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The Mammal Fauna of the Early Middle Pleistocene Cavern infill Site of Western-Sub-Mendip Somerset

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SPECIAL PAPERS IN PALAEONTOLOGY NO. 28

THE MAMMAL FAUNA OF THE EARLY MIDDLE PLEISTOCENE CAVERN INFILL SITE OF WESTBURY-SUB-MENDIP, SOMERSET

BY

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Systematic Descriptions

ABSTRACT. The mammalian remains from the cavern infill site near Westbury-sub-Mendip, Somerset, comprising forty-eight species, are described in detail for the first time. Three faunas can be recognized on stratigraphic and palaeoecological grounds. The first, Westbury 1, is a derived open woodland fauna recovered from the basal waterlaid sands and gravels, and may be a mixed assemblage, the faunal elements indicating any age between the Lower Pleistocene and the Cromerian. The second, Westbury 2, is a carnivore lair assemblage dominated by *Ursus deningeri*, recovered from a well-stratified series of cave sediments. The third, Westbury 3, is a small mammal fauna derived from an owl pellet accumulation, belonging to the same but slightly later part of the Westbury 2 temperate stage. The faunas of Westbury 2 and 3 probably belong to a temperate stage between the Cromerian and the Hoxnian, hitherto unrecognized in the British Pleistocene sequence. The Westbury stage almost certainly precedes the Anglian Glaciation, may represent a protracted temperate period following the end of the Cromerian Interglacial, and is tentatively correlated with palaeotemperature stage 13 of deep-sea cores. In Britain the only correlations that can be made are with Ostend, Norfolk, and possibly with the basal fauna of Kent's Cavern, but on the Continent correlations with a number of important sites are made, in particular Mosbach and Hundsheim.

Westbury has yielded the richest carnivore assemblage and small mammal assemblage of any Pleistocene site in the British Isles, of which eight species described are new to the British Pleistocene.

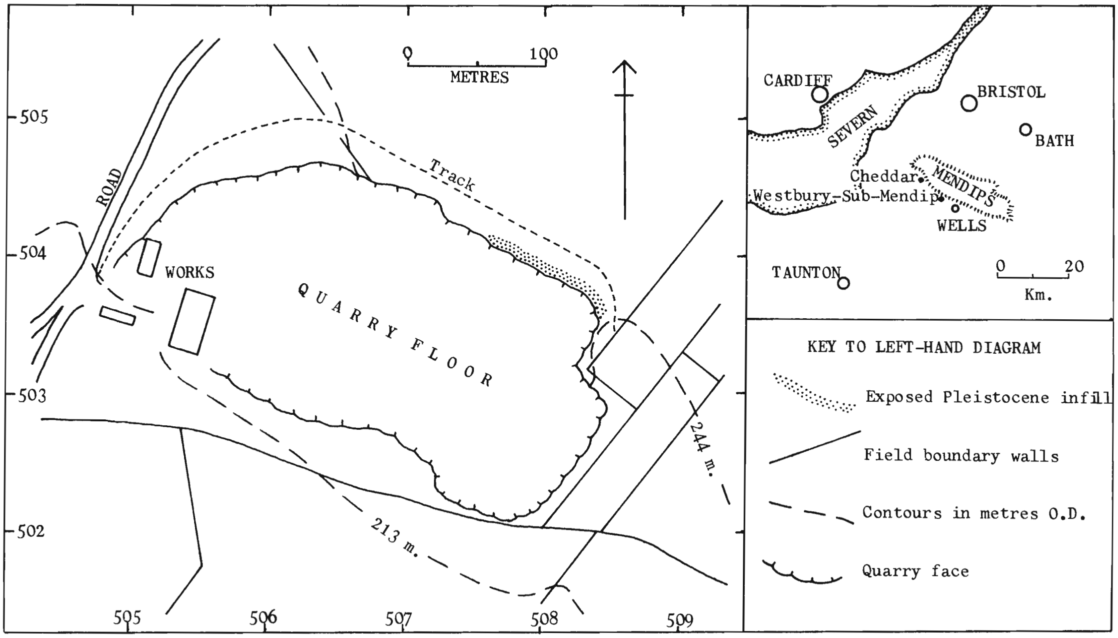
The Westbury 2 fauna is associated with finds of flints which may be artefacts, and as such would mark the earliest record of man's presence in Britain.

INTRODUCTION

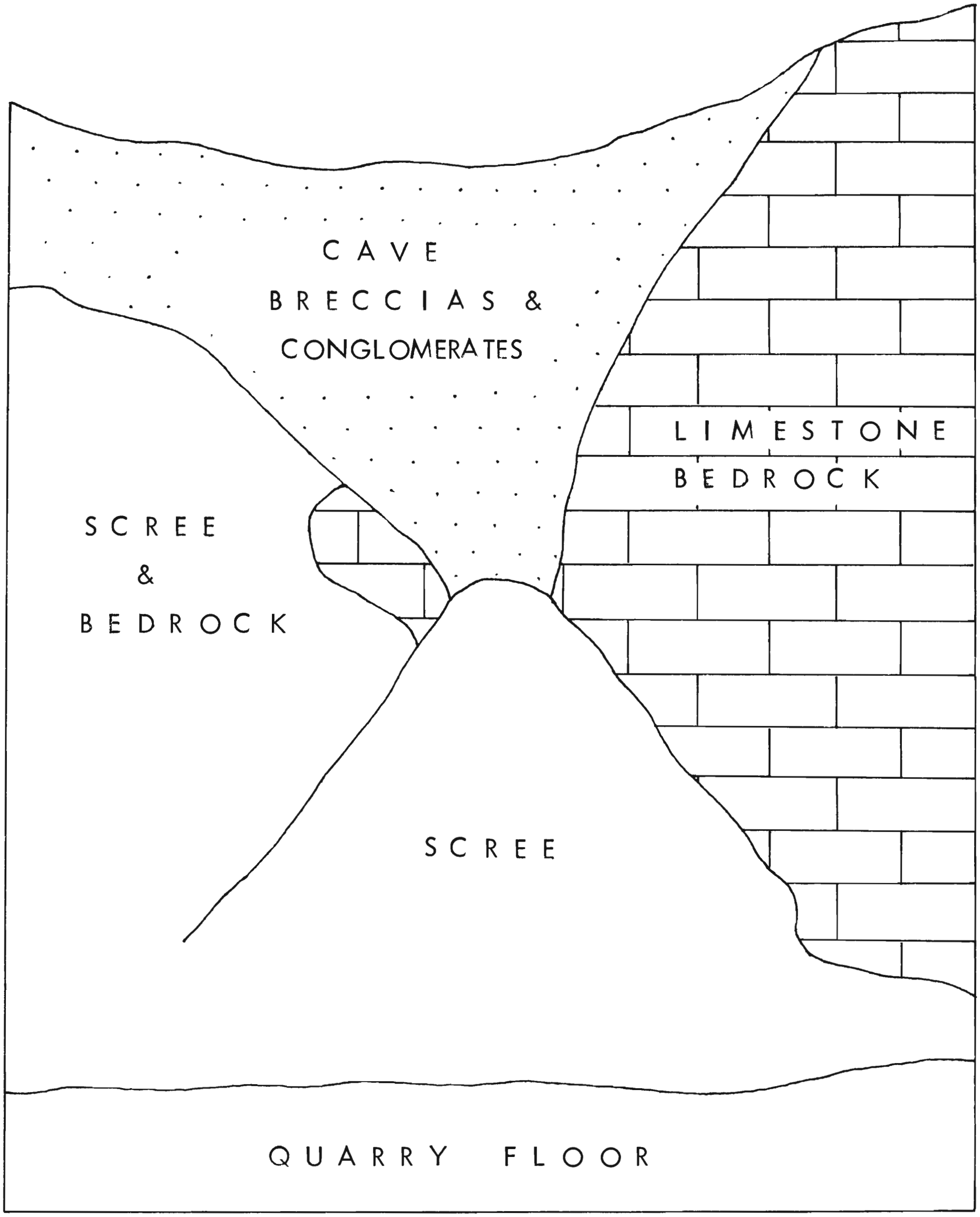
THE Westbury mammalian fauna is probably the most important British Pleistocene fauna discovered this century, and is the only known cave fauna of early Middle Pleistocene age in Britain. In species and numbers Westbury has yielded the richest Pleistocene carnivore assemblage in Britain, and the 'Rodent Earth' (Bed 10) is probably one of the richest small-mammal deposits in Europe. With the discovery of possible artefacts associated with these faunas, which correlate with the early Middle Pleistocene hominid-bearing sites of Mauer and Vertesszollos, Westbury ranks as one of the most important Pleistocene sites of Europe.

The faunal remains from Westbury also include abundant remains of reptiles, fish, birds, and amphibians, and these groups are being studied by other workers whose results are begining to appear in print (e.g. Stuart 1979). The study of these other vertebrate classes, in particular the birds and reptiles, is very important in view of the restricted climatic tolerances and habitats of many species. Sediments from Westbury have also been investigated for pollen but, as expected for cave sediments, pollen concentrations are extremely low, and the resulting pollen counts are very difficult to interpret with any degree of confidence, though pursuance of this line of inquiry is highly desirable.

