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Phil. Trans. R. Soc. Lond. B 1990 **328**, 359-385
doi: 10.1098/rstb.1990.0117

Phil. Trans. R. Soc. Lond. B **328**, 359–385 (1990) [359]
Printed in Great Britain

THE EARLY MIDDLE PLEISTOCENE VERTEBRATE FAUNA FROM LITTLE OAKLEY, ESSEX

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(*Communicated by R. G. West, F.R.S. – Received* 4 *March* 1988 – *Revised* 3 *October* 1989)

[Plate 1]

CONTENTS

The Little Oakley channel has provided one of very few stratified early Middle Pleistocene vertebrate faunas from the British Isles. This study is based both on material recovered by S. H. Warren in 1939, and new material excavated in 1982–87.

The vertebrate fauna is entirely consistent with a temperate climate and vegetation, in keeping with palaeobotanical and invertebrate evidence from the site. Mammals include taxa indicative of both woodland (e.g. *Apodemus sylvaticus*, *Sus scrofa*), and more open areas (e.g. *Equus* sp., *Sorex minutus*). At least 12 species of freshwater fishes have been identified, including the first British Pleistocene records of carp (*Cyprinus carpio*), freshwater burbot (*Lota lota*), and probably zander (*Stizostedion* sp.). The herpetofauna includes the earliest dated British record of European pond tortoise (*Emys orbicularis*), which together with the fish fauna indicates fully interglacial conditions.

The early giant deer *Megaloceros verticornis* and probably *M. dawkinsi* are recorded for the first time in Britain outside the Cromer Forest-bed Formation. These species, together with the ancestral water vole *Mimomys savini*, are of considerable stratigraphic significance, strongly supporting an age for the channel later than Pastonian but pre-dating faunas 2 and 3 of Westbury-sub-Mendip.

1. Historical introduction and provenance of fossils

The existence of a broad channel of fossiliferous silts and sands at Little Oakley, Essex, was first recognized in 1939 by S. H. Warren and A. S. Kennard, who discovered molluscan and

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vertebrate remains in the spoil heap of a sewer trench (Warren 1940). Kennard noted the affinity of the molluscan fauna to that of the 'Cromer Forest Bed' of West Runton (Preece 1990), and Warren & Davis (*ca.* 1955) supported this with the tentative identification of an antler of the extinct elk *Cervalces latifrons* (Johnson).

Sutcliffe, Currant & Oakley (1979) drew attention to the potential importance of the Little Oakley channel, and the existence of a manuscript by Warren indicating the precise position of the 1939 trench. Reinvestigation of the site began in 1982, with a series of boreholes which demonstrated the extent of the channel and its lithology (Bridgland *et al.* 1990). From the boreholes, pollen, mollusc and ostracod samples were obtained, providing biostratigraphical evidence that the deposits accumulated during an interglacial stage of the early Middle Pleistocene (Gibbard & Peglar 1990; Preece 1990; Robinson 1990).

The borehole samples also yielded a few small vertebrate remains, after sieving of sediment through a 0.25 mm mesh. Only borehole LOO contained identifiable remains, those from LOA and LOH being too fragmentary for specific identification. The sedimentology and molluscan fauna of borehole LOO indicate that it represents a marginal, quiet-water facies. In addition, pollen evidence suggests that the deposits accumulated during the pre-temperate substage of the interglacial.

In addition to the boreholes, vertebrate remains were collected from several large pits, dug through the channel deposits with the aid of a mechanical excavator. Pits LOAB, LOAC, LOAF and LOAH corresponded to the central part of the channel, immediately adjacent to borehole LOA. Pit LOAG was more marginal. The pollen sequence from LOA indicates that all excavated levels in LOAB, LOAC, LOAF and LOAH, and probably also LOAG, correspond to the early temperate substage of the interglacial. Several large bones were collected in the field during the excavation. In addition, from pits LOAC, LOAF, LOAG and LOAH, 50 kg bulk samples were collected from successive grabs of 25 cm thickness through the deposit, to a depth of 350 cm. These samples, amounting to approximately 1.5 t of sediment, were later wet-sieved through mesh sizes of 1 cm and 1 mm, and the retained fractions dried and carefully sorted for small vertebrate material. Fish were the most abundant remains, with mammals giving a rather low yield, generally between one and six identifiable specimens per 50 kg sample. It is likely that some very small vertebrate remains (e.g. shrew incisors) were lost through the 1 mm mesh, but sieving a sufficient quantity of material through a finer mesh would have been impracticable.

All vertebrate remains from the 1982–87 boreholes and pits have been placed in the collection of the University Museum of Zoology, Cambridge (UMZC). The vertebrate material collected by Warren in 1939, and now at the British Museum (Natural History) (BM(NH)), is also included in this study. Although the precise provenance of Warren's specimens is unknown, it is clear from Warren's sketch (unpublished data) that the main part of the 1939 trench ran along the central part of the channel, with its eastern extremity passing within a few metres of the position of LOA, and a small extension of the trench entering a more marginal area close to the position of LOO (Bridgland *et al.* 1990). Sediment scraped from one of the large mammal bones collected by Warren (an antler base of cf. *Megaloceros dawkinsi*, M20414) yielded a pollen spectrum palynologically indistinguishable from the early temperate profile of the 1984 boreholes (Gibbard & Peglar 1990).

2. Description and taxonomy of material

In the following lists, each specimen from the 1982–87 excavations is listed by borehole or pit (LOO, LOAB, LOAC, LOAF, LOAG or LOAH), and level below surface (in centimetres) at which it was obtained. This is followed by its UMZC acquisition number, prefixed LO, and description. A few specimens, listed as 'unstratified', are from the private collection of Mr R. Wrayton, and are of uncertain level within the channel deposit. Specimens collected by Warren in 1939 bear BM(NH) acquisition numbers, prefixed M. All measurements are in millimetres. A complete faunal list is given in table 1.

Table 1. The vertebrate fauna from the Little Oakley channel

		Warren colln.	LOO	LOAB LOAC LOAF LOAG LOAH
Pisces				
(Haplomi)	*Esox lucius* L., pike	·	·	+
Cypriniformes	*Scardinius erythropthalmus* (L.), rudd	·	+	+
	Tinca tinca (L.), tench	·	+	+
	Rutilus rutilus (L.), roach	·	·	+
	Barbus barbus (L.), barbel	·	·	+
	Abramis brama (L.), bream	·	·	+
	Cyprinus carpio L., common carp	·	·	+
	Leuciscus sp.	·	·	+
Gadiformes	*Lota lota* (L.), burbot	·	·	+
Anguilliformes	*Anguilla anguilla* L., eel	·	·	+
Perciformes	*Perca fluviatilis* L., perch	·	·	+
	Stizostedion sp., zander	·	·	cf.
Amphibia				
Anura	*Rana arvalis* Nilsson, moor frog	·	·	cf.
	Rana sp., a frog	·	·	+
Reptilia				
Chelonia	*Emys orbicularis* L., European pond tortoise	·	·	+
Ophidia	*Natrix natrix* (L.), grass snake	·	·	+
Mammalia				
Insectivora	*Sorex minutus* L., pygmy shrew	·	cf.	·
	Sorex sp. 1 (size of *S. araneus* L. or *S. runtonensis* Hinton), a shrew	·	+	·
	Sorex sp. 2 (larger than *S. araneus* L.), a shrew	·	+	·
Rodentia	*Apodemus sylvaticus* (L.), wood mouse	·	·	+
	Clethrionomys glareolus (Schreber), bank vole	·	·	+
	Mimomys savini Hinton, extinct water vole	+	·	+
	Microtus oeconomus (Pallas), northern vole	·	·	+
	Microtus arvalis (Pallas), common vole	·	·	cf.
	Pitymys gregaloides Hinton, extinct pine vole	·	·	cf.
	Pitymys sp., pine vole	·	·	+
Carnivora	*Crocuta crocuta* Erxleben, spotted hyaena	cf.	·	cf.
Proboscidea	? Elephantidae gen. et sp. indet., elephant	?	·	·
Perissodactyla	*Equus* sp., horse ('caballine')	+	·	+
Artiodactyla	*Sus scrofa* L., wild boar	+	·	·
	Megaloceros verticornis (Dawkins), extinct giant deer	cf.	·	+
	Megaloceros dawkinsi (Newton), extinct giant deer	cf.	·	·
	medium-sized cervid (size of *Cervus elaphus* L., red deer)	·	·	+
	large bovid (size of *Bison schoetensacki* Freudenberg, extinct bison)	+	·	+

Pisces

All specimens identifiable as fish are included in the following list. Pharyngeal teeth have proved particularly valuable in allowing a number of cyprinids to be determined to species. It should be borne in mind, however, that other taxa are less easy to identify, and with the presence of many indeterminate fragments it is likely that the ichthyofauna was more diverse than represented here.

(Haplomi)

Esocidae

Esox lucius L., pike

LOAC 235–255	LO399: tooth
LOAC 275–295	LO613–4: 2 teeth
LOAC 275–315	LO539: tooth
LOAF 175–190	LO668: tooth
LOAF 190–205	LO314: tooth
LOAF 190–225	LO45: tooth
LOAF 225–235	LO166: tooth
LOAF 255–275	LO234: tooth
LOAG 115–140	LO856, LO1056: 2 teeth
LOAG 115–140	LO1036–1038, LO1073: 4 vertebrae
LOAH 325–350	LO716: tooth
LOAG unstrat	LO711: tooth

Cypriniformes

Cyprinidae

Scardinius erythropthalmus (L.), rudd

LOO 260–368	LO636: pharyngeal tooth
LOAC 220–235	LO384–8: 5 pharyngeal teeth
LOAC 235–255	LO403–405, LO421–422: 5 pharyngeal teeth
LOAC 255–275	LO464, LO493–4: 3 pharyngeal teeth
LOAC 275–295	LO595–6: 2 pharyngeal teeth
LOAC 275–315	LO535–6: 2 pharyngeal teeth
LOAC 315–325	LO565: pharyngeal tooth
LOAF 175–190	LO4, LO664–667: 5 pharyngeal teeth
LOAF 190–205	LO48–49, LO684–5: 4 pharyngeal teeth
LOAF 190–205	LO315: pharyngeal tooth + arch
LOAF 205–225	LO72: pharyngeal tooth
LOAF 205–235	LO112–113: 2 pharyngeal teeth
LOAF 220–240	LO141: pharyngeal tooth
LOAF 225–235	LO148, LO167: 2 pharyngeal teeth
LOAF 225–235	LO676: bone + tooth
LOAF 275–295	LO277: pharyngeal tooth
LOAH 200–225	LO673, LO1156: 2 pharyngeal teeth
LOAH 200–225	LO1144: arch + 2 pharyngeal teeth

