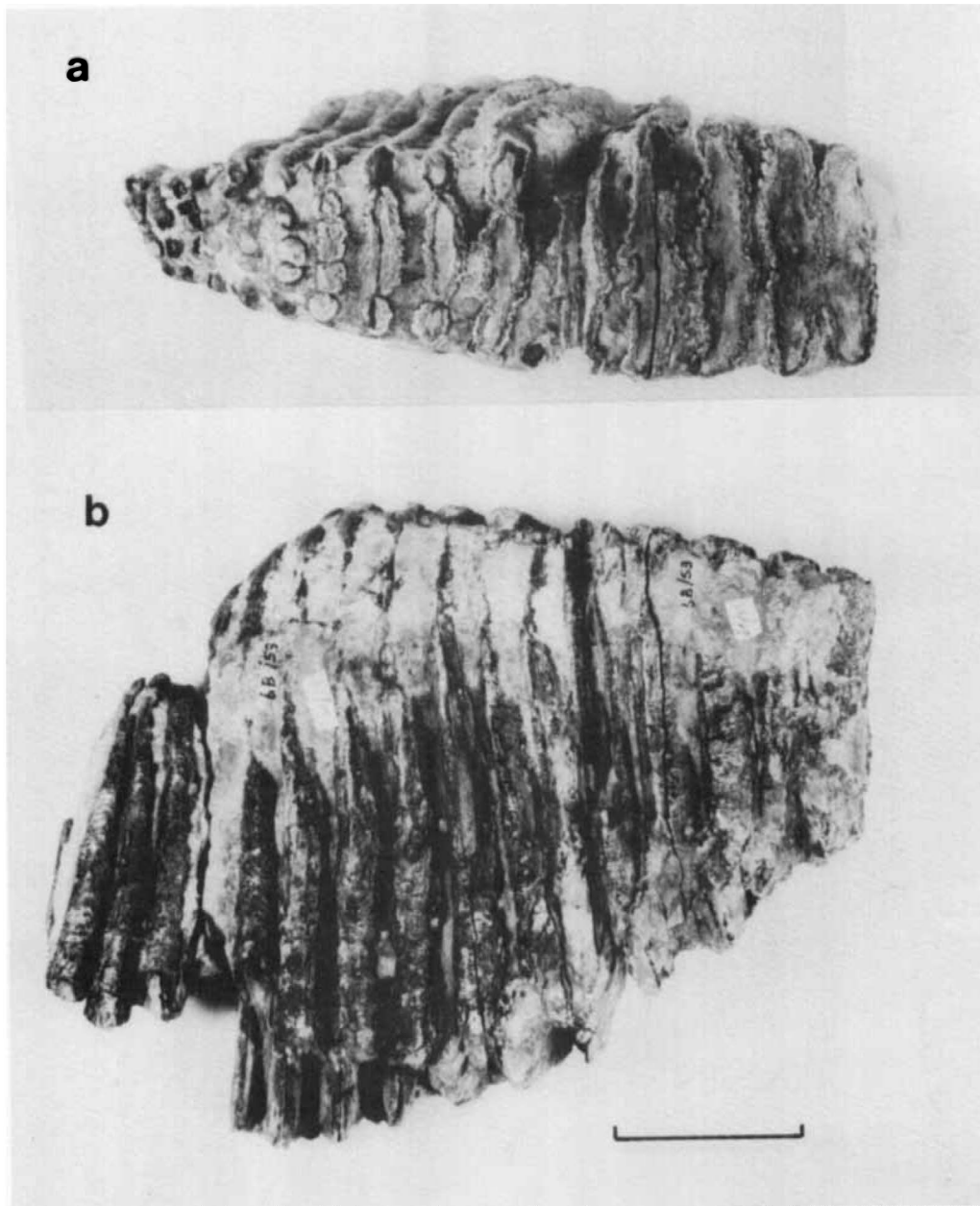


Figure 9 Right upper molar of straight-tusked elephant, *P. antiquus*, 6B/53, from Pit 2b. (a) Occlusal view, (b) lateral view. Scale bar 5 cm.

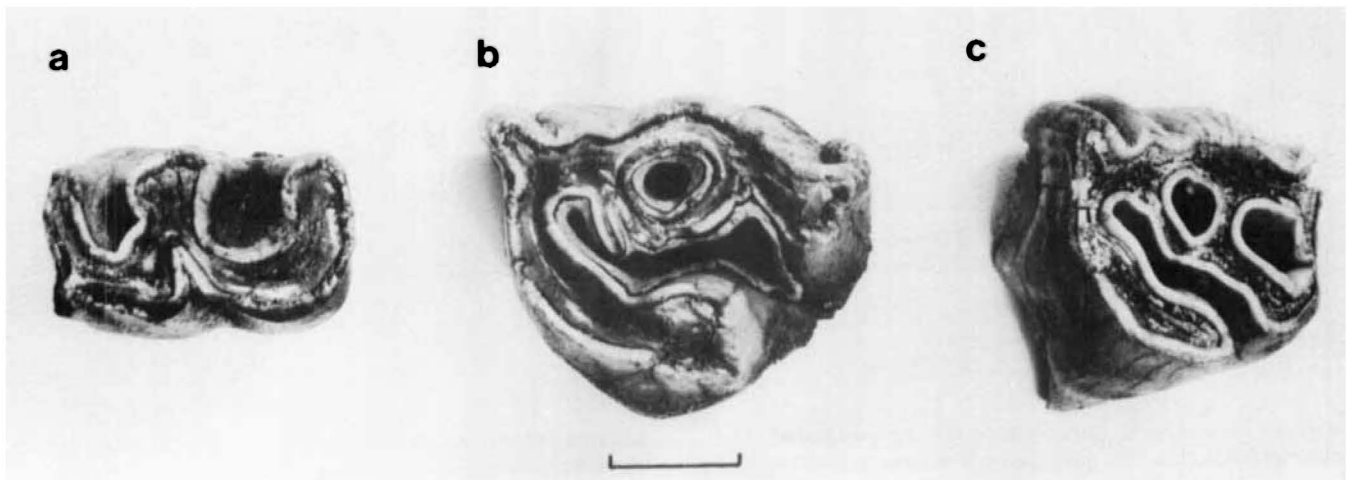


Figure 10 Molars of woolly rhinoceros, *C. antiquitatis* from Pit 2a, in occlusal view. (a) Lower molar 6A/32, (b) upper molar 6A/74, (c) upper molar 6A/191. Scale bar 2 cm.