Until the discovery of these deposits and their contained fauna, mammal-bearing sites of the Lower and early Middle Pleistocene consisted of the Crag and Cromer Forest Bed sites of East Anglia, and Dove Holes, Derbyshire. The exposure of the British Isles to successive ice sheets and intensive weathering and erosion has removed most early Pleistocene deposits, so any further discoveries of such sites will be rare. When they do occur, like Westbury, they might be expected to be in locations such as deep caves which have preserved the deposits against the ravages of denudation.



TEXT-FIG. 1. Location map of Westbury-sub-Mendip and plan of Westbury Quarry.



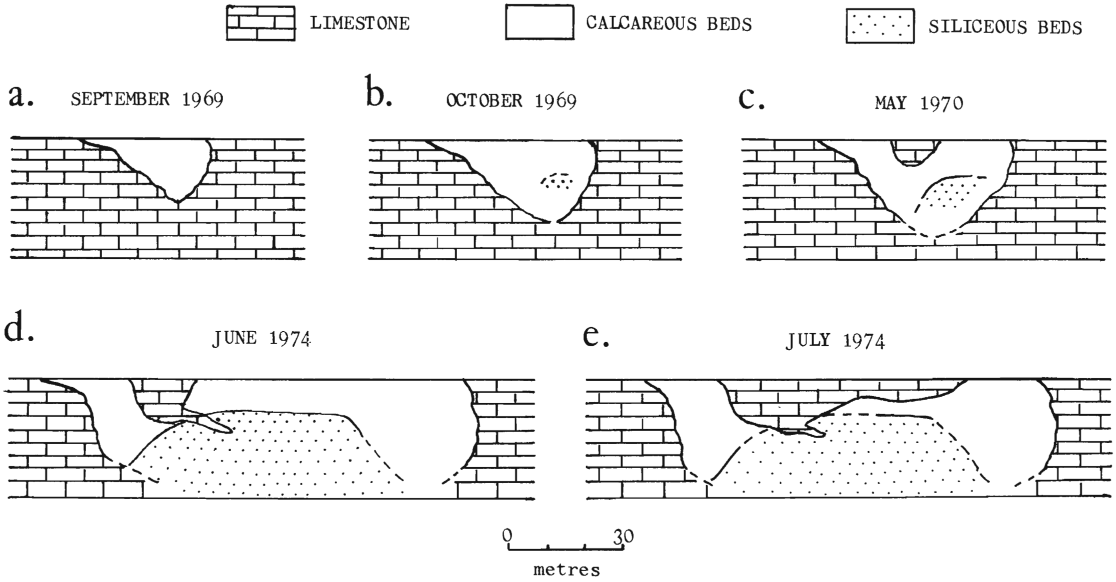
TEXT-FIG. 2. Explanatory sketch of the principal features in Plate 1, showing the V-shaped infilling of Pleistocene sediments within the surrounding limestone as exposed in 1969.

EXPLANATION OF PLATE 1

View of the Pleistocene deposits on the north-east corner of the quarry as they appeared in 1969. (Photograph courtesy of the University of Bristol Spelaeological Society.)

BISHOP, Pleistocene mammals

The Pleistocene deposits of Westbury-sub-Mendip were discovered in 1969 in a working limestone quarry on the southern edge of the Mendip Plateau (NGR ST506504). Formerly referred to as Broadmead Quarry (Green and Welch 1965), but now Westbury Quarry, it was opened up for the extraction of limestone aggregate, and after blasting operations in the north-east corner of the quarry in 1969, a V-shaped infilling appeared (Plate 1, text-fig. 2). Quarry employees noticed large bones and teeth going through the crushing plant, and examples of these were given to Bristol City Museum for identification, and subsequently to the University of Bristol Spelaeological Society. The late Professor E. K. Tratman initiated the collecting and recording of specimens and samples with the help of fellow members of the Society, and Heal (1970) announced the discovery of the site in a short note in their journal.



TEXT-FIG. 3. Diagrammatic sketches of the NE. quarry face showing the progressive exposure of the infilling between 1969 and 1974.

Tratman realized the possible importance of this site at an early stage, and pressed for a deeper investigation to be made. In 1972 the present writer was invited by undertake research into the site, based at the University of Bristol. By 1974 the east face of the quarry had been worked back to expose a well-stratified infilling about 30 m deep and nearly 100 m wide (Plate 2), and the author's studies had by this time established that the contained fauna was all pre-Hoxnian, and that there might be evidence of man (Bishop 1974). In the same year the quarry company, Mixconcrete Aggregates Ltd., decided to blast away the central stratified sequence as it was regarded as unsafe, despite efforts of the author to avert this course of action. Sadly this highly valuable sequence which yielded the richest carnivore remains and the most numerous flints is now lost for ever. The author's second paper on the site (Bishop 1975) was devoted to the discovery of the flint artefacts, the announcement of which, having more impact than the description of a unique mammal fauna, helped in securing the precarious future of what was left of the site, and happily the British Museum (Natural History) undertook to excavate the site from 1975 onwards.

The present paper is mainly devoted to an account of the mammalian remains recovered between 1969 and 1974, and the author's first-hand study of the site between 1972 and 1974. Much of this account, therefore, relates to the well-stratified central sequence (text-fig. 9) now almost entirely destroyed, whereas the British Museum (Natural History) excavations have concentrated on the remaining lateral sequences of the West and East Basins (text-fig. 9) into which some beds of the former central sequence intertongue or are lateral equivalents. It is hoped therefore that the detailed stratigraphic work of the British Museum (Natural History) excavations can be tied in with the present work where stratigraphic horizons can be correlated.

Within the last decade the study of the Quaternary has been revolutionized on a scale comparable to the plate tectonic theory in geology (summary in Bowen 1978), leading to many new interpretations of early Middle Pleistocene events though, as in so many disciplines, raising many new questions (papers in Butzer and Isaac 1975). Recent studies in Britain have seen to the publication of important work on classic British Pleistocene sites, notably the work of West (1980) on the early Pleistocene sites of Norfolk and Suffolk. Recent research has proved of fundamental importance in providing a framework for the conclusions drawn in this paper, and this paper hopefully shows that mammalian palaeontology still has an important place in understanding some Pleistocene sites.

ABBREVIATIONS AND TERMINOLOGY

Recent studies in Pleistocene stratigraphy have radically altered its subdivision (review in Bowen 1978), so new discoveries and correlations require well-defined terms of reference. In this paper the term 'Cromerian' strictly refers to the temperate interglacial stage in Great Britain as defined by West (1980) in the Cromer Forest-bed Formation. Within this stage the full cycle of pollen assemblage zones I to IV (defined in Turner and West 1968) can be recognized in the West Runton and Mundesley Members of the Cromer Forest-bed Formation (West 1980, p. 201). The term 'Cromerian' has also been used by many European authors to describe sites of broadly similar age to Cromer Forest-bed sites (which are now seen to cover several warm and cold stages), and although this usage should be suppressed, it is useful to include such sites under the term Cromerian *s.l.* until thay are redefined under local stage names. The term Cromerian *s.l.* therefore covers an undefined number of early Middle Pleistocene stages (Table 50).

Under Systematics, references to full synonomies are generally given within shortened synonomy lists. References within these lists may include a reference to an updated diagnosis, a review of the species, or a full synonomy list, and the nature of such a reference is given in parentheses if other than a straightforward synonomy. In a number of cases species described are extant, and good diagnostic descriptions of European species are given in Miller (1912). Other useful standard works on Pleistocene mammals are Kurten (1968), Stuart (1974), Sutcliffe and Kowalski (1976), Hinton (1926), Dawkins and Sandford (1866–1872), Reynolds (1902–1912), and Dawkins and Reynolds (1872–1939).

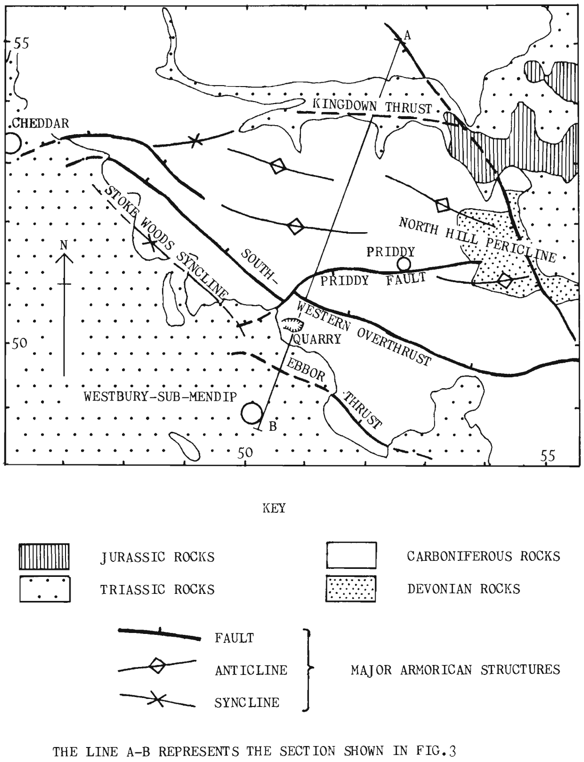
The majority of finds are housed in the Department of Palaeontology of the British Museum (Natural History), and so in this paper numbers prefixed by M and a stop (e.g. M.12345) refer to specimens in these collections. In other places this institution is abbreviated as the B.M.N.H. In many instances one registration number covers more than one specimen, and where distinction is necessary the number is followed by a letter of the alphabet, each representing one specimen. Some specimens do not bear numbers, and these represent unregistered specimens in the B.M.N.H. collections. The majority of other finds are housed in the Department of Geology of Bristol University and in Bristol City Museum.