LOAH 200–225	LO1142: pharyngeal tooth
LOAH 200–225	LO887–899: 13 pharyngeal teeth + bones
LOAH 250–275	LO1258: pharyngeal tooth
LOAH 250–275	LO851: pharyngeal tooth + bone
LOAH unstrat	LO709: 2 pharyngeal teeth + bone
LOAH unstrat	LO937–938: 2 pharyngeal teeth

Tinca tinca (L.), tench

LOO 350–360	LO645: pharyngeal tooth
LOAC 235–255	LO402, LO406–407, LO424: 4 pharyngeal teeth
LOAC 275–295	LO712: pharyngeal tooth
LOAF 225–235	LO149: pharyngeal tooth
LOAH 200–225	LO884, LO905–907: 4 pharyngeal teeth
LOAH 250–275	LO842–847: 6 pharyngeal teeth

Rutilus rutilus (L.), roach

LOAC 220–235	LO389: pharyngeal tooth
LOAC 235–255	LO423, LO425–427: 4 pharyngeal teeth
LOAC 255–275	LO465: pharyngeal tooth
LOAC 275–315	LO538: pharyngeal tooth
LOAF 225–235	LO168: pharyngeal tooth
LOAF 235–255	LO194: pharyngeal tooth
LOAH 200–225	LO900–904: 5 pharyngeal teeth
LOAH 250–275	LO848–850: 3 pharyngeal teeth
LOAH 325–350	LO705: pharyngeal tooth
LOAH unstrat	LO939: pharyngeal tooth

Barbus barbus (L.), barbel

LOAC 275–295	LO597: pharyngeal tooth
LOAG 115–140	LO855: pharyngeal tooth
LOAH unstrat	LO761: pharyngeal tooth + bone

Abramis brama (L.), bream

LOAC 165–220	LO362: pharyngeal tooth
LOAC 255–275	LO672: pharyngeal tooth
LOAC 275–295	LO598–601: 4 pharyngeal teeth
LOAC 275–315	LO537: pharyngeal tooth
LOAF 190–205	LO46, LO50–51: 3 pharyngeal teeth
LOAF 205–225	LO75: pharyngeal tooth
LOAF 255–275	LO232–233: 2 pharyngeal teeth
LOAG 115–140	LO857: pharyngeal tooth
LOAH 200–225	LO1141: pharyngeal tooth
LOAH 200–225	LO908–911, LO1143, LO1145: 6 pharyngeal teeth
LOAH 325–350	LO713: pharyngeal tooth

Cyprinus carpio L., common carp

LOAC 255–275 LO463: pharyngeal tooth
LOAC 275–295 LO531: pharyngeal tooth (figure 1)

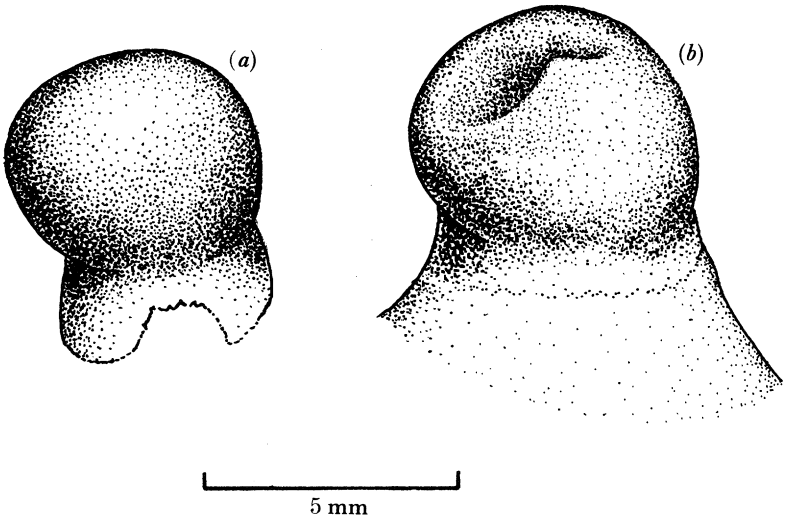


FIGURE 1. Right posterior pharyngeal teeth of common carp *Cyprinus carpio*, in posterior view. (*a*) Little Oakley LO531; (*b*) modern comparative specimen, BM(NH) collection.

The identification of these specimens as *C. carpio* was based on comparison with all available material of carp in the BM(NH) collection (confirmed by P. H. Greenwood and A. Wheeler). The only difference is the absence of an apical papilla or ridge (figure 1); however, this could easily have been lost through wear.

Leuciscus sp.

LOAH unstrat LO1259: hyomandibular

The genus *Leuciscus* includes chubb (*L. cephalus* (L.)) and dace (*L. leuciscus* (L.)). The Little Oakley specimen was not determinable to species.

Unidentified Cyprinidae

LOAH 220–225 LO886: pharyngeal tooth (figure 2). This specimen, although clearly a cyprinid pharyngeal tooth, could not be matched to any species in the available comparative collections.

Unidentified Cypriniformes

In the following, specimens are listed by horizon, but accession numbers are omitted. v, vertebrae.

LOAC 165–220 (2v); 235–255 (5v, pharyngeal arch + bones); 255–275 (6v); 275–295 (5v); 275–315 (2v); 315–325 (4v, lateral line scale 5 yr old); *LOAF* 175–190 (3v); 190–205 (10v, pharyngeal arch); 205–225 (12v, pharyngeal arch); 205–235 (5v); 220–240 (1v, 2 pharyngeal arch bones); 225–235 (3v); 235–255 (7v); 255–275 (5v); 275–295 (4v); *LOAG* 115–140 (20v); *LOAH* 135–200 (1v); 200–225 (37v); 250–275 (6v, 2 pharyngeal bones); unstrat. (15v)

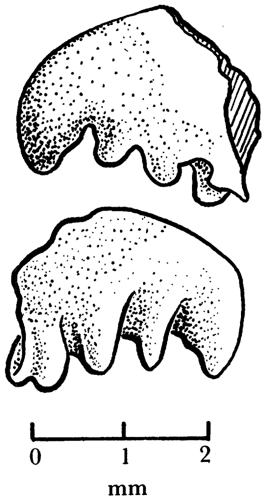


Figure 2. Pharyngeal tooth of unidentified cyprinid, LO886.

Gadiformes

Gadidae

Lota lota (L.), burbot

LOAH 325–350	LO717: otolith

Anguilliformes

Anguillidae

Anguilla anguilla L., eel

LOAC 235–255	LO429–431: 3 vertebrae
LOAC 255–275	LO468, LO495–496: 3 vertebrae
LOAC 275–295	LO602: vertebra
LOAC 315–325	LO571–572: 2 vertebrae
LOAF 175–190	LO5: vertebra
LOAF 190–205	LO32–33, LO319–321: 5 vertebrae
LOAF 205–225	LO88–89: 2 vertebrae
LOAF 205–235	LO119: vertebra
LOAF 220–240	LO142: vertebra
LOAF 225–235	LO150–152: 3 vertebrae
LOAF 235–255	LO196–205: 10 vertebrae
LOAF 255–275	LO236: vertebra
LOAF 275–295	LO268–278: 11 vertebrae
LOAG 115–140	LO854, LO1032–1033, LO1234–1235: 5 vertebrae
LOAH 200–225	LO885, LO912–918, LO1220–1229: 18 vertebrae
LOAH 250–275	LO1041: vertebra
LOAH 325–350	LO714–715, LO1219: 3 vertebrae
LOAH unstrat	LO760, LO1230–1233: 5 vertebrae

Perciformes

Percidae

Perca fluviatilis L., perch

LOAC 165–220	LO365–366: 2 vertebrae
LOAC 275–315	LO540: vertebra
LOAF 190–205	LO318: vertebra
LOAF 205–225	LO90: vertebra
LOAF 275–295	LO283–284: 2 vertebrae
LOAG 115–140	LO1208: vertebra

cf. *Stizostedion* sp., zander (pikeperch)

LOAG 115–140	LO1209–1210: 2 vertebrae

The common zander of Europe at the present day is *S. lucioperca*, although other species occur in Eastern Europe and North America. The specific identity of the Little Oakley specimen could not be determined with certainty from the fossil material available.

Unidentified Perciformes

In the following, specimens are listed by horizon, but accession numbers are omitted. v, vertebra.

LOAC 255–275 (4v); 275–295 (2v); 315–325 (2v); *LOAF* 175–190 (2v); 190–205 (6v); 205–235 (4v); 225–235 (4v); 235–255 (3v); 255–275 (1v); *LOAG* 115–140 (3v); *LOAH* 200–225 (18v); 250–275 (1v); unstrat. (6v)

Unidentified fish remains

In the following, specimens are listed by horizon, but accession numbers are omitted. f, bone fragment, p, pharyngeal bone, s, spines and rays, t, tooth, v, vertebra.

LOAC 220–235 (2v); 235–255 (8v); 255–275 (8v, 3f); 275–295 (5v); 275–315 (3v); 315–325 (1v); *LOAF* 175–190 (12s, 27f); 190–205 (12v, 1f); 205–225 (4v, 1s); 205–235 (6v); 220–240 (1v); 225–235 (1v); 235–255 (4v); 255–275 (7v); 275–295 (5v); *LOAG* 115–140 (9f, 3s, 1t, 16v) *LOAH* 200–225 (26f, 13s, 36v, 7s/v); 220–225 (45f, 29s, 3v); 250–270 (2v); 250–275 (10f, 8s, 10v); 325–350 (5f, 2p, 8s, 3v); unstrat. (80f, 16s, 7v)

In addition, several reworked fish teeth from Eocene and Lower Pleistocene Crag deposits were found in the channel.

AMPHIBIA

Anura

Rana cf. *R. arvalis* Nilsson, moor frog

LOAH 220–225	LO1003: R ilium fragment.

This species, currently distributed across much of temperate Europe but absent from Britain, has recently been recorded from the type Cromerian of West Runton (Holman *et al.* 1988).