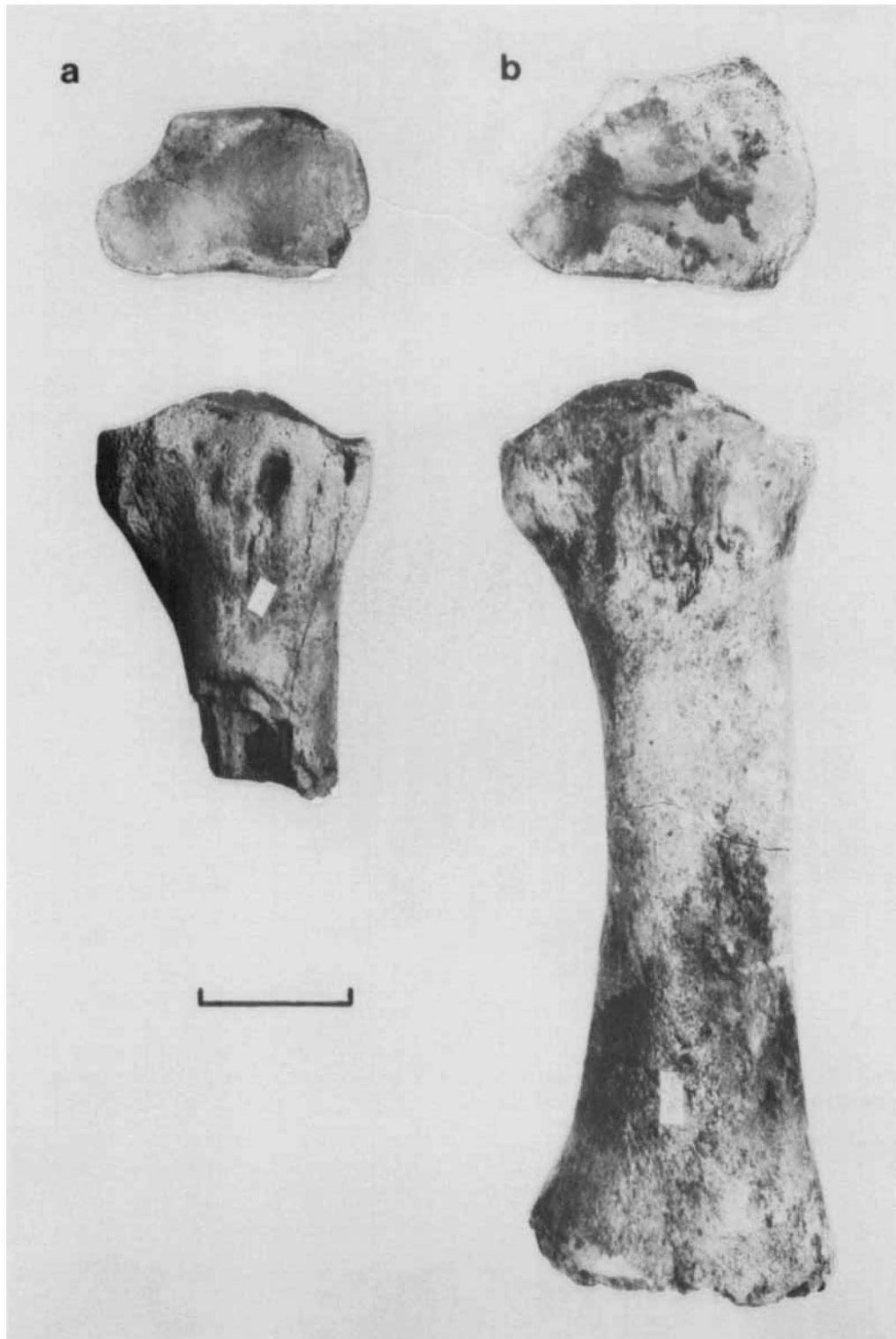


Figure 11 Right radii of rhinoceroses in proximal and anterior views. (a) *Dicerorhinus cf. hemitoechus*, 6A/82, from Pit 2a, (b) *C. antiquitatis*, 7A/49, from Pit 1a (NB distal epiphysis missing). Scale bar 5 cm.

sandy silt in channels; grey, orange and pale-coloured (i.e. colourless or buff) sands; and (usually medium to deep orange) sandy gravels. The fossils show a correspondingly wide range of preservation types, most evident in their coloration. In

addition, many fossils have original sediment adhering to them, and an attempt was made to classify them accordingly. Identifiable and unidentifiable remains were pooled for this analysis (Table 6). Of a total of 193 such specimens, 42%