All measurements are in millimetres unless otherwise stated, and the abbreviation for different teeth in the text and tables is as follows: I = incisor, C = canine, P = premolar, and M = molar. Estimated measurements are followed by (e). Mean values are italicized.

LOCAL GEOLOGY

The quarry in which the Pleistocene deposits are exposed is excavated on the southerly edge of the Mendip plateau, between 213 m and 244 m above O.D. The quarry exposes the Clifton Down Limestone, a grey well-bedded calcite mudstone, which on average dips at 40° to the south, and has a strike averaging 290°.

The Carboniferous limestone of this area is a part of the southerly limb of the North Hill Pericline (text-fig. 4), and Westbury quarry lies along the line of the complex Cheddar–Wells thrust belt, an Armorican structure belonging to the same phase of movement as the main Mendip periclines (Green and Welch 1965). Within this structural belt the Clifton Down Limestone is a part of the northerly



TEXT-FIG. 4. Geological sketch-map of the Central Mendips showing the major Armorican structures, adapted from Green and Welch (1965) and the 1-inch Geological Sheet 280 (Geological Survey, New Series).

limb of the south-easterly pitching Stoke Woods Syncline, a major syncline whose axis runs about 700 m to the south-west of the quarry (text-fig. 4). The South-Western Overthrust lies about 500 m to the north-east of the quarry (text-figs. 4, 5), and the roadway running past the quarry entrance (text-fig. 1) is sited upon the Priddy Fault, a normal fault with a downthrow to the east which displaces the South-Western Overthrust.

Within the quarry there are few structural features of any special importance. There is evidence of a minor vertical fault, trending east–west, in the limestone bluff projecting from the middle of the infill (Pl. 2), but dip and strike in the limestone in the rest of the quarry is relatively uniform, and it is difficult to assess the importance or otherwise of this fault in terms of the origin of the cavity. Bedding and vertical jointing in beds is well developed throughout the exposed limestone.

The Triassic Dolomitic Conglomerate lies unconformably against the Carboniferous rocks forming the southern flank of Mendip (text-fig. 4). In the vicinity of the quarry the Dolomitic Conglomerate tongues up the valley sited over the Priddy Fault, thus infilling one of the many Triassic cut valleys along the south flank of Mendip, which have now been partially exhumed. As Ford and Stanton (1968) note, however, these ancient features are never precisely revealed by the modern feature which cuts across the valley walls and Conglomerate/Limestone contacts. The Dolomitic Conglomerate reaches to about 230 m above O.D. up the valley, within a few metres of the quarry entrance.

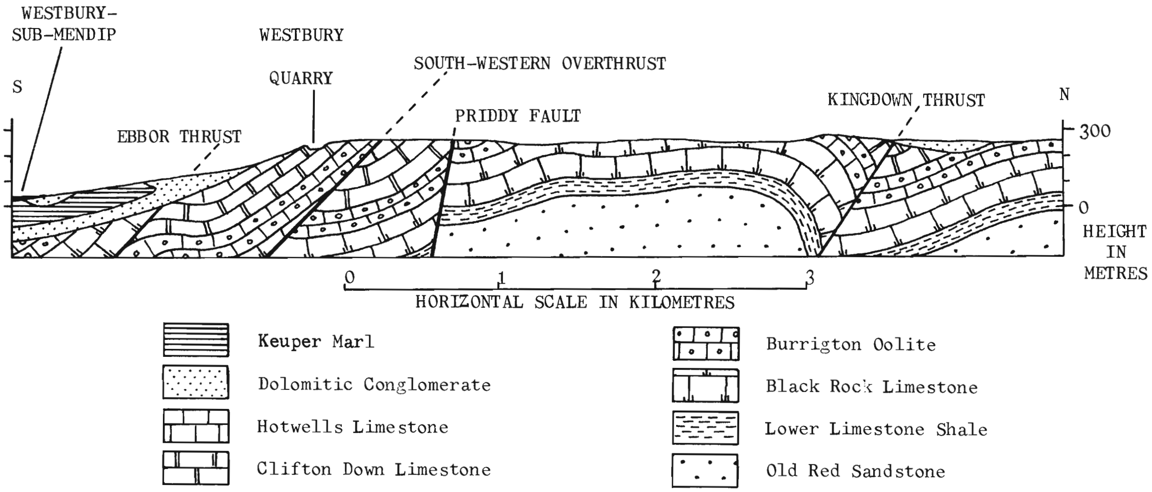
No other rocks are in evidence on the south Mendip plateau surface in the vicinity of the quarry. About 4 km to the north-east of the quarry Green and Welch (1965) note Rhaetic sands and Lower Lias (Downside Stone) recorded in a borehole, and in the same area (Castle of Comfort) they note surface finds of Jurassic chert ascribed to the Harptree Beds. The author could confirm the presence of this Jurassic chert in the Castle of Comfort area, but found no traces of the Jurassic rock type retrieved from the Pleistocene infilling described later.

On the ground surface around the quarry there is a shallow brown soil, which becomes more red-brown where it comes into contact with the underlying limestone. Apart from limestone fragments, the only other rock types found in the soil are pieces of flint. These invariably show signs of human workmanship, and are probably of Upper Palaeolithic age. Nearly all these flints are of the characteristic flinty grey colour, or have rather patinated surfaces, but all are quite different from flint found in the Pleistocene infilling, described later.

LOCAL GEOMORPHOLOGY

The Mendip Plateau mainly comprises gently rolling land between 245 and 260 m above O.D. In the vicinity of the quarry the Plateau surface is at around about 245 m. To the north-east of the quarry there is a large shallow closed basin in which Brimble Pit Pool lies. Ford and Stanton (1968) describe this basin as being made up of thirteen tightly bunched depressions on a flat clay floor with a col on the south edge into which an overflow channel has been cut. This channel forms the feature immediately to the east of the quarry (text-fig. 1) running over the edge of the Plateau southwards. Ford and Stanton (1968) interpret these basins as the product of the development of an interior drainage system (usually sited over major faults and thrusts providing open groundwater routes) to which each depression contributes, formed by desiccation in a temperate climate, subsequent to which their sinks were blocked by permafrost during a glacial phase. Ponding of meltwater would deposit clay, increasing impermeability, and overflow would have cut a channel through the col.

As Donovan (1969) and others have noted, the Mendip Plateau is not an exhumed Triassic surface, and not wholly an exhumed Jurassic erosion surface since gently folded Jurassic cover is itself truncated. Green (Green and Welch 1965) regarded the surface as of late Tertiary age, and Ford and Stanton (1968) regarded it as Pliocene, incorporating large areas of Rhaetic–Liassic erosion surface. Donovan (1969), while agreeing that parts of the surface may be of Jurassic origin, believes that mid-Cretaceous erosion may have played a part, for in south-east England Jurassic structures are truncated by the Gault erosion surface. The location of the Pleistocene cavern infill at such a high level, and the eroded relief which can be inferred from studying the cave's history (see below), indicate that a considerable amount of erosion has taken place since its formation, and much of this erosion has taken place since Middle Pleistocene times. The Plateau seen today would, therefore, seem to be the result of a long history of successive denudation from Triassic times. The Rhaetic–Liassic erosion surface was especially important in levelling the stronger relief of the Triassic Mendip landscape to a



TEXT-FIG. 5. Section across the North Hill Pericline passing through Westbury Quarry, adapted from Green and Welch (1965) and the 1-inch Geological Sheet 280 (Geological Survey, New Series). Line of section in text-fig. 3.

plateau, forming a 'proto-plateau' which was subsequently always an important influence upon further erosion. The mid-Cretaceous erosion undoubtedly removed Jurassic cover from the Mendips, probably exhuming in parts the Jurassic erosion surface, and Upper Cretaceous sediments were probably deposited over the whole area. The presence of flint artefacts in the upper levels of the infill, and its absence amongst deposits below containing fragments of pre-existing cover rocks, suggests that by Middle Pleistocene times Cretaceous cover had been stripped from the Plateau surface, but probably closely flanked the Mendips. Late Tertiary erosion probably removed Cretaceous cover and some of the remaining Jurassic cover in turn, exhuming both Cretaceous and Jurassic erosion surfaces, but probably had limited effect below these levels. The importance of erosion during the Pleistocene would seem to be that soils were able to develop directly over Carboniferous Limestone denuded of various cover rocks and residues derived from them. Recent studies of erosion distribution in the Mendips have shown that over 60% of erosion takes place at the junction of the soil and limestone (Atkinson and Smith 1976), though actual rates of erosion, while calculated for several areas of the Mendips, are fraught with uncertainties when extrapolating back in time. The erosion rate for sites in the South Mendip area given by Atkinson and Smith (1976) is 81 $m^3/km^2/year$, giving a surface lowering equivalent of 81 mm per thousand years, but clearly such rates would have varied enormously during the Pleistocene. Whatever the details, a significant degree of surface lowering probably took place during the Pleistocene once limestone areas were exposed to soil development, and the Plateau feature evident today is the product of several superimposed cycles of denudation, the most important of which span Rhaetic to Pleistocene times.