Rana sp. (frog)

LOAC 235–255 LO415: L ilium fragment

Rana sp. (frog) or *Bufo* sp. (toad)

LOAF 190–205 LO31: tibia fragment
LOAF 190–205 LO313: radio-ulna
LOAF 190–205 LO316: urostyle
LOAF 225–235 LO157: radio-ulna
LOAH 220–225 LO1004: humerus

REPTILIA

Chelonia

Emys orbicularis L., European pond tortoise

LOAG 115–140 LO1006: neural plate (figure 3, plate 1)

The specimen has the 'grainy' texture characteristic of much reptilian bone. The flattened dorsal surface and the two parallel ridges on the ventral side – part of the neural arch of the underlying vertebra – show that it is a neural plate (cf. Stuart 1979, figures 3A and 11). The small size of the bone indicates a young individual.

Ophidia

Natrix natrix (L.), grass snake

LOAH 250–275 LO1005: caudal vertebra with lymphapophyses intact

MAMMALIA

Insectivora

Sorex cf. *S. minutus* L., pygmy shrew

LOO 350–360 LO644: upper molar frag.
LOO 360–368 LO632: RM$_1$ (figure 4*a*)

Sorex sp. 1 (size of *S. araneus* L. or *S. runtonensis* Hinton)

LOO 360–368 LO633–634: two RI^1's (figure 4*b*, *c*)
LOO 360–368 LO635: RP^4 frag.

Sorex sp. 2 (larger than *S. araneus*)

LOO 350–360 LO641–643: 3 upper unicuspids

Three species of *Sorex* are known from the British early Middle Pleistocene: in ascending order of size these are *S. minutus*, conspecific with the living pygmy shrew; *S. runtonensis*, of similar size to the living common shrew *S. araneus*; and *S. savini*. In addition to size, the species are separated by distinctive mandibular morphology. *S. runtonensis* and *S. savini* are known from both the West Runton Freshwater Bed and faunas 2 and 3 at Westbury-sub-Mendip, and on current evidence, neither species survived into the Hoxnian (Stuart 1982; Bishop 1982), although Hoxnian small mammal faunas are in general not well known.

The Little Oakley material falls into three size categories which probably represent distinct

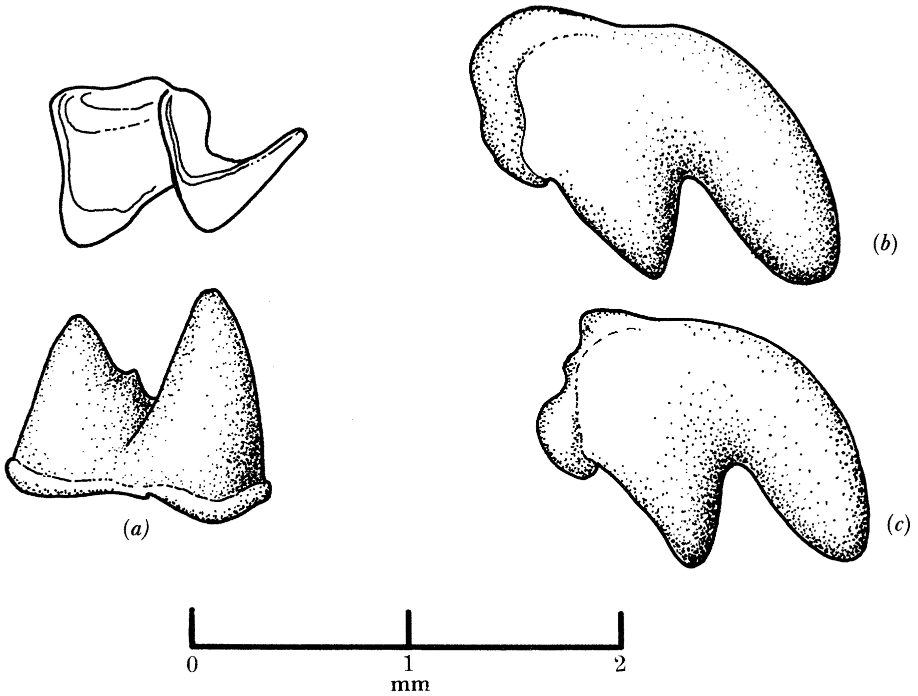


FIGURE 4. Shrew teeth. (*a*) Right M_1 referred to pygmy shrew *Sorex* cf. *S. minutus*, LO632, in crown and buccal views. (*b*, *c*) Right I^1s of *Sorex* sp. 1, LO633–34, in buccal view.

taxa. The smallest category is closely comparable to *S. minutus* on the basis both of its size, and the morphology of the M_1, on which the anterior faces of the cusps rise at a steep angle (figure 4*a*). The middle size category could correspond to either *S. araneus* or *S. runtonensis*, but this cannot be resolved in the absence of mandibular material. The existence of a large size category is suggestive of *S. savini*, but again this is speculative in the absence of a mandible.

The finding of shrew remains only in borehole LOO requires some discussion. This may be a facies effect, as molluscan and lithological evidence suggests that the deposits here represent a more marginal facies than the other boreholes and pits. This would conform to the general tendency for Pleistocene shrew remains to be found most commonly in marginal freshwater deposits. However, it is also possible that shrew incisors were present in the sediment samples from LOAC, LOAF, LOAG and LOAH, but were lost due to coarser sieving (1 mm, compared with 0.25 mm for LOO). None the less, they were absent from samples of LOA, sieved to 0.25 mm.

Rodentia

Apodemus sylvaticus (L.), wood mouse

LOAC 315–325	LO561: RM_1 (figure 5*a*)
LOAF 190–205	LO311: LI^1
LOAF 225–235	LO147: RM_1 (figure 5*b*)
LOAH 220–225	LO1013: LM^1
LOAH 220–225	LO1014: M^2

Measurements

LO561 length 1.40, width 0.92

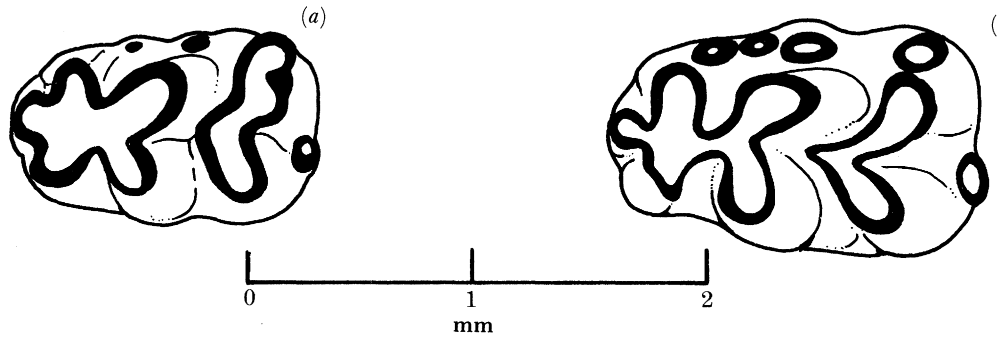


FIGURE 5. Right M_1s of wood mouse *Apodemus sylvaticus*, in crown view. (*a*) LO561, (*b*) LO147.

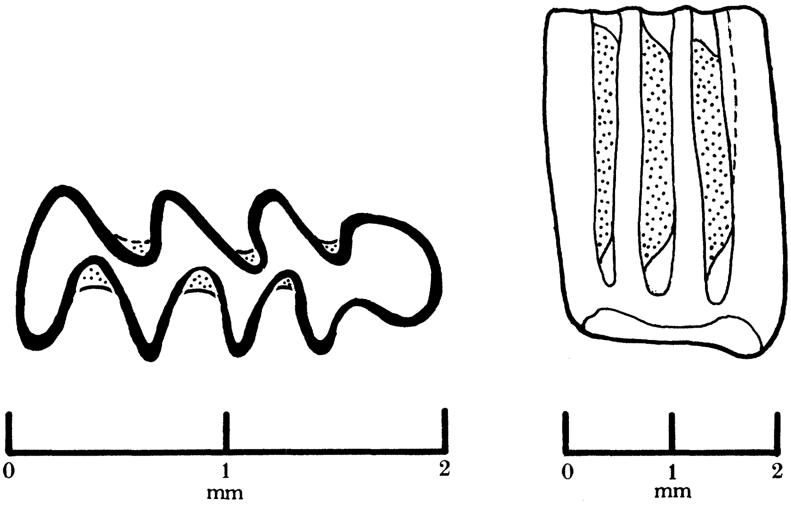


FIGURE 6. Left M_1 of bank vole *Clethrionomys glareolus*, LO191, in crown and lingual views.

LO147	length 1.72, width 1.10
LO1013	length 1.79, width 1.26

Clethrionomys glareolus (Schreber), bank vole

LOAF 235–255	LO191: LM_1 (figure 6)
LOAF 235–255	LO192: LM_2

Measurements

LO191	length 1.94, width 0.78

Mimomys savini Hinton, extinct water vole

LOAH 220–225	LO1007: LM_1 (figure 7*a*)
LOAH 250–275	LO1022: LM_3 (figure 7*b*)
	M49694: LM_3 (figure 7*c*)

Measurements

LO1007	length 3.08, width 1.45
LO1022	length 2.00, width 1.03
M49694	length 1.76, width 0.94