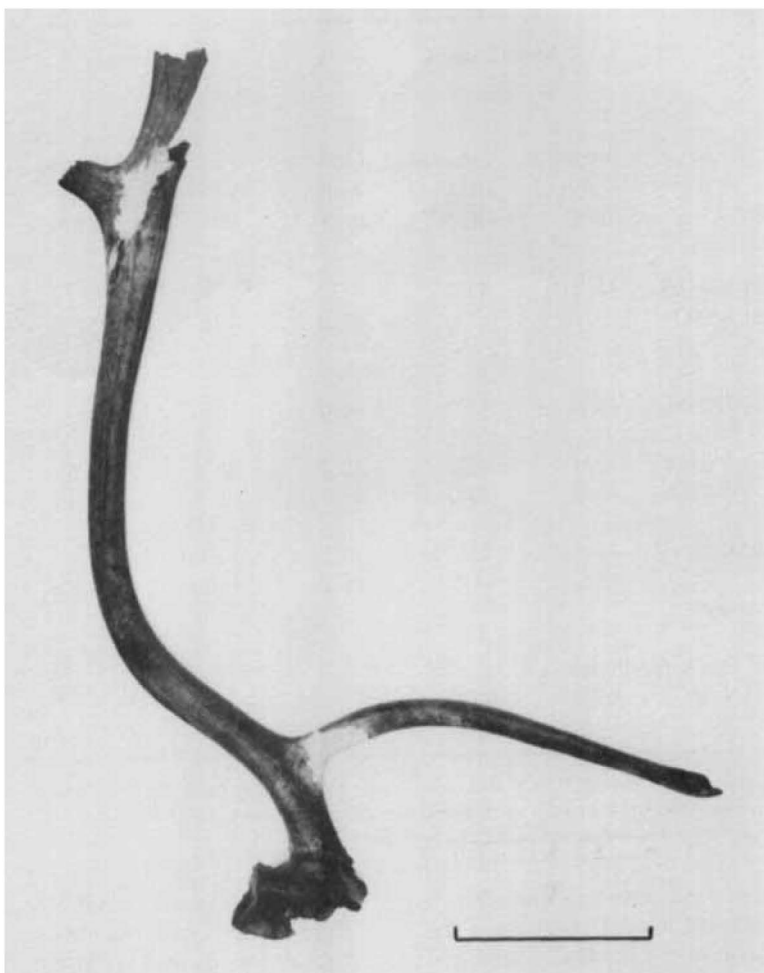


Figure 12 Partial skull and left antler of reindeer, *R. tarandus*, 4E/6, from Pit 4e, in medial view. Scale bar 20 cm.

Table 4 Dimensions of a metatarsal and astragalus referred to bison from the Balderton Sand and Gravel, and comparison with British Ipswichian and Devensian samples, the latter from Gee (1991)

	Metatarsal				Astragalus		
	Length (mm)	Proximal width (mm)	Distal width (mm)	<i>n</i>	Length (mm)	Distal width (mm)	<i>n</i>
Balderton 6B/34	297	72.5	82.0	1			
Balderton 6A/188					95.5	61.5	1
<i>British Ipswichian</i> Barrington	254–286			12	71.0–98.0		70
<i>British Devensian</i> Isleworth	231–276			35	72.7–92.7		11
Wretton					67.2–87.6		23
Windy Knoll	272–295			6	69.0–88.3		25
Kent's Cavern	252–289			3	79.6–101.3		20

Table 5 Dimensions of a metatarsal and axis vertebra of musk ox from the Balderton Sand and Gravel, and comparison with Recent and Weichselian material

Specimen ^a	Metatarsal		Axis vertebra			
	Proximal width (mm)	Proximal depth (mm)	Odontoid width (mm)	Anterior width (mm)	Ventral length (mm)	Ventral minimum width (mm)
Balderton 6A/189	47.5	43.5				
Balderton 6A/31			52.0	130	75	99
<i>Recent</i>						
53.9.20.1 (NHM, male)	43.6	42.0	40.0	108	58	91
16.3.28.3 (NHM)	39.9	40.8	38.7	90.3	50.3	73.2
55.5.14.5 (NHM, female)	40.8	39.0	39.8	95.3	51.5	76.3
612.f (NHM)	43.8	42.7	38.7	110.0	53.6	98.7
H.27,501 (UMZC, male)	43.5	41.5	41.2	110.0	56.6	90.4
<i>Last Cold Stage, North Sea</i>						
5167 (V.T.v.S) ^b	48.5	43.0				
Stolzenb. ^c	43.5	43.0				

^a NHM, Natural History museum; UMZC, University Museum of Zoology, Cambridge

^b V.T.v.S, private collection Van Tuyll van Serooskerken (Bosscha Erdbrink, 1986)

^c Stolzenb., private collection Stolzenbach (Bosscha Erdbrink, 1986)

bear a silt or silty sand, and commonly have a medium brown and grey coloration. This sediment implies origin from the silt-filled channels near the base of the Balderton Sand and Gravel. The basal ca. 2 m at all pits contains all but one of the known organic silt-filled channels and is below the lowest ice-wedge truncation surface (Brandon and Sumbler, 1991). It is significant that quarry workers report that fossils are commonly found when particular areas at or near the base of the deposits are being worked. It is conceivable that a few bones, resting at the very base of the Balderton Sand and Gravel, might have picked up a grey silty sediment direct from the underlying Lias bedrock, but the large majority associated with silt are from channel fills. The only two bones found *in situ*, a wolf femur and unidentified large rib, are from a basal silt-filled channel at Pit 1a.

The remaining fossils (58%) have sand or sand and gravel, of various grades and colours, attached (see Table 6). Many of the fossils with sand and/or gravel attached have orange or brown staining, but others, even some of those bearing orange sediment, have a grey and brown preservation similar to those from silty deposits. Thus it is not always possible to deduce the nature of the enclosing sediment from fossil preservation type alone.

Table 6 also shows some clear differences in the proportions of adhering sediment types between the three main pits. Pit 2a has a far higher proportion of silt-covered specimens than Pit 1a, with 2b intermediate. Orange sand is more predominant in 2b, while 2a has more grey sand, despite the close proximity of these two pits (Brandon and Sumbler, 1991). A high proportion of specimens with pale sand is found only in Pit 1a, corresponding to a high proportion of bones from Pit 1a with very light coloration, whether or not they have adhering sediment. Finally, two mammoth molars from locality 3 and one from locality 2 are stained reddish brown, and are partly coated with cemented reddish brown silty

sand. These could possibly have originated in the Whisby Sand or the locally rubified top of the Balderton Sand and Gravel, though they could equally have come from the base of the sand and gravel, which, at the bottom of the workings, is commonly red-stained owing to seepage of iron-rich water.