THE CAVERN AND CAVE GENESIS

The cavity in the limestone which is infilled with Pleistocene sediments, is in exposed section about 90 m wide and up to 30 m deep. To the west the infill deposits rise steeply and thin out to ground level, whereas to the east the infill deposits rise steeply towards ground level but are partially roofed over by the enclosing limestone. The tendency of the east side to be roofed by limestone has been in evidence throughout the working back of the east face since 1969 (text-fig. 3). In 1974 the central portion of the infill was removed by blasting, and this revealed a limestone roof rising from the back (north) of the infill (text-fig. 3*e*). Thus, in the central area, there existed a roofed cavern roughly orientated along the strike of the limestone i.e. in a north-west–south-east direction, which has been breached by erosion of the ground surface. The exposed limestone walls in this central area have in a number of places adhering flowstone near the present ground surface, indicating a former cavern environment. In both the west and east basins (text-fig. 9) the contained sediments rise to ground level, and the two sequences suggest that there were two entrances into the main cavern exposed today.

The limestone walls of the cavity show a number of features that bear on the history of the cave. Most dramatic are those surfaces exposed through the yellow silts and gravels (Bed 1) which occur 10 m from the surface downwards. The limestone is extremely eroded, with angular chert fragments projecting from smooth scalloped limestone surfaces. These surfaces are not scalloped in the regular fashion which forms a common feature covering the sides and bottoms of cave streams, but tend to be asymmetric and of variable size and depth. They tend to follow weaknesses in the bedrock, picking out bedding planes, joints, and other areas where limestone was more susceptible to physical erosion (corrasion) or chemical erosion (corrosion). it seems likely that both erosive processes must have been very active, the water-laid sands and gravels which are in direct contact with these features providing the mechanical means for a highly corrasive stream load, and the totally non-calcareous nature of these same sediments indicating that calcium carbonate was being entirely dissolved out of the system. A common product of the chemical corrosion of limestone is the insoluble red-brown clay residue which makes up a high proportion of cave sediments. This residue was seen around much of the limestone in contact with the sands and gravels, and in some cases could be seen to entirely infill deep round hollows in the exposed bedrock, similar features of which Bretz (1956) has described as 'phreatic pockets' though offered no explanation as to their mode of origin. The presence of this residue appears to be post-depositional, probably forming by corrosion when the sands and gravels were still receiving large volumes of water percolating through the system.

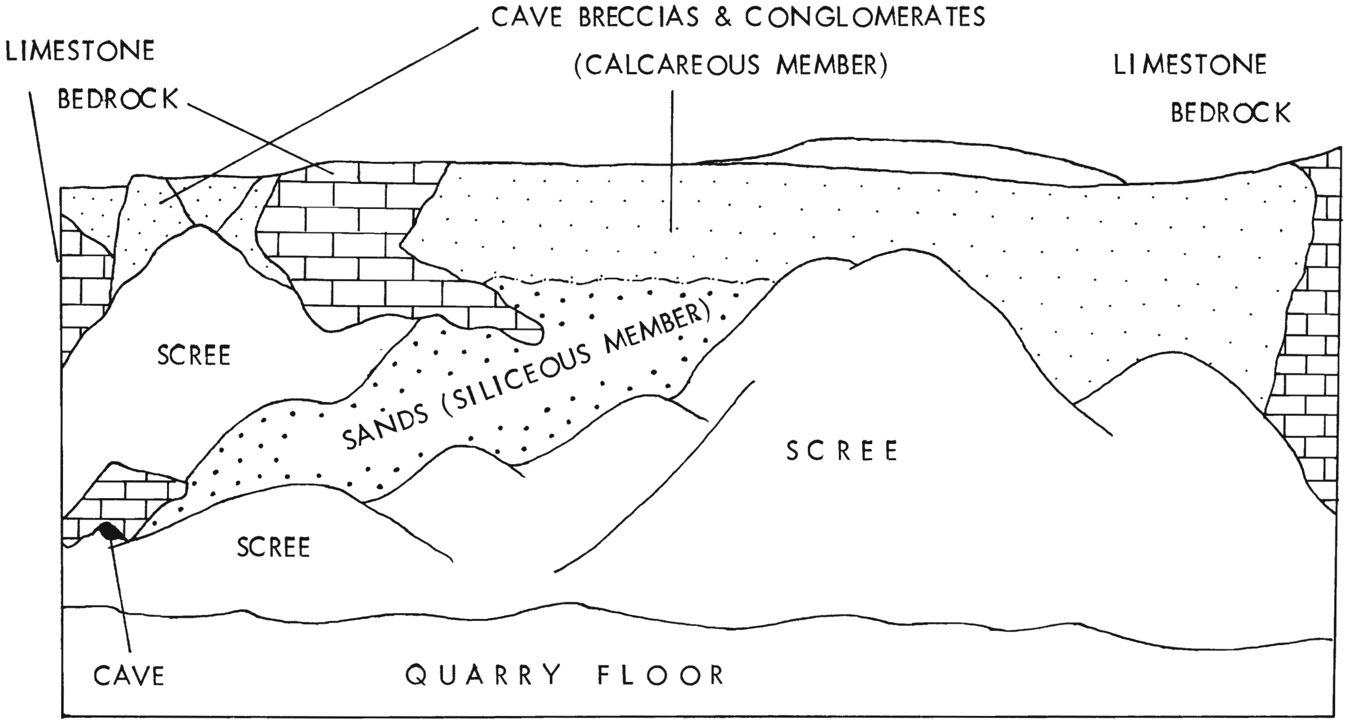
In a small number of cases direct evidence of erosion by corrasional activity was found. Most notable was the presence of small series of rills incised into the upper surfaces of limestone bedrock associated with Bed 1, west of the central area. These features indicate that at the level found, sand-laden water was entering the system from the west side, and was running over the exposed bedrock above any standing water. A steady supply of sand-laden water of relatively low velocity might thus have incised the rivulet system of rills observed.

The significance of these features is that at the time of deposition of the sands and gravels of Bed 1, the cavern appears to have been infilling under vadose conditions, that is, above the water table. Phreatic features associated with this cavern are therefore probably partially superimposed by solutional features associated with the sands and gravels, but probably include the scalloping of limestone particularly on vertical bedrock faces. These phreatic features date back to pre-depositional times when the cavern was waterfilled, and were part of the process of the original cavern formation. Associated phreatic features include the small tube caves which came to light at the base of the present cavern and in the east quarry face as it was being worked back. These smooth-walled caves commonly form complex networks, and those in the vicinity of the main cave are probably all a part of a former phreatic network joining one another.

Bedrock above the level of the sands and gravels and in contact with the Calcareous Member sediments (text-fig. 9) shows very different surface features. None of the solutional features seen below were present, but instead limestone walls were either irregular with fracture, joint, or bedding planes exposed, or old cave wall surfaces were rather rough and bore layers of stalagmitic flowstone. In many cases large blocks of limestone could be found within the infill which had clearly fallen directly from a limestone roof above on to a soft cushion of sediment. These blocks often fell preserving the dip and strike positions that they held *in situ* and, interestingly, a major roof collapse is in evidence at the junction of the Siliceous and Calcareous Member sediments by way of a series of such blocks along the transition zone (text-fig. 9).

In reviewing the possible history of the formation of Westbury cavern it must be borne in mind that the cavity observed today is only a part of a formerly more extensive system. This is clear since: we know that surface lowering takes place; the sedimentary infill requires considerably more topography above the existing site to provide the source rocks; the contained mammal fauna indicates a sheltered lair environment and the whole has been transported into the present cavern; transported blocks of stalagmite have been recovered which must have formed in a cave environment further up in the cave system. Thus text-fig. 8*d* reconstructs the type of situation that might have existed, where the large cavern visible today formed a sedimentary trap at the end of a cave passage or passages, which became inhabited by cave-dwelling mammals. As mentioned above, and as reiterated later, there is evidence for two main entrances to the cavern, one to the east and the other to the west side (text-figs. 7, 11).