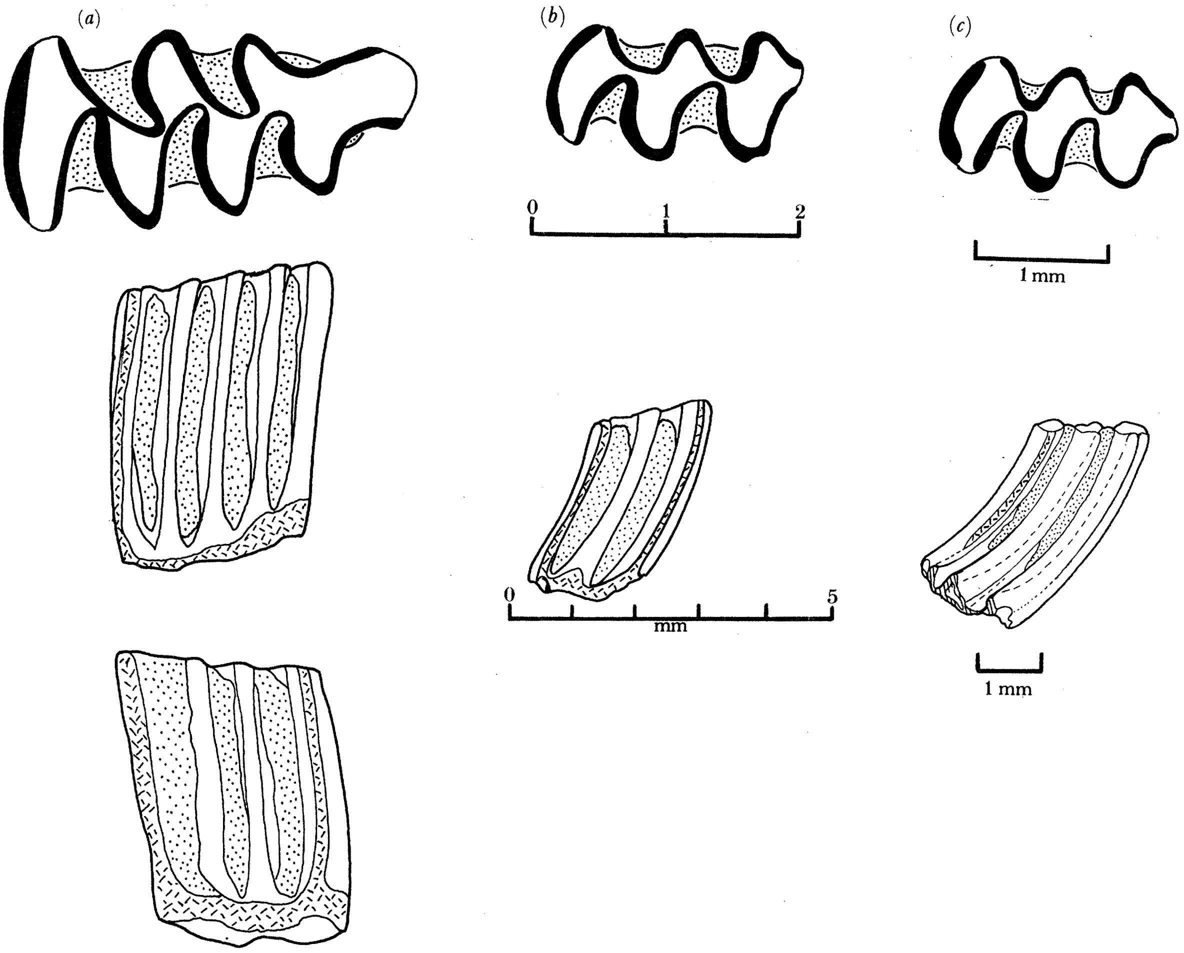


Figure 7. Lower molars of extinct water vole *Mimomys savini*. (*a*) Left M_1, LO1007, in crown, lingual and buccal views; (*b*) left M_3, LO1022, in crown and buccal views; (*c*) left M_3, M49694, in crown and buccal views.

Mimomys savini Hinton (or *Arvicola cantiana* (Hinton)), extinct water vole

LOAC 315–325	LO562: RM_2, incomplete (figure 8*a*)
LOAF 255–275	LO231: molar frag.
LOAG 115–140	LO1026: LM^3 (figure 8*b*)
LOAG 115–140	LO1023: LI^1
LOAH 200–225	LO1019: molar fragment

The lineage of the water vole is represented in Europe by a series of chronospecies: *Mimomys pliocaenicus* (Lower Pleistocene), *M. savini* (latest Lower and early Middle Pleistocene), *Arvicola cantiana* (late Middle & early Upper Pleistocene), and finally the living *A. terrestris* (Koenigswald 1973; Stuart 1982; and see below).

All the molars listed here are high crowned (in contrast to *Mimomys pliocaenicus*) and the differentiation of the enamel is thicker on the convex side of the molar angles than on the concave side (in contrast to *Arvicola terrestris*). Specimens LO1007 and LO1022 are rooted and

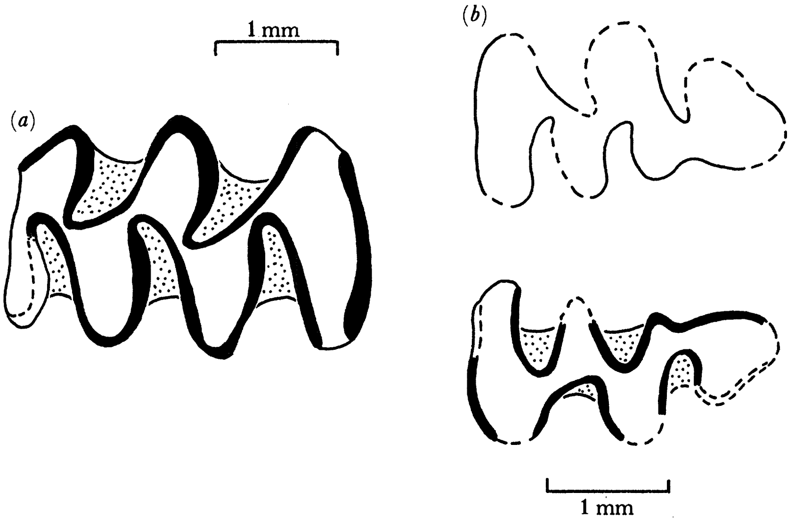


FIGURE 8. Molars of extinct water vole *Mimomys savini* (or *Arvicola cantiana*). (*a*) Right M_2, LO562, in crown view; (*b*) left M^3, LO1026, in basal and crown views. The basal view in (*b*) illustrates the characteristic crown outline, which is obscured in crown view because of the young age of the specimen.

are therefore referred to *Mimomys savini* rather than *Arvicola cantiana*. Specimen M49694 can also be assigned to *M. savini*, because the external longitudinal ridges can be seen to converge slightly towards the crown base showing an early stage of root formation (figure 7). The other molars show no trace of root development and could therefore correspond either to *A. cantiana* or to immature *M. savini* (figure 8).

Microtus oeconomus (Pallas), northern vole

LOAC 315–325 LO563: RM_1 (figure 9*a*)

Measurements

LO563 length 2.48 (estimated), width 0.92

Microtus cf. *M. arvalis* (Pallas), common vole

LOAH 220–225 LO1008: RM_1 (figure 9*b*)
LOAH 220–225 LO1009: RM_1

Measurements

LO1008 length 2.40, width 0.91

Pitymys cf. *P. gregaloides* Hinton, extinct pine vole

LOAH unstrat LO1020: LM_1 (figure 9*c*)

Pitymys sp., pine vole

LOAC 275–315 LO532: RM_1 frag. (figure 9*d*)

The above two specimens are referred to the genus *Pitymys* on the basis of the characteristic confluent angles behind the anterior loop of the first lower molar (figure 9*c*, *d*). Two species,

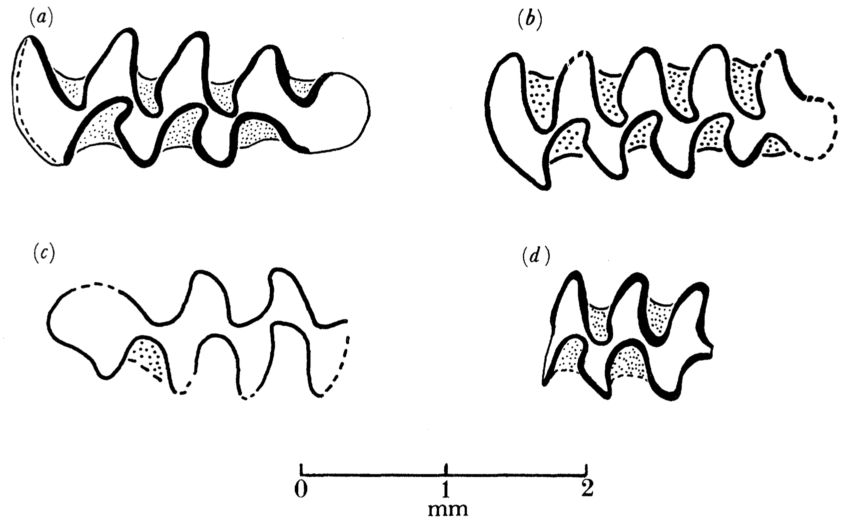


FIGURE 9. Lower molars of voles, *Microtus* spp. and *Pitymys* spp., in crown view. (*a*) Right M_1 of northern vole *M. oeconomus*, LO563; (*b*) right M_1 referred to common vole *M. cf. arvalis*, LO1008; (*c*) left M_1 referred to extinct pine vole *P. cf. gregaloides*, LO1020; (*d*) right M_1 fragment of pine vole *Pitymys* sp., LO532.

P. arvaloides and *P. gregaloides*, occur in the British Pleistocene. One of the Little Oakley specimens (LO1020) can be tentatively referred to *P. gregaloides* on the characteristic shape of the anterior loop.

Microtus or *Pitymys*

(material not distinguishable between the two genera)

LOAC 220–235	LO381: RM^1
LOAC 220–235	LO382: RM^1 incomplete
LOAC 220–235	LO383: M^3 frag.
LOAC 235–255	LO401: LM_2
LOAC 255–275	LO461: LM^2
LOAC 275–315	LO533: LM^2
LOAC 275–295	LO592: RM^1
LOAF 190–205	LO312: molar frag.
LOAF 275–295	LO276: RM^1
LOAH 200–225	LO1017: LM^1
LOAH 200–225	LO1027: RM^1
LOAH 200–225	LO1028: LM^2
LOAH 220–225	LO1010: LM^2
LOAH 220–225	LO1011: RM_2
LOAH unstrat	LO1021: RM_2

None of the M^2s has the 'extra' posterior angle characteristic of the species *Microtus agrestis* (see Stuart 1982, p. 36).

Unidentifiable small vole

LOAC 235–255	LO400: I^1 frag.
LOAF 205–225	LO71: I_1
LOAF 235–255	LO193: I_1 frag.

LOAH 200–225 LO1018: I$_1$ frag.
LOAH 200–225 LO1028: molar frag.
LOAH 220–225 LO1015: I frag.
LOAH 220–225 LO1016: I frag.