Table 7 shows the ratios of the adhering sediments for different fossil species. In general, there is no association of particular mammalian species or groups of species with particular sediment types. Calculated as a percentage of the total number of fossils for each sediment type, mammoth comprises 54% of the specimens with silt or silty sand matrix, and 62% of the specimens with sand and/or gravel matrix. For woolly rhino, the figures are 17% and 19%, respectively. Some possible imbalances in other species are evident, although small sample sizes make the significance of these uncertain. For the major species at least, the remains appear to be most abundant in whatever sediment type is predominant or most fossiliferous in each pit.

Ecological significance

The Balderton assemblage as a whole points clearly to a cold climate and a largely open biotope, including one or more stadial phases of a cold stage. It is possible, however, that parts of the assemblage pertain to one or more interstadial phases. The following list commences with the most diagnostically arctic species, and progresses towards the more temperate species.

Musk ox, *Ovibos moschatus*, is today distributed in the arctic tundra of North America and Greenland, where it feeds on grasses, sedges and herbaceous plants (Nowak and Paradiso, 1983). This may be a somewhat relict distribution, as there is evidence that the species was more widely distributed before the activities of humans (Kennard, 1944; Nowak and

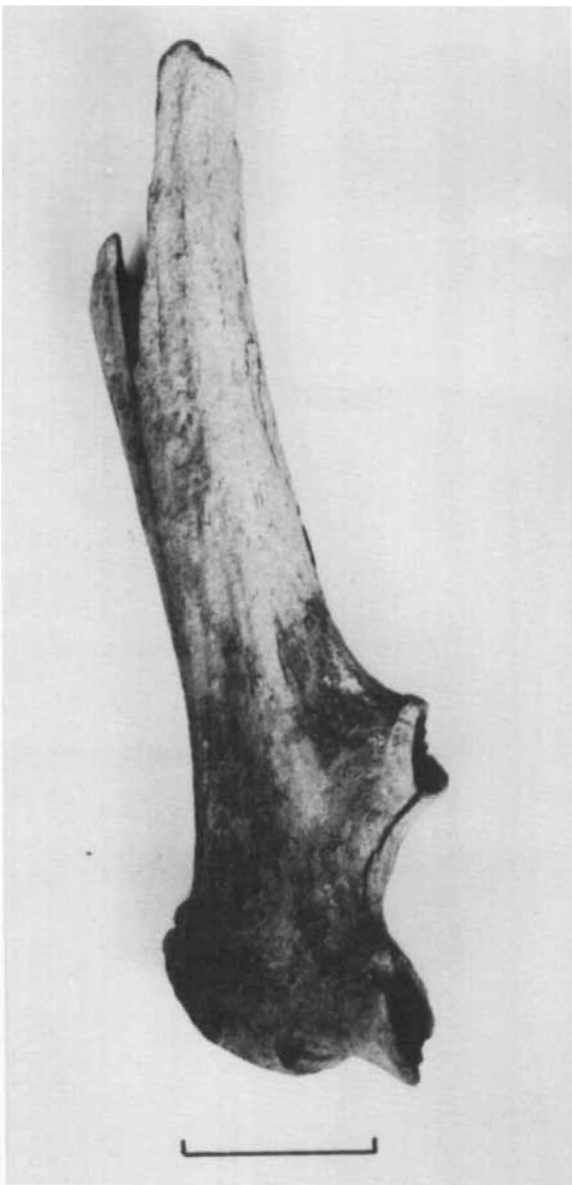


Figure 13 Shed left antler base of red deer, *C. elaphus*, 6A/142, from Pit 2a, in medial view. Scale bar 5 cm.

Paradiso, 1983). There are relatively few records of musk ox from the British Pleistocene (Dawkins, 1872; Reynolds, 1934), leading Stuart (1982) to suggest that even within cold stages they may have been restricted to the more arctic climatic phases.

Reindeer, *Rangifer tarandus*, occurs today in tundra and boreal forest ecotypes, but attempts to assign Pleistocene material to particular living forms have not been successful (Delpech, 1975). The diet of reindeer is dominated by lichens and herbaceous plants (Nowak and Paradiso, 1983). The Balderton skull is of interest because it provides seasonal information, the presence of a male with fully grown but unshed antlers indicating late summer or autumn occurrence of reindeer at the site (cf. Stuart, 1982).

Woolly rhinoceros, *Coelodonta antiquitatis*, is characteristic of Middle and Upper Pleistocene cold stages in Britain, its skull and dental morphology corresponding to open-ground feeding on low vegetation (Loose, 1975). Mammoth, *Mammuthus primigenius*, is similarly most commonly associated with cold stage deposits in Britain, although it also occurred during the more open phases of some interglacials (Stuart,

1976). Its body form and dentition were adapted to living in a cool climate and feeding on a diet dominated by grasses (Garutt, 1964).

A few of the remains of large bovids from Balderton are tentatively identified as *Bison priscus*; this species was a herding grazer and occurred commonly in both cold stages and interglacials in Britain. Similarly, horse, *Equus caballus*, with its almost exclusively grassy diet, was a common component of cold stage faunas in Britain. It also occurred during parts of the interglacials, presumably frequenting locally open areas.

Carnivores are extremely poorly represented in the assemblage, but the three taxa recovered, wolf, lion and bear (probably brown bear), were common elements of both interglacial and cold stage faunas in the British Middle and Upper Pleistocene (Stuart, 1982). Their distributions appear to have been less affected by climatic changes than those of many of the herbivore species.