The initial development of a cave system must have been under phreatic conditions when the Carboniferous Limestone of the Mendips was flanked by Triassic, Jurassic, and possibly later rocks. These rocks would have the effect of perching the water table where impermeable beds existed, and some Jurassic cover rocks may have still been present on the plateau surface. Under these conditions surface drainage would have predominated, and drainage systems would have run off the plateau edge. The development of underground drainage passages takes place ideally when the contained water finds a localized point at which to discharge, i.e. at a spring. As Ford (1968) has shown, in the Mendips cave development predominantly starts within the phreatic zone, with groundwater opening out passages down bedding planes and up joints in step fashion, each component descent and ascent being termed a phreatic loop. As solution along the network of phreatic loops increases and the resurgance point becomes more important, so passage enlargement occurs. Strike passages are common between dip tubes in steeply dipping rocks, and strike drainage is common in the Mendips (Ford 1971). It seems quite probable that the cavern at Westbury may have developed in just this way, the east and west entrances being the end product of the greatly enlarged original dip tubes,



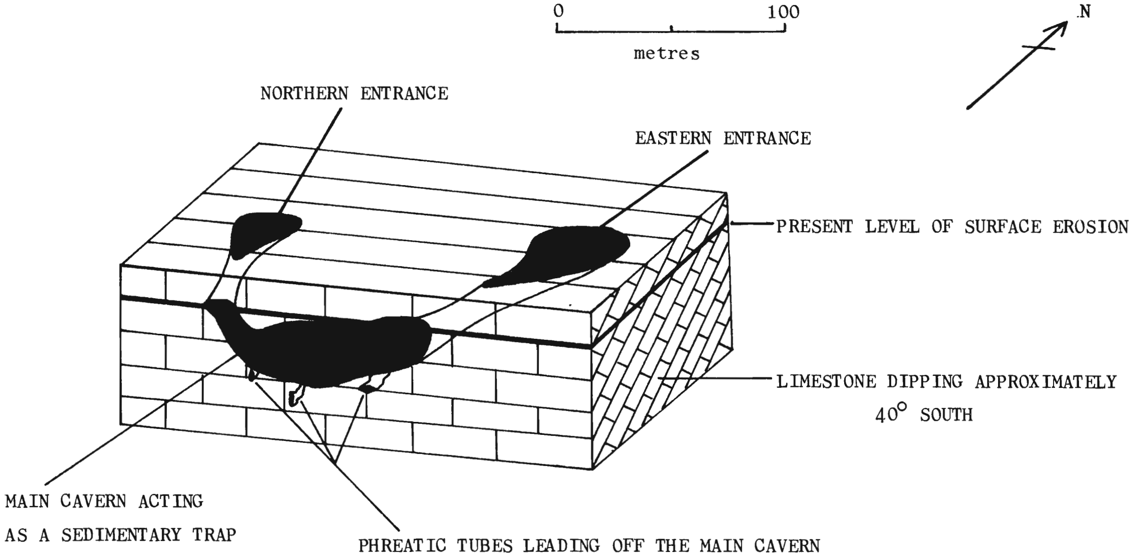
TEXT-FIG. 6. Explanatory sketch of the principal features in Plate 2, showing the very large infilling of Pleistocene sediments bounded to the far left and right by the enclosing limestone bedrock. A limestone bluff projects from the sequence on the left side, and a drainage cave is located to the left below it.

EXPLANATION OF PLATE 2

View of the Pleistocene deposits on the north face of the quarry (see text-fig. 1), taken in 1974.

PLATE 2

BISHOP, Pleistocene mammals

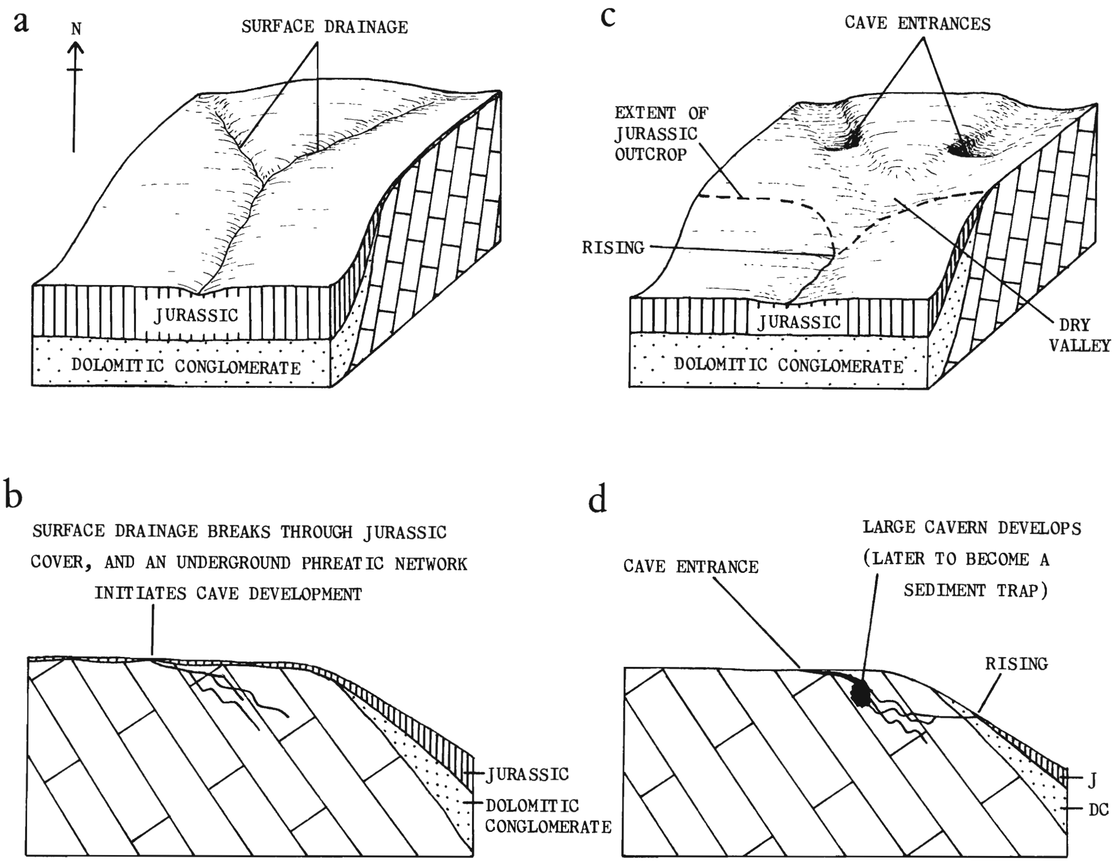


TEXT-FIG. 7. Block diagram showing a hypothetical reconstruction of Westbury cavern and its possible ingoing and outgoing passages.

and the main sedimentary infill cavern being the greatly enlarged product of a connecting strike passage.

Text-fig. 8 shows a possible mode of origin for the cavern developing from a surface drainage pattern. The greatest erosion potential for drainage over the plateau is from the plateau edge downwards where the change in gradient leads to a higher-energy stream course, and the downcutting of such a stream could thus remove cover rocks to initiate a spring (text-fig. 8*c*, *d*). This rising would occur when the impermeable cover rocks had been downcut sufficiently to reach the hydraulic gradient necessary for a groundwater resurgence. The process would be gradual, and over a long period drainage would gradually change from surface to surface and underground, to predominantly underground. As underground drainage became more important, old stream courses would be abandoned, underground passages would be enlarged, and upper cave passages would become air filled. The high position of the cave is consistent with its great antiquity compared with other Mendip caves, given that flanking cover rocks have been denuded over a long time period which determined cave formation. The cave is also in the expected position right at the edge of the Mendip Plateau, since the gradient between sink and rising (the hydraulic gradient) would be achieved more quickly the nearer the sink to the plateau edge. It is quite possible that the valley descending from the east side of the quarry (text-fig. 1) over the Mendip edge to Foxhills Wood (ST507505), though clearly active in last glaciation times as an overflow channel (Ford and Stanton 1968), is in fact a rejuvenated relic of the ancient surface overflow channel in text-fig. 8*a*. This would also imply that the ancient rising may be in this area, possibly at about 200 m above O.D.

The downcutting of surface drainage is most likely to have been accentuated by a drop in sea level (i.e. at the beginning of a glacial episode) when streams cut down in sympathy to the lowered base level. During glacial periods any drainage would probably remain on the surface where permafrost prevented solution entering the ground, except where caves were open to the ground surface and could accept streams. As Newson (1971) has pointed out, however, cave development itself tends to be inhibited during glacial episodes, though large volumes of water may suddenly enter systems as meltwater often infilling caves with superficial deposits. Thus the development of the main cavern