Carnivora

cf. *Crocuta crocuta* Erxleben, spotted hyaena

LOAG 115–140 LO1029: part of a coprolite
LOAH 135–200 LO1030: part of a coprolite
M49692: diaphysis of right femur (figure 10, plate 1)

Measurements (M49692)

Preserved length of specimen 167
Minimum antero-posterior diameter of shaft 20.4
Minimum transverse diameter of shaft *ca.* 22.5

Three species of hyaena occur in the European early Middle Pleistocene: *Crocuta crocuta*, *Hyaena perrieri* Croizet & Jobert, and *Hyaena brevirostris* Aymard (Schütt 1971). The two *Hyaena* species were survivors from the Lower Pleistocene and did persist through the Anglian–Elsterian, while *C. crocuta* was a new arrival and persisted through to the late Pleistocene. Both genera are recorded at Mosbach and Süssenborn (Schütt 1971), and in fauna 2 at Westbury-sub-Mendip (Bishop 1982). Only *C. crocuta* is so far known from West Runton (Stuart 1982), although the absence of any record of *Hyaena* from this site could be due to accidents of collecting.

The Little Oakley femur is identical in size and morphology to specimens of Upper Pleistocene *Crocuta crocuta* (Kent's Cavern, Devon, BM(NH) collection), and so is tentatively assigned to that species. However, as comparative material of *Hyaena* was not available, the occurrence of this genus at Little Oakley cannot be entirely ruled out. However, the large size of *H. brevirostris* (Schütt 1971) makes identification to this species unlikely.

The coprolites have the spherical form and calcareous structure characteristic of hyaena.

Proboscidea

?Elephantidae, gen. et sp. indet., elephant

Warren & Davis (*ca.* 1955) recorded the collecting of 'a single plate of an elephant molar' from the site, but the specimen cannot now be traced.

Perissodactyla

Equus sp. (caballine), horse

LOAG 115–140 LO1031: left D^3 or D^4, very little worn (figure 11*a* and figure 12, plate 1)
M49693: left P$_2$, worn (figure 11*b* and figure 13, plate 1)
M20419: left P$_3$ or P$_4$ (figure 11*c* and figure 14, plate 1)
M20418: right M^3 (figure 11*d* and figure 15, plate 1)
M20423: distal end of left humerus
M20420: proximal fragment of first phalanx

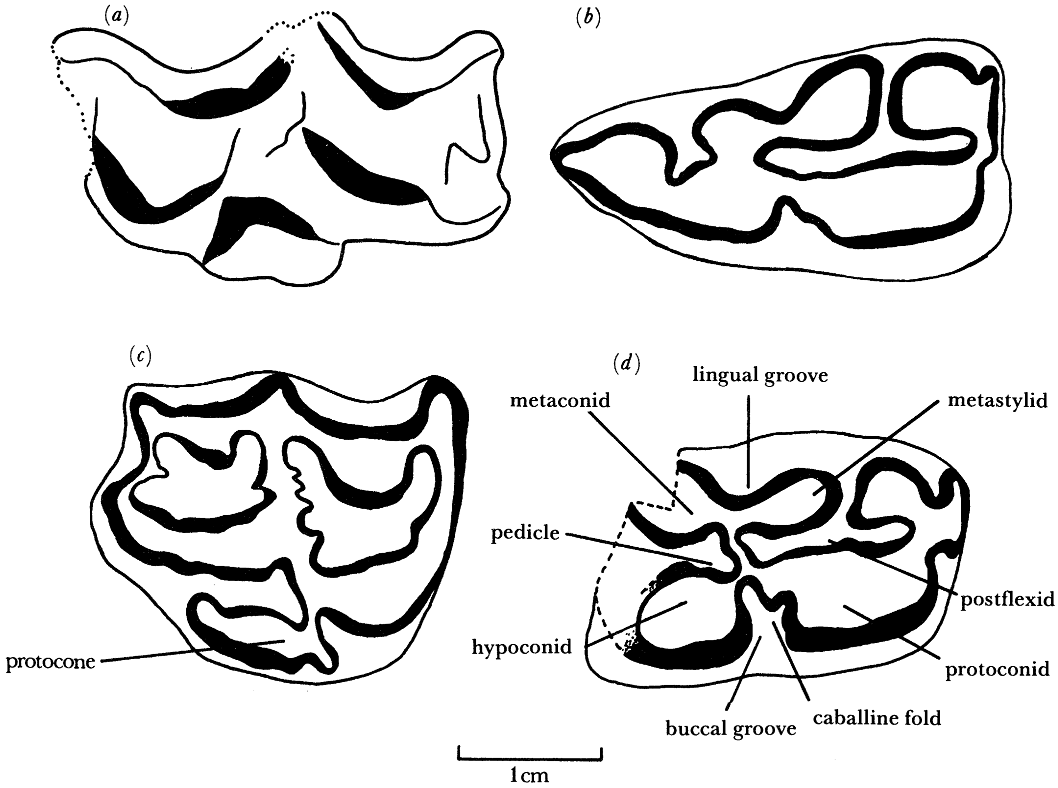


FIGURE 11. Cheek teeth of horse, *Equus* sp.,S in crown view. (*a*) Left D$^{3/4}$, very little worn, LO1031; (*b*) left P$_2$, M49693; (*c*) left P$_{3/4}$, M20419; (*d*) right M^3, M20418.

Measurements

M20423 epiphysis width 82 ± 2 (estimated when complete).

	occlusal length (excluding cement)	occlusal width (excluding cement)	crown height
LO1031	30.0	—	*ca.* 33
M49693	32.4	18.0	*ca.* 12
M20419	26.0	16.3	> 58
M20418	25.0	21.5	*ca.* 46

The taxonomy of Pleistocene horses is complicated, with many named species. The two largest groupings are the more primitive 'stenonines' and the more derived 'caballines'. The former are most characteristic of the Lower Pleistocene, but persist into the early Middle Pleistocene. The latter are first known from Europe in the early Middle Pleistocene, and survive at the present day as *Equus ferus* (= *E. caballus*) (Prat 1976; Eisenmann 1980, 1981).

The Little Oakley sample of four teeth is very small, and because of considerable intraspecific variation in equine dental characters, conclusions are tentative. None the less, considering the main taxonomic features discussed by Prat (1976) and Eisenmann (1980, 1981), the teeth are overall clearly of 'caballine' rather than 'stenonine' morphology (cf. figure 11, and figures 12–15, plate 1): (i) On P$_{3-4}$, the lingual groove separating the metastylid and metaconid is broad and gently curved, rather than narrow and sharp; (ii) on P$_{3-4}$, the buccal groove separating the protoconid and hypoconid is relatively shallow, not penetrating the 'pedicle' which connects these structures to the metastylid and metaconid. (iii) On D$^{3/4}$ and M^3, the 'protocone index' (100 × occlusal length of protocone/occlusal length of tooth) is above the range of *E. stenonis*, but within that of *E. ferus* (table 2).

A fourth feature given by Eisenmann (1981) is the postfixed index (100 × occlusal length of postflexid/occlusal length of tooth). On P_2 and P_{3-4}, however, the teeth available from Little Oakley, the ranges for this index overlap greatly between stenonine and caballine horses, and the Little Oakley values fall within both (table 2).

The 'caballine fold' (a small loop of enamel between protocone and hypocone on the upper cheek teeth, and between protoconid and hypoconid on the lowers), is present on the $P_{3/4}$ from Little Oakley, but not on the M^3 (figure 11). This character, however, is known to occur at variable frequencies in both stenonine and caballine horses (Eisenmann 1980, 1981), and cannot be given taxonomic weight on such a small sample.

Finally, the three Little Oakley teeth are below the size range of the early Middle Pleistocene caballines from Mosbach, F.R.G. (correlated with the late Cromerian or early Anglian) (table 2), and are also markedly smaller than the few available specimens from West Runton (BM(NH)).

TABLE 2. COMPARISONS OF SIZE AND MORPHOLOGICAL INDICES OF LITTLE OAKLEY HORSE TEETH WITH LOWER PLEISTOCENE *EQUUS STENONIS* (SENÈZE), EARLY MIDDLE PLEISTOCENE *E. MOSBACHENSIS* (MOSBACH), AND UPPER PLEISTOCENE *E. FERUS*

(Data (except for Little Oakley) from Eisenmann (1980, 1981). See text for discussion.)

	E. stenonis			*E. mosbachensis*			*E. ferus*			Little Oakley
	n	$\bar{x}$	range	*n*	$\bar{x}$	range	*n*	$\bar{x}$	range	
P_2 length	24	33.6	30.4–38.0	19	37.4	34.0–39.0	14	33.2	27.3–39.0	32.4
$P_{3/4}$ length	47	29.3	26.0–33.0	46	32.4	29.5–36.0	28	27.8	22.0–33.0	26.0
$D^{3/4}$ length	15	31.7	30.0–34.0	—	—	—	23	29.2	23.0–33.6	30.0
M^3 length	12	27.9	24.0–30.5	7	30.9	29.5–33.0	21	29.1	21.0–34.5	25.0
P_2 postflexid index	27	43.0	35.0–50.3	19	49.2	43.7–58.1	14	49.1	41.9–54.5	50
$P_{3/4}$ postflexid index	46	45.2	37.0–53.6	45	46.0	35.9–53.2	28	48.8	40.7–56.8	49.2
$D^{3/4}$ protocone index	11	26.4	23.5–31.3	—	—	—	23	31.3	25.5–38.3	32.3
M^3 protocone index	12	37.1	33.3–44.4	7	50.8	46.8–54.5	21	50.3	44.0–54.8	46.8

In summary, the Little Oakley horse is probably a caballine species, but is of unusually small size for the early Middle Pleistocene.

Artiodactyla

Sus cf. *S. scrofa* L., wild boar

M20417: tip of lower canine
M20421: distal end of right humerus diaphysis (figure 16, plate 1)

Measurements (M20421)

Diaphysis antero-posterior diameter (probably close to minimum)	26.7
Diaphysis transverse diameter (probably close to minimum)	17.4

As the articular end of the humerus is broken away, the state of epiphysial fusion cannot be assessed. However, it is unlikely that this is a juvenile specimen, as the diaphysis wall had already attained considerable thickness.

All British Pleistocene pigs found to date have been referred to *Sus scrofa* (Stuart 1982). The Little Oakley humerus is of relatively small size, toward the lower end of the range of variation of a sample of Recent and subfossil European wild boar (minimum transverse shaft diameters

17.1–20.7, $n = 7$, UMZC and BM(NH) collections). No humeri from British early Middle Pleistocene deposits are available for comparison, but dental and other remains from West Runton and Trimingham (BM(NH)) indicate animals of relatively large size, clustering around the upper end of the Recent range of variation. Thus the Little Oakley specimen may represent a population of significantly smaller body size that at West Runton and Trimingham, although more evidence would be required for certainty. Suggestion of variation in body size of *Sus scrofa* within the early Middle Pleistocene also comes from an M_3 from the CF–bF at Pakefield in the BM(NH) collection, considerably smaller than the West Runton and Trimingham specimens.