Red deer, *Cervus elaphus*, is a species ubiquitous in all Middle and Upper Pleistocene interglacials in Britain, but which is also found in a variety of cold stage contexts (Lister, 1984). Where detailed evidence is available, the latter appear largely restricted to interstadials, when climate was less severe and some tree or shrub vegetation often occurred. Especially in areas of little natural relief such as the English Midlands and East Anglia, including the area of the Balderton deposits, the species was rare or absent in the stadial phases of cold stages, corresponding to its known environmental limitations at the present day (Lister, 1984).

The extinct straight-tusked elephant, *Palaeoloxodon antiquus*, was characteristic of temperate, wooded interglacials in the British Middle and Upper Pleistocene, and is absent from typical cold stage mammalian assemblages (Stuart, 1982). However, the discovery of a skull of *P. antiquus* *in situ* in fluvial gravels referred to the Wolstonian or Anglian Cold Stage at Snitterfield, Warwickshire, in association with a molluscan fauna including some temperate elements (Lister *et al.*, 1990) indicates that the species existed in Britain during some interstadial phases.

The single specimen of rhinoceros, *Dicerorhinus* cf. *hemioechus*, could also have pertained to an intra-Wolstonian interstadial. Like *P. antiquus*, its remains are very largely restricted to interglacials in the British Middle and Upper Pleistocene, and do not occur in typical cold stage assemblages. However, a record from the Lower Breccia at Pontnewydd Cave, Clwyd, of Wolstonian age and in a broadly interstadial context (Green, 1986), provides a precedent for the Balderton find.

It is conceivable that the entire vertebrate assemblage from the Balderton Sand and Gravel could be penecontemporaneous, in which case, in order to accommodate the more temperate elements, it would most likely correspond to an interstadial phase. It is more likely, however, that the assemblage spans a period of time encompassing a range of climatic phases within a cold stage. The lack of ice-wedge casts in the main mammaliferous levels of the Balderton Sand and Gravel (see above, and Brandon and Sumbler (1991)) implies that the available assemblage did not accumulate in a fully arctic phase. Pollen analyses from silt bands at Localities 1, 3, 5 and 6 (Brandon and Sumbler, 1991) indicate a rich, open herbaceous vegetation, with little or no tree or shrub cover, i.e. not interstadial in the vegetational sense. There is no lithological or non-mammalian biostatigraphical evidence of a temperate episode within the Balderton Sand and Gravel, although this does not preclude the possibility that some levels within the fossiliferous deposit might have accumulated under temperate conditions. We may envisage

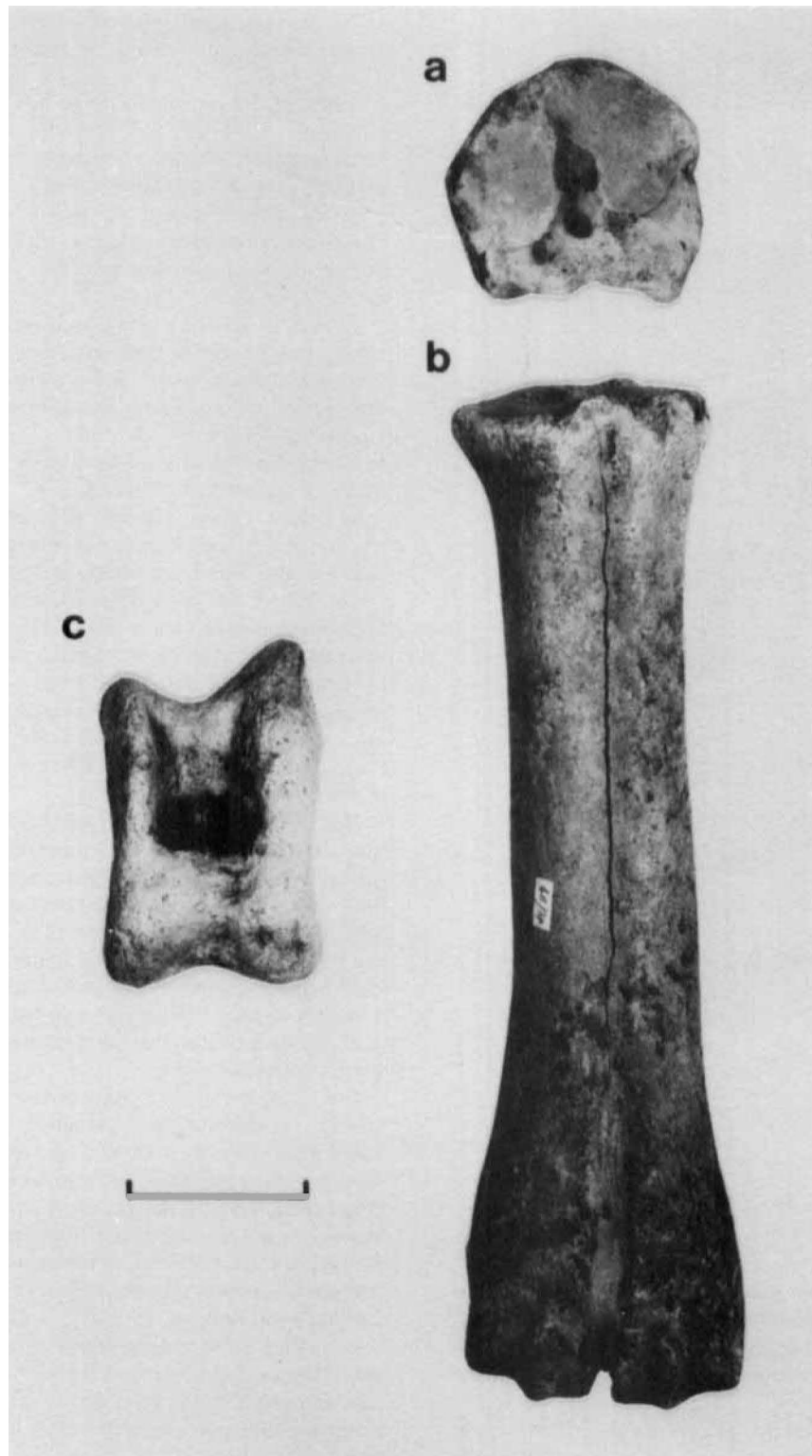


Figure 14 Astragalus and metatarsal of large bovid, cf. bison *B. priscus*. (a and b) Left metatarsal 6B/34 from Pit 2b, in proximal and anterior views, (c) left astragalus 6A/188 from Pit 2a, in anterior view. Scale bar 5 cm.