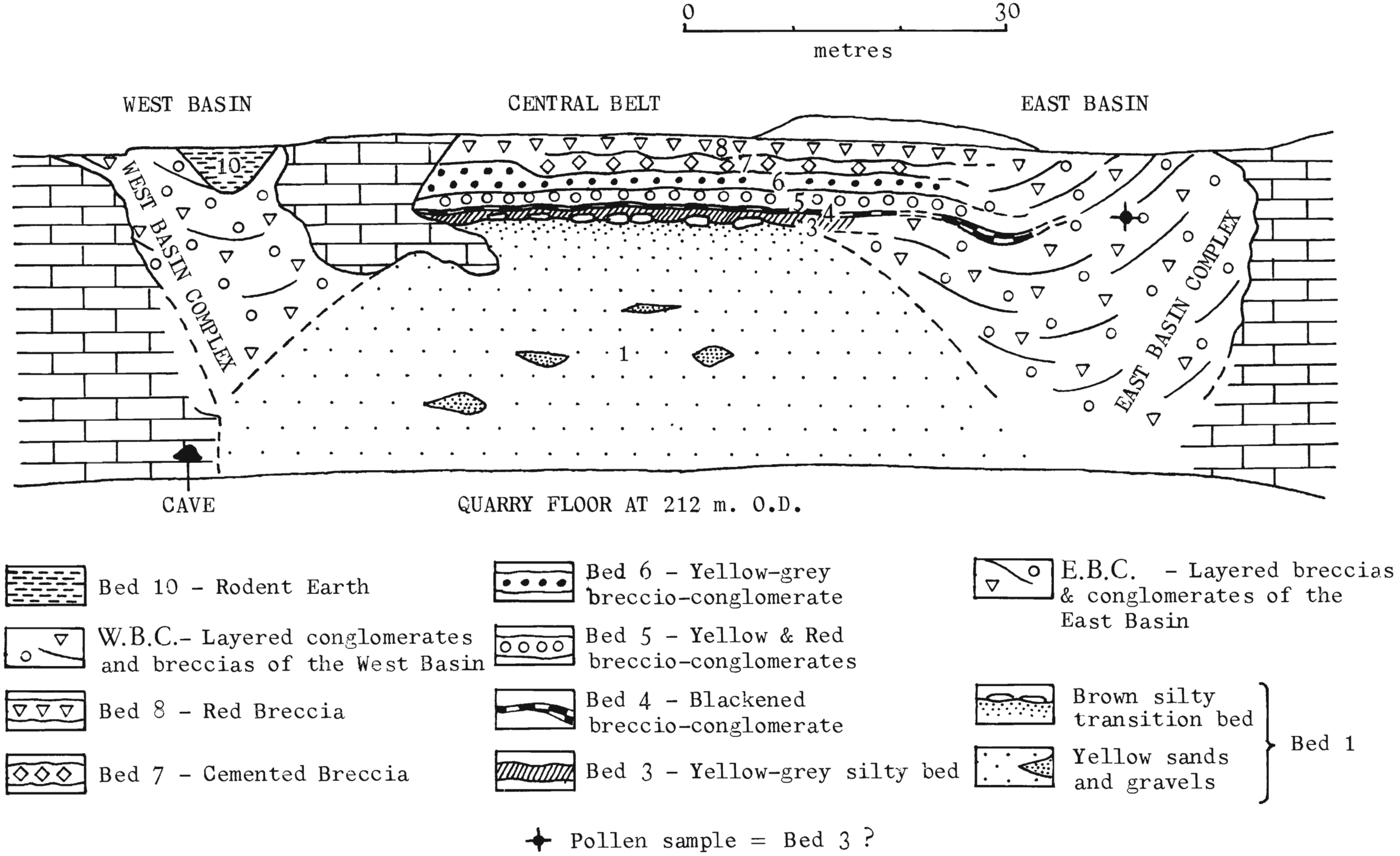
TEXT-FIG. 8. Block diagrams and sections showing hypothetical reconstructions of: (*a*) the surface drainage pattern before erosion of Jurassic cover; and (*b*) the underground drainage system of *a*; (*c*) and (*d*) the development of underground drainage following the denudation of cover rocks.

system would probably be during a temperate period under phreatic conditions, followed by opening and draining of the system in glacial times and initiation of sedimentary infilling.

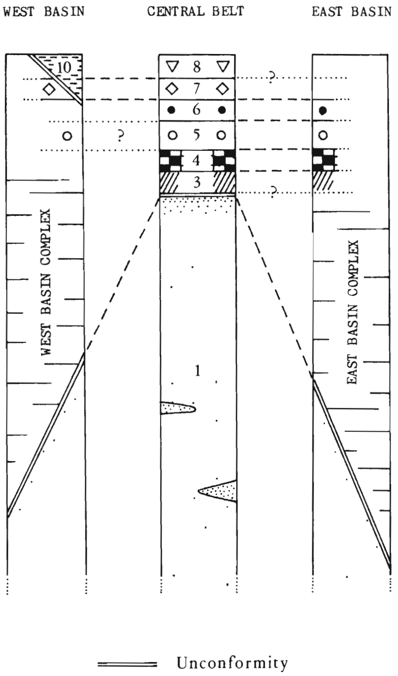
A relic of the ancient surface stream that must once have existed on the Mendip Plateau is preserved in the gravels of Bed 1. This is the presence of remains of the beaver and an extinct water vole both of which rely on permanent surface waters. As discussed later, this fauna, though older than the main cave fauna above, belongs to an early part of the Pleistocene to which time surface drainage must therefore also be ascribed.

STRATIGRAPHY

The stratigraphy of the Pleistocene infilling is shown in text-figs. 9 and 10. The well-layered sequence of the Central Belt is now almost entirely lost, but the layered cave deposits of the West and East Basins and the waterlaid sands and gravels of Bed 1 are still preserved. For convenience in the present work, beds constituting the East Basin Complex and West Basin Complex are abbreviated to EBC and WBC in places.



TEXT-FIG. 9. Sketch-section of the NE. quarry face demonstrating the stratigraphy of the Pleistocene infill up to 1974.



TEXT-FIG. 10. Columnar sections through the West Basin, Central Belt, and East Basin (see text-fig. 8) showing demonstrable and uncertain correlations between beds (bed thickness not to scale).

Bed 1. This thick sequence comprises over 15 m of fine sands, and gravels, of which almost the entire constituents are silica-based rock particles, hence the over-all term for this unit, the Siliceous Member. As a whole this sedimentary unit has a pale-yellow appearance while, in detail, layers range from dark brown (n.b. the gravels) to yellow to very pale yellow. The silica-sand constituent is almost entirely within the fine sand grade 3·25–4·25 ∅ (0·10–0·05 mm), and a considerable thickness of these fine sands are present exclusive of other sedimentary grades except mica particles which are common throughout.

Bedding in the fine sands is variable, from well-bedded bands of 3–4 mm thickness to uniform beds a metre or more thick. Grading and cross bedding are common, indicating deposition by water, and contortions and minor faulting occur indicating slumping and settlement of the deposits. The lighter-coloured layers, usually a few centimetres thick, invariably contained a high silt percentage giving them a clayey feel, so their light-coloured appearance probably relates to the impermeable nature of the sediment where mineral-enriched waters were permeating through the sands elsewhere.

Gravels occur at various levels as lenses or channel fills, predominantly up to 30 cm thick and 150 cm wide in cross-section, but in places fine gravels also formed thin basal layers under sands where beds were graded. The coarsest gravels of 3–4 cm size, occurred at the lowest levels of the Siliceous Member, and tended to be of smaller particle size further up, until the uppermost 4 m after which no gravels were encountered, which suggests that the higher-energy water supply that brought in the gravels gradually diminished. Gravels over 0·5 cm pebble size are mainly composed of a well-rounded pale yellow-white siliceous rock, which is heavily weathered and extensively bored by a small organism. Occasionally fragmentary macrofossils were seen, such as small ammonite whorls and Rhynchonellids, all of which tended to suggest a Jurassic age, though specific identification was difficult. The gravels also contained subangular pebbles of yellow chert probably also of Jurassic origin, angular pebbles of Carboniferous Limestone chert, vein quartz, and small round pebbles of clear quartz. The only other constituent of the coarse gravels and the finer gravels are the bone fragments and teeth of mammals (Table 44). They are highly mineralized and rolled, so much so that they closely resemble the condition found in similar remains from the Red Crag of Norfolk.

In the finer gravels, below 1·5 cm pebble size, limonite is a common constituent, both as small rounded pebbles and as a matrix encrusting the gravels themselves. This encrusting 'pan' is very common in the fine gravels, and often totally infilled voids between the pebbles indicating that the limonitic matrix built up after the deposition of the gravel lenses. This might be expected where iron-rich solution could drain or permeate out of the sand and gravel body most easily through the interstices of the gravels.

At about 1·5 m from the top of the Siliceous Member, the sediments contain a higher proportion of silt and clay, and darken to a brown colour. The uppermost part of this deposit is a brown silty clay in which there lies a series of massive limestone boulders, the whole forming a very definite transition before the overlying sediments of the Calcareous Member. Cessation of deposition in Bed 1 apparently coincided or was followed by partial collapse of the limestone roof of the cavern. The transition horizon was only seen in the Central Belt and was here a horizontal feature, whereas the Calcareous Member sediments occupy lower levels in the East and West Basins than the top of Bed 1 as text-fig. 10 shows. The only contact between the sediments of these basins and Bed 1 observed was in the West Basin where there was no evidence of a transitional zone. This strongly suggests that large parts of the west and east extremities of Bed 1 were slumped and remobilized, and their place has been taken by the heavy overburden of the West and East Basin Complexes.

All deposits overlying the Siliceous Member have limestone constituents and some have calcareous matrices, and are thus collectively referred to as the Calcareous Member.

The East Basin Complex. This thick sequence of beds forming the eastern portion of the infill, mainly comprises layers of angular to rounded limestone pebbles set in silty or clayey matrices mostly of red-brown colour. Mammalian remains occur at all levels, but this part of the infill has not been studied in any great detail by the present writer. The base of the sequence has never been seen due to covering scree material. The beds making up this easterly sequence sag downwards possibly as a result of slumping during and after deposition, which may well have occurred if the East Basin is sited over a drainage cave as suggested earlier. At the level of the Central Belt of deposits, beds from that Belt run into the East Basin Complex, intertonguing with additional beds. Thus layers such as Bed 4 (text-fig. 9) can be traced into this sequence, and characteristically they are thicker and sedimentologically of a different character. All the features of this sequence indicate that it was an area of incoming sediment where cave sediments sludged in to fill an actively slumping basin, until the height of the top of Bed 1 was reached, when incoming sediments traversed the East Basin depositing a particular portion of the sedimentary load, and swept over the top of Bed 1 depositing the rest of the load as a horizontal bed.