Megaloceros verticornis (Dawkins), extinct giant deer

LOAF 225–235 LO661 (figure 17*a*, *b*, plate 1; table 3): part of right frontal and parietal bones with attached pedicle and lower part of right antler, broken above second tine.

The morphology of this specimen corresponds in all respects to *Megaloceros verticornis* (see descriptions in Kahlke (1956*a*, *b*), Azzaroli (1953) and Lister (1987)), and it can be referred without doubt to that species. The main diagnostic features are: (i) the very obtuse angle of departure of the antler from the skull: the angle between the lower part of the beam, and the skull table between the pedicles, seen in anterior view, is 170°; (ii) the position and shape of the first tine, high above the burr and of circular cross-section, arising antero-dorsally on the beam but curving anteriorly above its base; (iii) the position and shape of the second tine, centred 83 mm from the first but about 90° anterior to it on the beam, dorso-ventrally flattened into an ovoid cross-section and turning gently dorsally above its base. The stout pedicle and complete burr correspond to the fully grown antler of an adult male which died between autumn and spring.

cf. *Megaloceros verticornis* (Dawkins), extinct giant deer

M43363: portion of antler beam (figure 18, plate 1)

This specimen is an unbranched portion of beam. It bears a broad longitudinal furrow, bounded toward the convex side of the beam by a ridge which begins to flatten into a tine where the fragment is broken off. By comparison with material from the CF–bF (e.g.

DESCRIPTION OF PLATE 1

FIGURE 3. Neural plate of European pond tortoise *Emys orbicularis*, LO1006, in ventral view. (Magn. × 5.)

FIGURE 10. Diaphysis of right femur referred to spotted hyaena cf. *Crocuta crocuta*, M49692, in anterior view. (Magn. × 0.5.)

FIGURES 12–15. Cheek teeth of horse, *Equus* sp., in crown and buccal views. (Magn. × 1.)

FIGURE 12. Left $D^{3/4}$, LO1031 (cf. figure 11*a*).

FIGURE 13. Left P_2, M49693 (cf. figure 11*b*).

FIGURE 14. Left $P_{3/4}$, M20419 (cf. figure 11*c*).

FIGURE 15. Right M^3, M20418 (cf. figure 11*d*).

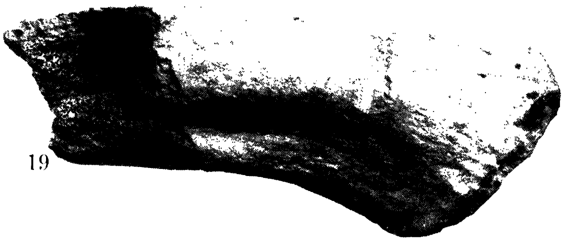
FIGURE 16. Distal end of right humerus diaphysis of wild boar *Sus scrofa*, M20421, in posterior view. (Magn. × 1.)

FIGURE 17. Right antler base and frontal bone of extinct giant deer *Megaloceros verticornis*, LO661. (*a*) Ventral view, (*b*) anterior view. (Magn. × 0.5.)

FIGURE 18. Portion of left antler beam referred to extinct giant deer *Megaloceros* cf. *M. verticornis*, M43363, in dorsal view. (Magn. × 0.5.)

FIGURES 19 AND 20. Right shed antler bases referred to extinct giant deer *Megaloceros dawkinsi*, M20414 and M20416, in anterior view. (Magn. × 0.5.)

FIGURE 21. Cervical vertebra of large bovine cf. *Bison* sp., LO662, in anterior view. (Magn. × 0.5.)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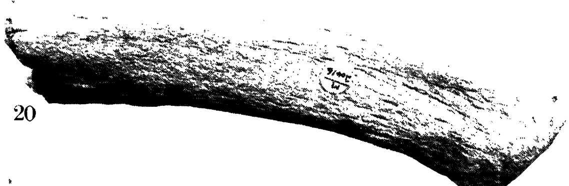
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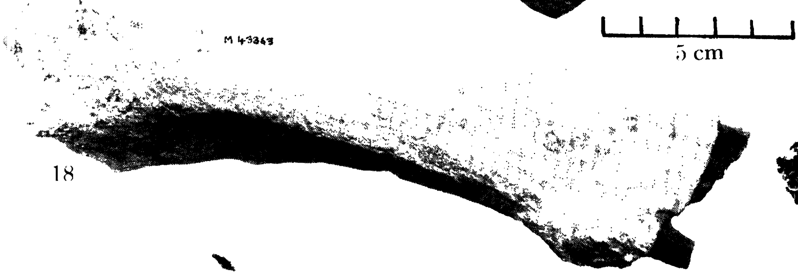
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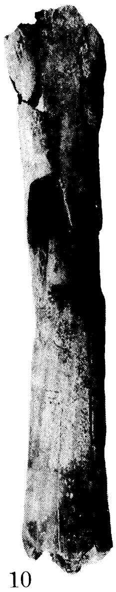
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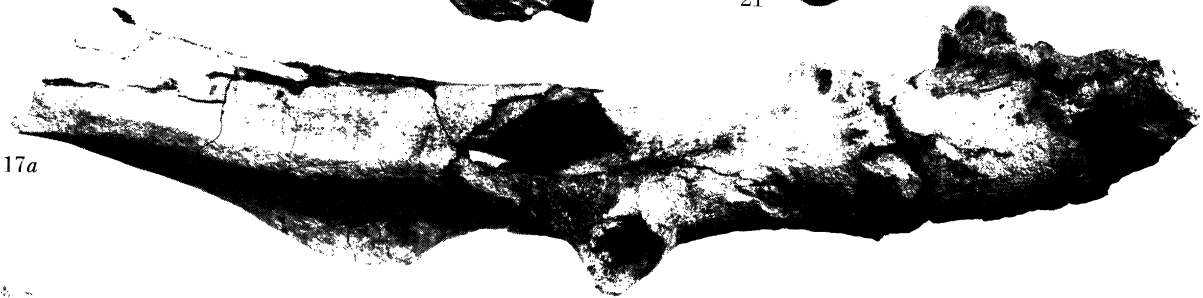
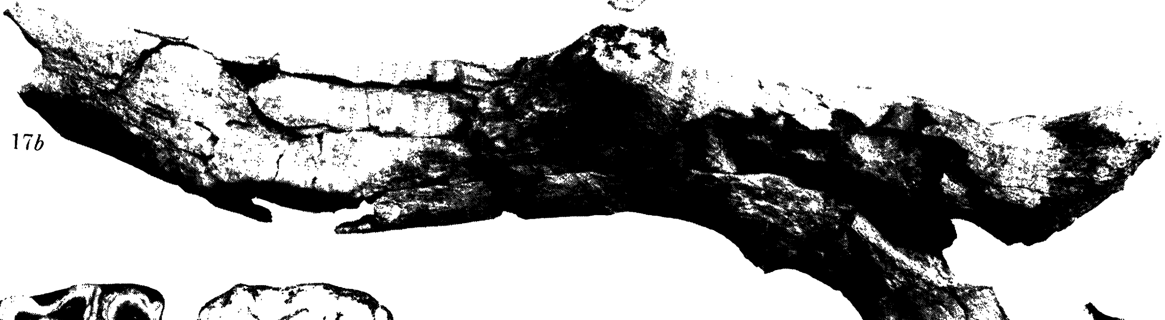

17*a*


17*b*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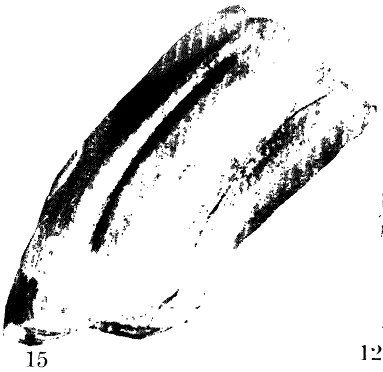
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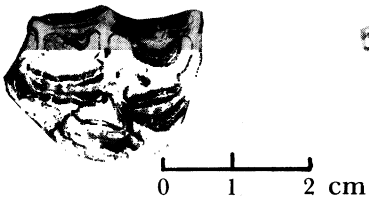

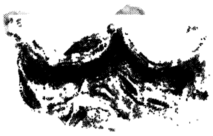


16

Figures 3, 10 and 12–21. For description see opposite.

Trimingham, BM(NH) specimen M6098), this fragment corresponds exactly to part of a left antler beam of *Megaloceros verticornis*, from above the first tine to the base of the second tine. *Megaloceros dawkinsi* (Newton) can be ruled out because its beam is much flatter in this region.

cf. *Megaloceros dawkinsi* (Newton), extinct giant deer

M20414, M20415, M20416: three bases of right shed antlers, each broken below the first tine. M20416 is juvenile (figures 19 and 20, plate 1).

Warren & Davis (*ca.* 1955), and initially one of the present authors (see Sutcliffe *et al.* 1979, p. 8), referred these specimens, as well as M43363 described above, to the primitive elk *Cervalces* (= *Alces*, = *Cervus*) *latifrons* (Johnson), known from the CF–bF. This was because the preserved parts of the beam in the Little Oakley specimens, like *C. latifrons*, show no clear evidence of branching. However, more careful examination demonstrates that the shape of the beams is unlike that of *C. latifrons*, but is consistent rather with *Megaloceros*: (i) the maximum proximal extension of the rose is on the convex (antero-dorsal) side of the beam, as in *Megaloceros*, not on the concave (anterior) side of the beam as in *Cervalces*; (ii) there is a broad furrow anteriorly on the beam, common on the lower part of *Megaloceros* antlers, but absent in *Cervalces*.