periods of sub-arctic climate in which probably only a restricted mammalian fauna existed, including musk ox and reindeer. At the other end of the spectrum, the presence of straight-tusked elephant, rhinoceros and red deer suggests more temperate phase(s). Other species, such as mammoth, bison, horse and woolly rhino, could have persisted across a range of climatic phases.

Stratigraphical significance

In Table 8, the Balderton assemblage is compared with other essentially cold climate, British large-mammal faunas that have been referred to the interval between the Hoxnian and Ipswichian Interglacials, and generally classified as

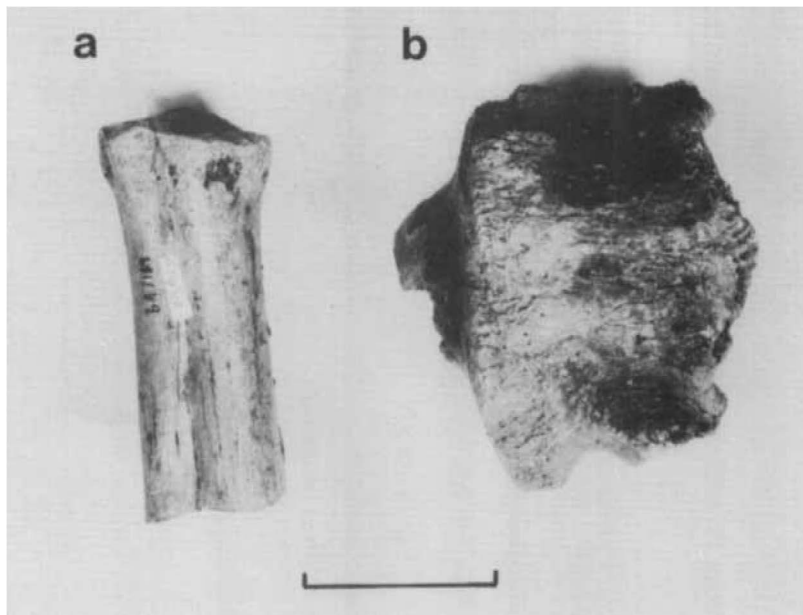


Figure 15 Metatarsal and axis vertebra of musk ox, *O. moschatus* from Pit 2a. (a) Right metatarsal 6A/189 in anterior view, (b) axis 6A/31 in ventral view. Scale bar 5 cm.

Table 6 Sediment types adhering to fossils, by pit. The figures give the number of specimens bearing each sediment type, and in brackets this is expressed as a percentage of the total number of sediment-bearing fossils from that pit

Pit	Sediment type					Total
	Silt or silty sand	Grey sand	Orange sand	Pale sand	Other sand and/or gravel	
1a	6 (25)		2 (8)	7 (29)	9 (38)	24 (100)
2a	51 (58)	12 (14)	14 (16)		11 (13)	88 (100)
2b	12 (19)	4 (6)	35 (56)	3 (5)	9 (14)	63 (100)
All pits (1–5) pooled	81 (42)	18 (9)	51 (26)	10 (5)	33 (17)	193 (100)

Table 7 Sediment types adhering to fossils, classified by species arranged in order of abundance, all pits pooled. The figures give the number of specimens of each species bearing each sediment type, and in brackets this is expressed as a percentage of the total number of fossils bearing that sediment type. The sixth (rightmost) column is a summation of columns two to five

Taxon	Sediment type					All sands and gravels pooled
	Silt or silty sand	Grey sand	Orange sand	Pale sand	Other sand and/or gravel	
<i>Mammuthus</i>	29 (54)	8 (57)	22 (59)	6 (75)	20 (65)	56 (62)
<i>Coelodonta</i>	9 (17)	5 (33)	8 (22)		4 (13)	17 (19)
<i>Equus</i>	6 (11)		2 (5)		1 (3)	3 (3)
<i>Cervus</i>	3 (6)	1 (7)	1 (3)	1 (13)	1 (3)	4 (4)
<i>Palaeoloxodon</i>	1 (2)		1 (3)		5 (16)	6 (7)
<i>Bison/Bos</i>	2 (4)		2 (5)	1 (13)		3 (3)
<i>Rangifer</i>	1 (2)					
<i>Ovibos</i>	2 (4)					
<i>Canis</i>	1 (2)					
<i>Ursus</i>			1 (3)			
Total	54 (100)	14 (100)	37 (100)	8 (100)	31 (100)	89 (100)

Table 8. Large mammal faunas from British deposits that have been referred to the cold stage between the Hoxnian and Ipswichian