Bed 3. This lies directly over the transitional layer of the Siliceous Member in the Central Belt. Its contact with the brown silty clay below was very marked suggesting discontinuous sedimentation, which would be in keeping with basal sediments of the East Basin partly representing sedimentation between Bed 1 and Bed 3 times. Bed 3 formed a uniform layer 1–1·2 m thick, was pale yellow to grey-white in colour, and consisted of small agglomerations of fine sand and silt. Sub-angular limestone fragments of all sizes occurred within this matrix, mostly rather corroded, but less limestone was present in this bed relative to any other in the Calcareous Member except perhaps Bed 10. Mammalian teeth and bones were extremely abundant in this bed, the bones represented by broken splinters to entire long bones and mandibles. This was the only horizon in which articulated bones were recovered, which ranged from finds of bear limb bones to associated mustelid bones to bat bones. Large bones and mandibles were recovered in all attitudes within the matrix, and this and the above features suggest the whole entered the cavern as a water-laden mud or sludge from the cave habitation area.

Nearly 30 m of this bed was exposed laterally, but after the destruction of the Central Belt in 1974 no exact equivalent remained. It seems most likely that this bed, like others above it, probably has a facies equivalent within the East Basin, or tongues out in the East Basin. A sample of grey silty matrix analysed for pollen was recovered from a point below Bed 4 in the East Basin (text-fig. 9), and was possibly the equivalent of Bed 3.

Bed 4. At the top of Bed 3 well-rounded limestone pebbles become common, and a black deposit coats pebbles and occurs as flecks within the silty matrix. The black appearance of this bed and the high proportion of small, well-rounded pebbles differentiates it from beds above and below. Where matrix occurs, it is similar to the matrix of Bed 3, but has been stained to variable degrees by a black deposit. Analysis of the black-coated pebbles has shown that this stain is iron-manganese based, and can thus be equated with iron and manganese oxides and hydrates coating stream-bed pebbles in caves described by White (1976). The mineral coating is characteristically very thin, and concentrations of it on pebbles mark where beds of streams flow into caves from the surface.

In the Central Belt the bed averages about 0·3 m thick, but to the east Bed 4 could be traced into the East Basin Complex, where it is thicker and of different sedimentological character. Here the bed has lost nearly all traces of matrix and the pebbles, while still well rounded, no longer are stained black but are covered by a thin film of brown silt. Bones and teeth are abundant in all parts of Bed 4, and tend to be stained black in both areas where this bed is found. The freshness of the contained bones suggests they have had a short depositional history, so the very rounded pebbles of Bed 4 may have washed in rapidly, though derive from a source area where they were exposed to a high degree of rounding. On deposition of the main sedimentary load the bed appears to have been exposed to active stream flow, encrusting large parts of it with the black iron-manganese deposit.

Bed 5. This bed which averages 1·2–1·5 m thick, is characteristically made up of rounded pebbles and cobbles in a substantial matrix of silt of pale-yellow colour. Near the top and bottom of the bed are bands in which the matrix is stained a red-brown colour and the pebbles are stained black. Fragmentary bones and teeth were extremely abundant, the bone remains frequently including many small bone fragments, suggesting much of the material was derived from a cave habitation area where animal debris had accumulated over a period of time. Of special importance here is the fact that this bed yielded relatively large numbers of small fragments of flint, as well as a smaller number of large flints showing signs of human workmanship. As no trace of flint was found in the Siliceous Member sediments which include an abundance of siliceous rocks derived from the land surface, the presence of flint immediately suggests derivation by a human agency.

Bed 5 was commonly indurated by calcareous solution making large portions of the bed hard and well cemented, often to the extent that its entire thickness was affected along a few metres of exposed section.

Bed 5 could be traced across the Central Belt and into the East Basin, and although there is no clear trace of this bed in the West Basin today, Tratman's notes (typescript, University of Bristol) describe a similar bed within the West Basin at about the equivalent level (text-fig. 10) in 1969.

Bed 6. This bed, about 1·5 m thick, was similar to Bed 5 except that its matrix was more pale in colour and was not cemented to the same degree. The concentration of bone remains was lower than Bed 5, but otherwise the bed was so similar that it could be grouped with Bed 5, though the upper red band of the latter provided a continuous division across the Central Belt.

Bed 7. This bed was easily differentiated from Bed 6 in consisting of angular fragments and blocks of limestone, often cemented together with calcite flowstone. Voids between the limestone were either open, filled with calcite, or were filled with a red-brown silty clay. Bone remains were common, but larger bones were invariably splintered and crushed as a result of the inter-boulder contact due to the lack of matrix sediment. The nature of the limestone debris suggests that much of this material fell directly from cave walls, so unlike beds below this horizon may have largely accumluated *in situ*. This and the presence of abundant calcite cementing the deposit indicates a profound change in the sedimentary regime and cave morphology, suggesting possibly a deterioration in climate leading to increased cavern breakdown, and an advancing cavern entrance bringing with it conditions sympathetic to flowstone formation.

Tratman's notes (typescript, University of Bristol) indicate that this bed was present in the West Basin in 1969 at about the same level (text-fig. 10).

Bed 8. This bed also contains a high proportion of angular limestone debris, but lacks the calcite cement of Bed 7, and has between the limestone blocks a red-brown silt characteristic of many cave earths. Bone remains were relatively scarce. This bed reached ground level, and with Bed 7 was of irregular thickness, the bed probably being partly *in situ* cave debris, and partly sludged in debris, forming the terminal depositional phase within the cavern.

The West Basin Complex. This sequence of beds is even more variable than those of the East Basin, but probably accumulated under similar circumstances. In exposed section the beds of this Basin have been physically separated from beds of the Central Belt by a limestone bluff (text-figs. 6, 9). This natural barrier within the cavern is traversed at the base by the sands of Bed 1, and at an early stage in the exposure of the infill beds of the West Basin covered the face of this feature extending to the Central Belt. The series of sediments connecting the West Basin and Central Belt were only seen for the last few months of 1969 before the east face was worked back, and they subsequently fell away from the face to reveal the limestone bluff. Sadly, the short life of this section never allowed close investigation to elucidate correlations between beds of the Central Belt and West Basin. In 1969 beds belonging to the Central Belt sequence certainly extended westwards around the bluff dipping down into the West Basin, but all well-stratified beds on either side of the Basin were interrupted by a massive amorphous earthy infill which stretched down from the surface deep into the Basin. The remnants of this infill are seen in Bed 10 described below. The more extensive sequence originally seen on the east side of the West Basin, and the apparent absence of correlatives of Central Belt beds on the west side of the West Basin, suggests that beds of the Central Belt tongued out into the Basin within a mass of further cave sediments unique to this Basin, The West Basin sequence must, it would seem, have to have accumulated via a different entrance to the East Basin, and its basinal morphology may, like the East Basin, relate to it being sited over a drainage cave or caves, one of which has in the past been exposed.

Bed 10. This unit termed the 'Rodent Earth' is actually a V-shaped infilling at the top of the West Basin which cuts across bedding in that Basin. The 'bed' is a large mass of red-brown cave earth containing angular corroded limestone fragments and a concentrated layer of bones and teeth of small mammals. This fossil-rich horizon lies within the mass approximately following the basin contour, though the whole unit inclusive of the small-mammal deposit is designated as Bed 10. As mentioned above, this bed was a part of a much larger infill excavated into the beds of the West Basin, which earlier excavators found to be largely barren of faunal remains. An analagous structure in the Mendips is Nod's Pot doline (see Ford and Stanton 1968) where a vertical clay-filled shaft over 20 m deep is excavated through a breccia mass, though the mode of origin of the structure is unexplained. In the case of Westbury, it is possible that the West Basin sequence was exposed to a downcutting stream that excavated a conduit to a drainage cave at the base of the Basin, and the resulting pit was infilled by a mass of cave earth. The exact circumstances of the formation of Bed 10 are very puzzling, and while this unconformable structure is clearly the youngest unit in the infill, the fauna from it belongs, within the limits of Pleistocene faunal discrimination, to the same faunal group as the rest of the Calcareous Member fauna. The interesting feature of its fauna, as discussed later, is the fact that it appears to be derived from an owl-pellet accumulation, and this suggests that the cavern entrance was nearby by Bed 10 times, which probably played an important part in the formation of this unit.