Specimens M20414, M20415 and M20416 are incompatible with *M. verticornis* because there is no tine between the base of the antler and at least 100 mm up the beam (table 3). Among the large sample of *M. verticornis* from the CF–bF (BM(NH) collection), the greatest distance from burr to base of first tine is 78 mm. However, the long unbranched lower region in the Little Oakley antlers, as well as the curvature and position of the groove, correspond precisely with specimens of *M. dawkinsi* from Trimingham and Mundesley in the CF–bF. (A further difference between *M. verticornis* and *M. dawkinsi* is the angle of departure of the beam from the burr, which is more acute in *M. dawkinsi* (55°–70° in a sample of eight CF–bF specimens) than in *M. verticornis* (70°–85° in a sample of six CF–bF specimens). However, this feature is not diagnostic on the Little Oakley antlers, as all three have an angle of 70°.)

TABLE 3. MEASUREMENTS OF *MEGALOCEROS* ANTLERS FROM LITTLE OAKLEY

	M. verticornis		cf. *M. dawkinsi*		
	LO661	M43363	M20414	M20415	M20416
width of frontal bone, from midline to side wall of braincase	*ca.* 75	—	—	—	—
length of pedicle	34	—	—	—	—
circumference of pedicle below burr	165	—	187	190	113
major and minor axes of pedicle below burr	55 × 44	—	59 × 50	65 × 53	36 × 34
circumference of burr	*ca.* 178	—	205	210	125
circumference of beam above burr	139	—	175	185	110
distance from burr to base of first tine	*ca.* 68	—	> 130	> 100	> 140
distance between centres of first and second tine bases	83	> 150	—	—	—
circumference of first tine at base	85	—	—	—	—
circumference of second tine at base	*ca.* 120	—	—	—	—
circumference of beam between first and second tines	135	*ca.* 150	—	—	—
angle between lower part of beam and skull table	170°	—	—	—	—
angle between lower part of beam and burr	70°	—	70°	70°	70°

Large cervid, sp. indet., a deer

M20422: left lateral or right medial ungual phalanx, incomplete.

The specimen is intermediate in size between large Upper Pleistocene *Cervus elaphus* (e.g. Ilford, BM(NH) collection), and Late Devensian *Megaloceros giganteus* (Ireland, BM(NH) collection). Morphologically, it is more similar to the latter; for example, the dorsal edge of the articular facet is rather square. It could well pertain to either *M. verticornis* or *M. dawkinsi*, although direct comparative material of these species is not available. *Alces* or *Cervalces* are excluded morphologically.

Measurements

length	62
height	39
width	26

Medium-sized cervid, sp. indet., a deer

LOAB 165–280 LO663: two fragments, almost certainly from the same bone, of the distal part of a right metatarsal.

The specimen corresponds in size and morphology to red deer (*Cervus elaphus* L.). Reindeer (*Rangifer tarandus* (L.)) is excluded morphologically.

Measurements

transverse width of distal epiphysis when complete	48
antero-posterior depth of distal epiphysis when complete	28.2
transverse diameter of shaft	24.5

cf. *Bison* sp., large bovine

LOAC 275–295 LO662: partial 3rd or 4th cervical vertebra (figure 21, plate 1).
M49692: lateral fragment of distal end of left metatarsal diaphysis. The distal face shows the surface for connection with the epiphysis, which has been lost, indicating a juvenile individual.

Measurement

antero-posterior diameter of metatarsal diaphysis	41.5

The form of these specimens corresponds closely to *Bison* and *Bos*, but does not allow distinction between the two. They are tentatively referred to *Bison* on the basis of their small size, and because, of the two genera, only *Bison* is so far known from the European early Middle Pleistocene.

Bison from European sites of early Middle Pleistocene age (e.g. Voigtstedt, Mauer) have mostly been referred to *Bison schoetensacki* Freudenberg, a species of relatively small size and distinctive horn morphology (Fisher 1965; Flerov 1969). *Bison* remains from the West Runton Freshwater Bed (BM(NH) collection) are of small size, and may be referable to this species. The larger, longer-horned *Bison priscus* replaces it at Mosbach, and is the characteristic species of the remainder of the Pleistocene (Flerov 1969). At Westbury-sub-Mendip, Bishop (1982) recorded a small bison, which he referred to *B. schoetensacki*, from the W1 fauna (probably Lower Pleistocene), but a larger form, which he referred to cf. *B. priscus*, from the late Cromerian or early Anglian W2 fauna. The absence of horn material from Little Oakley prohibits definite attribution of the bovine remains to species. The Little Oakley vertebra is of relatively small size, consistent with *Bison schoetensacki*, although the existence of considerable size variation within *B. priscus* (H. E. Gee, personal communication) means the latter species cannot be ruled out.

3. Ecological significance of the vertebrate fauna

(*a*) *Local and regional environment of the Little Oakley channel*

The vertebrate fauna corresponds very well with the vegetational and climatic picture derived from pollen and molluscan evidence. This picture indicates a temperate climate, a regional vegetation of mixed deciduous woodland, extensive areas of dry grassland in the river floodplain, and swampy areas close to the river (Gibbard & Peglar 1990; Preece 1990).

Species whose almost exclusive habitat today is deciduous woodland, are wood mouse *Apodemus sylvaticus* and wild boar *Sus scrofa*. Both have relatively low-crowned teeth which are adapted to soft foods found in woodland, such as fruits, roots and invertebrates, and neither species has extended further north than southern Scandinavia in historical times, even before reduction of range due to human activities (Corbet 1966). Nor is there anatomical evidence that their adaptations have changed during the Pleistocene.

Species likely to have inhabited the dry grassland areas are horse *Equus* sp., large bovine cf. *Bison* sp., and pygmy shrew *Sorex minutus*. *Equus* and *Bison* are grazing animals with high-crowned cheek teeth. *S. minutus* today has a preference for dry areas with ample ground cover, rarely being found in closed woodland (Brink 1967).

The northern vole, *Microtus oeconomus*, is today an inhabitant of wet ground such as reed beds and marshes close to rivers, a habitat known to have been present at Little Oakley. Although currently largely boreal in distribution, it is known from the early temperate zone of the Cromerian interglacial at West Runton, a time of regional deciduous forest in Britain (Stuart 1982). The moor frog, *Rana arvalis*, currently absent from Britain but distributed in France, Belgium and Scandinavia, would have inhabited damp grassy areas close to the river (Arnold & Burton 1978).

Of particular climatic significance is the record of European pond tortoise *Emys orbicularis*. Today it is found in central, eastern and southern Europe, but not in the British Isles, Scandinavia or northern France. Consideration of the geographical distribution and biology of the species strongly suggests that ample summer sunshine, with mean July temperatures exceeding 18 °C are necessary for the eggs to hatch (Stuart 1979). The presence of pond tortoise at Little Oakley therefore indicates interglacial summer temperatures in excess of those at the present day. The species has previously been recorded from the Hoxnian, Ipswichian and Flandrian interglacial stages and from Westbury-sub-Mendip, Somerset which may date from the later part of the Cromerian interglacial (Stuart 1979, 1982). The Little Oakley find is the first definite record of Cromerian or earlier age.

Confirmation of temperate climate is provided by the fish fauna. Data on spawning of the recorded Cyprinidae and Percidae (Muus & Dahlstrom 1967; Wheeler 1969) indicate that from May to August water temperatures must have reached a minimum of 15 °C, with a maximum of 22 °C. Pike and burbot are winter spawners, and available data for burbot (Wheeler 1969) imply water temperatures from December to March of not lower than 0.5 °C.

The assemblage of fishes at Little Oakley is characteristic of standing or slow-flowing freshwater, in which weeds and grasses abound. These plants are used for the attachment of eggs by all the Cyprinidae. The bottom type must have included areas of gravel or stone, because the diets of all the identified species include crustaceans and gastropods, rather than mud-dwelling benthic fauna. Although the majority of the fish species could occur in either a large lake or the lower reaches of a river, the presence of eel *Anguilla anguilla*, a catadromous species requiring access to the sea, indicates the latter.

Other vertebrate taxa, while less diagnostic of specific habitat and climate, are nonetheless entirely consistent with the prevailing picture, as described below.

The living water vole, *Arvicola terrestris*, occupies habitats ranging from the overgrown banks of streams and lakes, to more open grassland in some areas. The habitat range of its precursor *Mimomys savini*, found at Little Oakley, may have been similar, although it probably subsisted on softer plant food, to judge by its rooted molars. Bank vole, *Clethrionomys glareolus*, today occurs in both woodland and scrub habitats.

The pine voles from Little Oakley cannot strictly be placed in ecological context as the specimens are referred to species which are either extinct (*Pitymys* cf. *P. gregaloides*), or of uncertain identity (*Pitymys* sp.). However, all four living European species of *Pitymys* are now restricted to the temperate regions of central and southern Europe, south of Britain at the present day.

Living spotted hyaenas (*Crocuta crocuta*) are restricted to sub-Saharan Africa, and these populations are the only guide to the possibly ecology of the species in the British Pleistocene. Although most conspicuous in open savannah, they also occur and forage in woodland (Bearder 1977). The dens are almost always dug on flat open ground, including small open spaces in generally wooded areas (Kruuk 1972).

The extinct deer *Megaloceros verticornis* and *M. dawkinsi*, and the unidentified cervids, would probably, like most living temperate-zone deer, have had a mixed diet of grasses, herbs, and arboreal vegetation, feeding in and around the edges of woodland.

(*b*) *Fish biogeography*

The history and origins of the British ichthyofauna are poorly understood. The presence at Little Oakley of several cyprinid species, including tench, roach, bream, barbel and rudd, is not unexpected, corroborating previous work on early Middle Pleistocene faunas (see, for example, Stuart 1975). All of these species have also recently been reported from Lower Pleistocene deposits (Kedichem Formation) in The Netherlands (Gaemers 1988). However, the occurrence of pharyngeal teeth of common carp *Cyprinus carpio* is of great interest, representing the first record of this species in Britain before its introduction as a pond-culture fish in Mediaeval times (Maxwell 1904). It indicates earlier natural dispersal of carp into Britain from its presumed origin further east. Also of interest are the presence of a gadoid otolith identified as freshwater burbot *Lota lota*, and two vertebrae referred to zander *Stizostedion*. Burbot is currently widespread in continental waters, but very rare in Britain, with a restricted distribution in eastern England. Zander also has a restricted distribution in Britain today, its presence there being the result of historical introduction from the Continent (Muus & Dahlstrom 1967; Wheeler 1969). It has been found in deposits as early as Lower Pleistocene (Kedichem Formation) in The Netherlands (Gaemers 1988).