	Type ^a																	
	Wolstonian of the Midlands				Thames Basin						Caves				Other sites			
	Sretton Sands (1) ^a	Baginton/Lillington Gravels (2)	Waverley Wood (3)	Snitterfield (4)	Baker's Hole (5)	Ebbsfleet (6)	Boyn Hill Gravel (7)	Lynch Hill Gravel (8)	Taplow Gravel (9)	Stanton Harcourt Gravel (10)	Crayford (11)	Tornewton C, Glutton and Bear Strata (12)	Pontnewydd, Lower Breccia (13)	Bacon Hole, Units B and C (14)	Marsworth, Lower Channel (15)	Broome Heath (16)	Avon Terrace no. 4 (17)	Balderton Sand and Gravel (18)
Carnivora																		
<i>Canis lupus</i> L., wolf											+	+	+		+			+
^b <i>Vulpes vulpes</i> (L.), red fox												+						
<i>Ursus arctos</i> L., brown bear										+	+	+	+		+			+
<i>Gulo gulo</i> L., wolverine												+						
^b <i>Meles meles</i> (L.), badger												+						
<i>Panthera leo</i> (L.), lion											+	+			+			+
<i>Panthera aff. pardus</i> , leopard-sized cat													+					
<i>Aonyx antiqua</i> Blainville, clawless otter												+						
Proboscidea																		
<i>Mammuthus primigenius</i> (Blum.), mammoth		+			+	+		+	+	+	+				+	+	+	+
^b <i>Palaeoloxodon antiquus</i> , Falc. & Caut., straight-tusked elephant	+		+	+				+										+
Perissodactyla																		
<i>Equus caballus</i> L., horse		+			+	+	+	+		+	+	+	+	+	+		+	+
<i>Coelodonta antiquitatis</i> Blum., woolly rhino		+			+	+		+	+	+	+	+					+	+
^b <i>Dicerorhinus</i> spp., rhinos											+		+					+
Artiodactyla																		
<i>Rangifer tarandus</i> (L.), reindeer		+					+					+					+	+
<i>Cervus elaphus</i> L., red deer		+					+			+	+		+					+
<i>Megaloceros giganteus</i> (Blum.), giant deer		+									+							
<i>Bison/Bos</i> , large bovid		+	+					+		+	+	+	+		+	+	+	+
<i>Ovibos moschatus</i> Zimmerman, musk ox									+		+							+

^a Numbers in parentheses are references to sites and faunas: (1) Shotton, 1973; Lister, 1989; (2) Shotton, 1953, Lister, 1989; (3) A. P. Currant, pers. comm.; (4) Lister et al., 1990; (5) Stuart, 1982, table 8.1; (6) Sutcliffe, 1985, p.138; (7)–(9) Gibbard, 1986; (10) Sandford, 1924; Briggs, 1988; (11) Stuart, 1982; (12) Sutcliffe and Zeuner, 1962; (13) Green, 1986; (14) Stringer et al., 1986; (15) Green et al., 1984; (16) Stuart, 1982, table 8.1; (17) Whitehead, 1989; Bridgland et al., 1989; (18) this paper.

^b Commonly associated elsewhere with temperate faunas.

Wolstonian. This interval was undoubtedly climatically complex, including interstadials and probably also an interglacial (Sutcliffe, 1976). The faunas are dominated by species indicative of cool, open conditions. At some of the sites, temperate elements also appear, which may indicate warmer phase(s) within the Wolstonian, although admixture of fossils from adjacent interglacial deposits may be responsible in some cases, particularly the occurrence of red fox and badger, recorded only from Tornewton Cave. Faunas from the type Wolstonian sequence and associated deposit in the Midlands have been included in Table 8, although some authors have suggested that they are of Anglian age (Sumbler, 1983; Rose, 1987). Also shown is the fauna from Crayford, Kent, of controversial age. Differing geomorphological interpretations place the Crayford deposits either in the late Ipswichian (Stuart, 1976), or between the Hoxnian and Ipswichian (Sutcliffe, 1976; Sutcliffe and Kowalski, 1976). Alternatively,

the fauna has been regarded as mixed, but with the 'cold element' belonging to the period between the Hoxnian and Ipswichian (Currant, 1986). Finally, the Avon Terrace no. 4 deposits have been included in Table 8. These had long been regarded as early Devensian, but recently have been reassigned to a post-Hoxnian, pre-Ipswichian phase (Whitehead, 1989; Bridgland et al., 1989).

Table 8 shows that each of the Balderton species is recorded from at least two of the other sites, or if the assemblages of possibly debatable age from the type Wolstonian and Crayford are excluded, from at least one other site. The Balderton fauna would therefore seem to be entirely consistent with the Wolstonian age deduced from other lines of evidence (cf. Brandon and Sumbler, 1991).

Most of the species also are found commonly in deposits of Devensian age (e.g. Stuart, 1982, Table 8.2). There are two exceptions to this, however: straight-tusked elephant

Palaeoloxodon aniquus, and cf. narrow-nosed rhinoceros *Dicerorhinus* cf. *hemiteochus*. Both of these taxa are now extinct, and although there is evidence that they persisted into the Last Cold Stage in southern Europe and the Middle East (Stuart, in preparation), there is no firm record of their survival in Britain after the end of the Ipswichian (Last Interglacial). There is no trace of either taxon among numerous Devensian deposits, both open and cave sites (Stuart, 1982, 1983). Stringer et al. (1986) recorded both *Palaeoloxodon* and *Dicerorhinus* from the Upper Cave Earth at Bacon Hole, Gower, which they attributed to an early Devensian interstadial, but in the absence of direct dating, this level might alternatively represent the late Ipswichian, as suggested by Stringer (1977) and Stuart (1982, p. 134).

It is believed that the *Palaeoloxodon* and *Dicerorhinus* remains were in primary position within the lower part of the Balderton Sand and Gravel. However, in view of the importance of these records, and the fact that none of the fossils was found *in situ*, some discussion of alternative possibilities is desirable.