The occurrence of eel *Anguilla anguilla* raises the question of their access to a marine environment given that they are catadromous and presently spawn in the Sargasso Sea. The Straits of Dover are believed not to have opened until later in the Pleistocene (Gibbard 1988), so their approach to an east-flowing river in southern England in the early Middle Pleistocene would presumably have been via the North Sea. Judging from the present-day migrations of the species (Muus & Dahlstrom 1967), the extra distance to be covered would probably have been within the known capabilities of the species.

4. Stratigraphical significance of the vertebrate fauna

Several of the mammalian species at Little Oakley are of great importance in relation to the stratigraphical position of the deposits. Only species actually present are considered in the following discussion, and not absences, as the collection is too small to place any significance on the latter. For location of sites mentioned, see Bridgland *et al.* (1990, figure 11). A summary of stratigraphically significant mammalian taxa is presented in table 4.

Megaloceros verticornis occurs widely in the European early Middle Pleistocene, but is unknown in any reliable context either of Lower Pleistocene age (Heintz 1970), or post-dating the Anglian–Elsterian glaciation (Kahlke 1975; Lister 1986). It occurs in the type Cromerian of West Runton, and abundantly at Mundesley, Bacton, Trimingham, Pakefield and Kessingland in the Cromer Forest-bed Formation (Lister 1981). Although the collections from the CF–bF contain material mixed from both Lower and early Middle Pleistocene horizons, the mammalian faunas from the last two sites mentioned are of very largely early Middle Pleistocene aspect. Moreover, *M. verticornis* is absent from the deposits at East Runton, of Pre-Pastonian and Pastonian age. Continental records of *M. verticornis* include Voigtstedt, Süssenborn, Mosbach and Mauer, all of which have been correlated with either the Cromerian interglacial or the early Anglian/Elsterian Cold Stage (Kahlke 1975; Stuart 1981). In sites referred to the Holsteinian or Hoxnian (e.g. Steinheim, Swanscombe, Clacton, Hoxne), *M. verticornis* is invariably absent, its place being taken by *M. giganteus* (Lister 1986). The record of *M. verticornis* from Little Oakley, the first from Britain outside the CF–bF, strongly supports an age later than Pastonian and preceding the Anglian glaciation.

This stratigraphical deduction is supported by the antlers referred to *Megaloceros dawkinsi*. This species, related to *M. verticornis*, was regarded as a mere variant of the latter by Kahlke (1956*a*), but its separate status has been defended by Azzaroli (1953, 1978–79), Radulesco & Samson (1967), and Lister (1987; see also above). *M. dawkinsi* is well known only from the British Cromer Forest-bed Formation, particularly Mundesley. Sediment scraped from an antler of *M. dawkinsi* from Mundesley yielded pollen suggesting a Cr III–IV age (Stuart 1982, p. 115). The absence of the species from the West Runton Freshwater Bed (Cr I–II) might be due to sampling error as very few antlers of large deer have been found at the site. There are no published records of *M. dawkinsi* from continental Europe, but several antlers from Mosbach, F.R.G., are closely similar to this species (observations by A. M. L. on material at the Naturhistorisches Museum, Mainz). Like *M. verticornis*, *M. dawkinsi* is absent from all sites of Hoxnian–Holsteinian age or later (Lister 1986).

A third species of particular stratigraphical interest at Little Oakley is the vole *Mimomys savini*. The species is abundant in the type Cromerian (substages I–II) of West Runton (Stuart 1975), and also occurs in deposits at Sugworth, Berkshire, assigned on the basis of palynology to the late temperate substage (biozone III b) of the Cromerian (Stuart 1980). In the Crag of pre-Pastonian or Pastonian age, underlying the type Cromerian, *M. savini* is absent, and its probable ancestor, *M. pliocaenicus* occurs instead (Mayhew & Stuart 1986). At Ostend, Norfolk, on the other hand, in deposits below the Anglian till and containing pollen assigned to the Cromerian post-temperate substage, *M. savini* is replaced by *Arvicola cantiana* (Stuart & West

Table 4. Stratigraphically significant mammalian taxa from Little Oakley, in comparison with other British localities

(Only significant genera present at Little Oakley, or their close relatives, are shown for the other localities. The latter have all yielded additional stratigraphically significant taxa, but the absence of these from Little Oakley, with its small sample size, cannot be given stratigraphical weight. A cross indicates absence from substantial samples, which is believed to represent genuine absence from the fauna. A dash indicates absence which is likely to be due to insufficient sampling.)

East Runton Pre-Pastonian and Pastonian (Stuart 1974, 1982)	West Runton Cr Ib–IIb (Stuart 1982)	Little Oakley	Westbury-sub-Mendip faunas 2 and 3 (Bishop 1982)	Clacton channel Ho II–III (Stuart 1982)	Swanscombe Basal & Lower Gravels (Sutcliffe 1964)
×	*Megaloceros verticornis*	*Megaloceros verticornis* and cf. *M. dawkinsi*	—	—	*Megaloceros giganteus*
Equus stenonis (stenonine)	*Equus* sp. (caballine)	*Equus* sp. (caballine)	*Equus ferus* (caballine)	*Equus ferus* (caballine)	*Equus ferus* (caballine)
—	*Crocuta crocuta*	cf. *Crocuta crocuta*	*Crocuta crocuta* and *Hyaena brevirostris*	×	×
Mimomys pliocaenicus	*Mimomys savini*	*Mimomys savini*	*Arvicola cantiana*	*Arvicola cantiana*	*Arvicola cantiana*
×	*Pitymys arvaloides* and *P. gregaloides*	*Pitymys* cf. *gregaloides*	*Pitymys arvaloides* and *P. gregaloides*	—	*Pitymys arvaloides*

1976). *A. cantiana* similarly occurs in faunas 2 and 3 at Westbury-sub-Mendip (Bishop 1982), and at Boxgrove (Roberts 1986), both regarded as dating either to the late Cromerian, or to a warm stage between the Cromerian and Hoxnian. On the Continent, *M. savini* occurs at Voigtstedt and Süssenborn, whereas Mauer and the main Mosbach fauna contain *Arvicola cantiana* (von Koenigswald 1973). Although there is evidence that the evolution of *Arvicola* from *Mimomys* may have taken place in the Near East as early as the Lower Pleistocene (Tchernov 1986), the transition between *M. savini* and *A. cantiana* in Europe, whether by evolution or by replacement, seems to have occurred either within the Cromerian (Stuart & West 1976), or between the Cromerian and Hoxnian (von Koenigswald 1973; Bishop 1982). In either case, the occurrence of *M. savini* at Little Oakley strongly corroborates an age after the Pastonian and before the glaciation of the Anglian Cold Stage.

Several other mammalian species provide a more limited contribution to the dating of the site. Neither pine voles (*Pitymys* sp.) nor caballine horses, have been clearly demonstrated from any European deposit before the early Middle Pleistocene (Prat 1976; Stuart 1982). *Pitymys gregaloides*, tentatively recorded at Little Oakley, has been identified in the British type Cromerian, but not thus far in any deposit of Hoxnian or later age in Britain (Stuart 1982). The probable presence of *Bison* and *Crocuta* is consistent, on current evidence, with an age other than Hoxnian, as these taxa, although they subsequently reappear in the Upper Pleistocene, are so far unknown from any British deposit of Hoxnian age (Stuart 1982).

In summary, the vertebrate fauna, particularly the occurrence of *Megaloceros verticornis* and *Mimomys savini*, and the probable presence of *Megaloceros dawkinsi*, strongly supports an age for the Little Oakley channel later than the Pastonian stage, but earlier than both Westbury-sub-Mendip (faunas 2 and 3), and Ostend and hence the Anglian glaciation of Britain.

At present, the vertebrate evidence does not of itself allow more precise dating within the British sequence. Although the Little Oakley fauna is entirely conformable with that of the Cromerian West Runton Freshwater Bed, our lack of knowledge of the mammal faunas between the Pastonian and Cromerian means that the Little Oakley assemblage could conceivably date from some time within this intervening period. In particular, Zagwijn (1985) has recognized a series of palynologically distinct temperate stages in The Netherlands, spanning the latest Lower Pleistocene (Bavel and Leerdam interglacials) and early Middle Pleistocene ('Cromerian Complex' interglacials I–IV). Sparse vertebrate material from the Bavel type locality includes molars of *Mimomys savini* very similar to those from West Runton (T. van Kolfschoten, personal communication), whereas the type deposits of 'Cromerian IV' at Noordbergum yielded remains of *Arvicola cantiana* (Schreuder 1943; van Kolfschoten 1988). No information exists on the vertebrate faunas of the Leerdam and 'Cromerian I–III' Stages. Thus the occurrence of *M. savini* at Little Oakley could correspond to any stage from the Bavelian to 'Cromerian III', or conceivably early in 'Cromerian IV' predating the Noordbergum deposits. Other key taxa, such as *Megaloceros verticornis*, may have more restricted stratigraphic ranges, but this is at present unknown. On palynological, malacological and palaeomagnetic grounds, correlation of Little Oakley with either the Bavel or Leerdam Stages, or interglacial 'I' of the 'Cromerian Complex', is highly unlikely (Bridgland *et al.* 1990; Gibbard & Peglar 1990). Therefore, combining the vertebrate and other lines of evidence, an early Middle Pleistocene age in the middle to late part of the 'Cromerian Complex', post-dating 'Cromerian I' but pre-dating Noordbergum and faunas 2 and 3 of Westbury-sub-Mendip, seems very probable.

We are most grateful to Dr R. C. Preece, Mr J. Clayden and Mr M. Warren for their help with collection and sieving of the bulk samples, and sorting them for small vertebrate remains. Mr R. Wrayton allowed us to study his collection of fossils from the site. Mr A. P. Currant and Dr A. J. Sutcliffe provided valuable discussion, and access to the fossils at the BM(NH). For access to comparative fish material, we are indebted to Dr P. H. Greenwood, Dr G. Howes and Mr A. Wheeler. Professor J. A. Holman very kindly identified the amphibian remains for us, and Dr V. Eisenmann suggested criteria for identification of the horse teeth. Dr T. van Kolfschoten generously provided unpublished information on Dutch faunas. The figures were drawn by Mr J. Rodford.

The hire of a mechanical excavator was financed by the Nature Conservancy Council (GCR Unit). A.M.L. acknowledges the support of a Research Fellowship from Girton College, Cambridge.

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FIGURES 3, 10 AND 12–21. For description see opposite.