First, the ESR results on two *P. antiquus* teeth might be taken to suggest that they are of Ipswichian (Last Interglacial) age, rather than pertaining to the pre-Ipswichian cold stage, since their mean dates, if early Uranium uptake is assumed, are 120 ka and 129 ka, respectively (Grün, in Brandon and Sumbler, 1991). However, ESR dates on individual specimens are themselves averaged from often rather widely spaced readings, and further depend on assumptions about the water level and the rate of U uptake. In the case of the two *P. antiquus* specimens, an assumption of linear U uptake would push the dates back to 169 ka and 144 ka, respectively, and Grün (in Brandon and Sumbler, 1991) suggests that the early and linear models bracket the true age. It seems safest to regard individual dates as giving only a broad indication of age: their value comes when data from many specimens are viewed together. Under either model of U uptake, the two results of *P. antiquus* are within the overall range of dates on six *M. primigenius* teeth from the Balderton Sand and Gravel (Grün, in Brandon and Sumbler, 1991).

Also against an Ipswichian age is the geological evidence (Brandon and Sumbler, 1991), which strongly indicates that the entire aggradation of the Balderton Sand and Gravel, and the overlying Whisby Sand, must pre-date the Last Interglacial. Moreover, there is no evidence of Ipswichian sedimentation on top of the Balderton Sand and Gravel, which formed a plateau-like interfluvium at this time. The Ipswichian is indicated only by rubification of the Whisby Sand and the upper part of the Balderton Sand and Gravel.

Second, it should be considered whether the *Palaeoloxodon* and *Dicerorhinus* remains could have originated in temperate channel deposits underlying the Balderton Sand and Gravel. This possibility is regarded as very unlikely since no such channel has ever been seen during extensive and regular observation of the Balderton Sand and Gravel, often down to bedrock, over the time that the fossils were being collected. All pollen and insect assemblages obtained from silt-filled channels indicated cold stage conditions, and all were within rather than below the Balderton Sand and Gravel (Brandon and Sumbler, 1991). At Pit 1a, several teeth of *P. antiquus* have been found at known times and in known areas of the pit, but there were no basal temperate channel deposits. Moreover, the colour and sediments cemented to these fossils (Table 7) suggest that they come from identical sand and gravel bed(s) to those that yielded *M. primigenius* molars, and not from organic silts. In January 1991, subsequent to compilation of the specimen lists given in this paper, further collecting produced two molars, one (7A/75) of *Mammuthus*

primigenius, the other (7A/73) of *Palaeoloxodon antiquus*, from the same part of Pit 1a at the same time, and with identical preservation. The implication is that they had come from the same bed.

Third, the question of reworking from older, temperate deposits, should be addressed. This is thought extremely unlikely, since the fossils have the same degree of freshness and an identical range of preservation types as other Balderton material, including typically cold stage forms such as *Coelodonta*. The ESR dates on two *Palaeoloxodon* specimens also militate against reworking. Some caution should perhaps attach to the Balderton *Dicerorhinus*, since this is based on a single, slightly rolled specimen, although it is still well within the preservation range of other Balderton material. However, the *Palaeoloxodon* remains at least seem unlikely to have been reworked, and can be taken to support a pre-Devensian date for the deposition of the Balderton Sand and Gravel.

The size and detailed morphology of certain species is also of stratigraphical interest.

The dental evolution of mammoths has often been invoked as a stratigraphical guide, with morphologies intermediate between typical early Middle Pleistocene *Mammuthus trogontherii* and late Upper Pleistocene *M. primigenius* expected at intervening times, including the Wolstonian/Saalian Stage (Adam, 1961; Guenther, 1971). The *primigenius*-like teeth from Balderton might, on this model, be taken as evidence of Devensian age. However, there is growing evidence that mammoths in northwest Europe had attained advanced form at least as early as the Wolstonian/Saalian, British examples coming from Broome Heath, Norfolk, the Baginton–Lillington Gravels, Warwickshire, and La Cotte, Jersey (Scott, 1986; Lister, 1989, in preparation). The advanced form of the Balderton mammoths is therefore entirely consistent with a Wolstonian age.

In general, the body size of mammalian species is a poor biostratigraphical indicator in the Quaternary, especially when based on evidence from only a few sites, since it is an extremely flexible biological attribute (Lister, 1986, 1991). Nonetheless, the large size of both the horse and cf. bison remains from the Balderton deposit is of interest, since both fall outside the range of samples from a considerable number of sites of Devensian age, while comparably large specimens are known for the Wolstonian/Saalian (see above). On current evidence, therefore, the large size of these species is more consistent with a Wolstonian than a Devensian age.

Discussion

The Balderton Sand and Gravel has yielded one of the largest collections of pre-Ipswichian cold stage mammalian fossils in the British Isles. The assemblage, essentially restricted to large herbivores, probably combines faunas from a range of cold stage environments. Its species composition is similar to that of many Devensian sites, illustrating the rather constant nature of cold stage mammalian faunas. A similar phenomenon is observed in the flora, and in molluscan and coleopteran faunas (Brandon and Sumbler, 1991). The occurrence of two mammalian taxa extinct in Britain by the Devensian, namely straight-tusked elephant and cf. narrow-nosed rhinoceros, provides a valuable addition to the previously limited evidence for these species in the Wolstonian, probably within interstadials.

The proportions of mammalian species also deserve mention. The Balderton assemblage has a very strong predominance of mammoth and woolly rhinoceros; bison is much

less common and reindeer extremely rare. Certain other British cold stage assemblages show a similar pattern, while in others the proportions are reversed. For example, Rackham (1978) compared the species proportions of two sites in Lincolnshire, Tattershall Castle and Tattershall Thorpe, only ca. 30 km east of the Balderton Terrace, and believed to date to warmer and cooler phases, respectively, of the Middle Devensian. The species representation at Tattershall Thorpe is very similar to that at Balderton, but Tattershall Castle is dominated by bison and reindeer. Species proportions in fossil assemblages should be treated with caution, since they can be influenced very strongly by taphonomic factors. However, the analogous depositional environments represented at these three geographically close sites implies that the relative species proportions in their fossil assemblages genuinely reflect parallel patterns in the composition of the living communities and their palaeoenvironments.

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