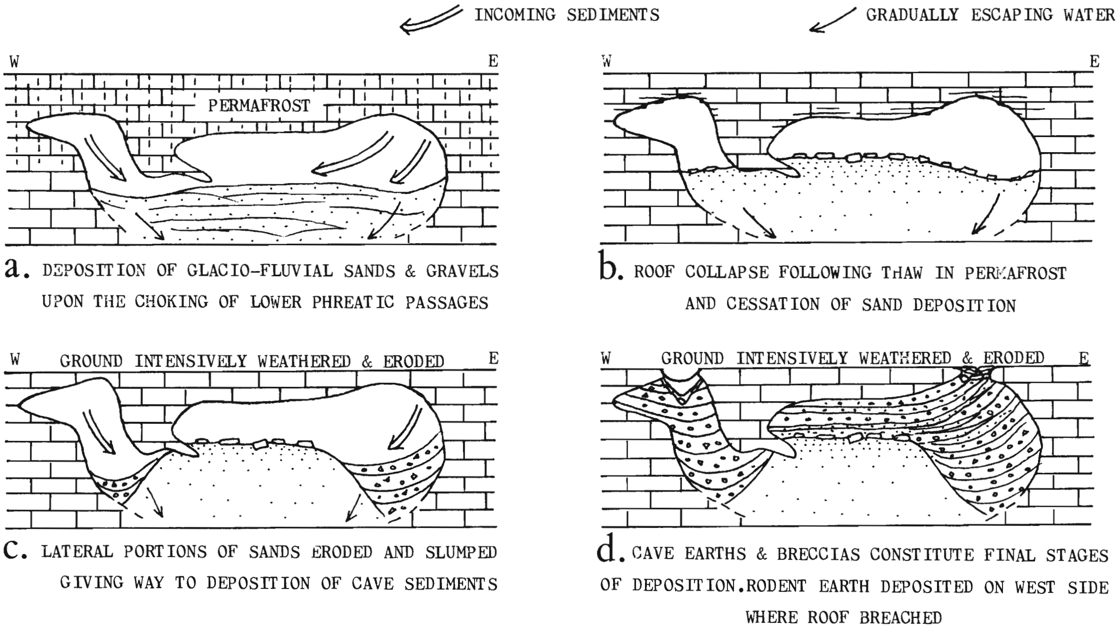
DEPOSITIONAL HISTORY

One of the greatest difficulties in discussing the depositional history of the infilling, lies in the fact that many of the sediments are quite unlike those seen in other caves. While sedimentary analyses would be invaluable in answering many areas of this study, they would still be limited given that no similar deposits of known depositional history are available for comparative study. All the cave sediments of the Calcareous Group are of polymodal origin, having a limestone constituent from breakdown scree, a fine-grained residue from limestone solution, constituents washed in from the land surface and cave entrance, biogenic remains, and probably some wind-blown material. These all working together as well as other processes such as calcite deposition, are bound to give rise to a sedimentary unit which is hard to interpret and, as Ford (1975) has noted, very few analyses or detailed descriptions of cave sediments have been reported in the literature. An in-depth study of the Westbury sediments and modern cave sedimentation would therefore be highly desirable, and any description of depositional history must be conjectural and open to considerable refinement.

Assuming that an east and west entrance to the cavern existed and that these led to drain caves at the base of the main cavern chamber (text-fig. 7), then it is likely that the cavern would have begun to infill with sediment soon after vadose conditions existed in the system. Main cavern enlargement probably occurred during a temperate period under phreatic conditions, and vadose conditions probably developed during a glacial period when the system became open to the surface. The close similarity of the fine sands of Bed 1 to last glaciation wind-blown material found elsewhere on the top of the Mendips, and the other sedimentary features of this bed, strongly suggest that it is deposited from meltwaters. Snowfields developing on the Plateau during a glaciation would be expected to contain a high proportion of this type of sedimentary grade, and the gradual diminution of water-borne load recorded in the full section of the Siliceous Member suggests transport by a limited water supply of ever-decreasing energy. The gravel channels in Bed 1 might thus represent higher-energy meltwater streams (possibly summer streams) whose load was scoured from the old river course containing pebbles of former cover rocks and earlier Pleistocene animal remains. It seems likely that the waters that bore the sediments of Bed 1 were probably considerably abrasive as a result of their sand load, and may well have played an important part in opening up the cave to the surface. As described, this abrasion has overprinted phreatic erosion features in the main cavern area. A relatively sudden influx of sediment may well have blocked exit passages of the main cavern chamber quite quickly, or these may have been previously blocked by clay fill so often found choking the lower reaches of caves. Bretz (1942) has attributed these blocking fills to the settling of fine-grained sediment between phreatic and vadose zones, while Ford (1975) has suggested that the sediment may have settled totally within a phreatic system, or may derive from glacial undermelt or from washed in loess cover. Once blocked, the cavern remained a sedimentary trap until totally infilled. The only escape of sediment from the system may have been from drain caves at the base of the East and West Basins, which may well have unblocked once a large head of water had been dammed back. This would account for the apparent slumping and poor representation of Bed 1 in these two Basins.

The transition zone at the top of Bed 1 marks the silting up of this unit, and the nature of the sediment strongly suggests that a high proportion may be the insoluble residue of weathered limestone, which might be expected to have accumulated once a permafrost zone thawed. The release of the permafrost zone would also explain the roof breakdown evident at the same level (text-fig. 11), where joints and bedding planes forced open by frozen groundwater would clearly precipitate collapse once thawed. Breakdown in and outside of the cave under these conditions would lead to a large amount of thermoclastic scree, which was probably the primary source of limestone debris for the Calcareous Member sediments.

Subsequent deposition occurred under a temperate climate, with the shift of large quantities of limestone scree and other cave debris from the two cave entrance areas down into the main cavern. Temperate conditions in the vadose zone of the cave and at the entrances would lead to the formation of fine-grained residues which would eventually become a major constituent of the matrices of Calcareous Member beds. It is difficult to know how long a hiatus in sedimentation exists between the cessation of Siliceous Member deposition and the begining of Calcareous Member deposition, but it is common in most caves for them to infill fairly rapidly once a route for sedimentary transport from the outside is established. Cave sediments, at first largely subangular limestone fragments and blocks in dark silty matrices, infilled the West and East Basins, probably as sludges charged by flood water or charged by water built up from cave streams. Beds with a high proportion of angular or subangular limestone and red-brown matrices, which includes Bed 8 and several beds within the East and West Basins, probably belong to the group that sludged into the cavern relatively slowly. Others, such as Beds 3, 5, and 6, may have entered as flood deposits, where waters picked out large quantities of



a. DEPOSITION OF GLACIO-FLUVIAL SANDS & GRAVELS UPON THE CHOKING OF LOWER PHREATIC PASSAGES

b. ROOF COLLAPSE FOLLOWING THAW IN PERMAFROST AND CESSATION OF SAND DEPOSITION

c. LATERAL PORTIONS OF SANDS ERODED AND SLUMPED GIVING WAY TO DEPOSITION OF CAVE SEDIMENTS

d. CAVE EARTHS & BRECCIAS CONSTITUTE FINAL STAGES OF DEPOSITION.RODENT EARTH DEPOSITED ON WEST SIDE WHERE ROOF BREACHED

TEXT-FIG. 11. Diagrammatic reconstructions across the cavern showing its possible mode of infilling with sediments.

sediments from the cave habitation areas. Another explanation for the concurrence of these three light-coloured conglomeratic beds at this level, is that with the vast amount of cave sediment removed from the higher cave passages to the East Basin, the sediments accumulating in the habitation area may have become susceptible to erosion by the gradual removal of supporting cave debris. The reverse might also have come into effect where the cave entrance was being worked back by erosion, to expose formerly sheltered cave floor areas. Whichever the case, and all three processes may have operated, the nature of Beds 3, 5, and 6 indicate derivation from a dry area (thus attracting animals seeking shelter) where light-coloured sediments would accumulate from mechanically abraded limestone debris, wind-blown material, and animal remains. Being a dry area, the dark residues from limestone solution would be excluded. In Bed 4 times an active cave stream appears to have reached the main cavern area from the upper east cave entrance depositing a black coating around an inwashed gravel bed.

Bed 7 heralds further breakdown of the cavern walls, and is highly suggestive of a thermoclastic deposit. It is probably entirely endogenetic (derived by internal processes) and probably accumulated *in situ* in the main cavern. Bed 8 appears to have sealed the main cavern, and this poorly sorted bed which belongs to the sedimentary group which probably sludged into the cavern, may well have entered by solifluction given the apparent evidence of a deterioration in climate.

As the top layers of the Central Belt could not be correlated with equivalents in the West Basin, the relative stratigraphic position of Bed 10 to the Central Belt is uncertain. Bed 10 is clearly the final sedimentary phase in the West Basin, but there is at present no evidence to establish it being younger than Bed 8. Drainage must have altered quite profoundly to have cut the channel in which Bed 10 lies, possibly in Bed 7 times when major cave wall breakdown may have altered the flow of an incoming stream. The same breakdown limestone may have been an important source rock in the formation of the Bed 10 cave earth. The abundance of this detritus from limestone solution indicates a considerable amount of weathering took place to form it, and it is therefore likely that the detrital sediment accumulated at the exposed mouth of the cave or even within what by Bed 10 times might have become an open ravine on the site of the West Basin.

SYSTEMATIC DESCRIPTIONS

Order INSECTIVORA Bowdich 1821
Family ERINACEIDAE Bonaparte 1838
Erinaceus sp.

Material. One fragmentary upper left M1 (M.33996a), and one fragmentary anterior portion of mandible (M.33996b), both from Bed 10.

Description. The tooth and jaw fragments are indistinguishable in morphology from the living *Erinaceus europaeus*, and appear to be close in size to the living species. Unfortunately both specimens are too fragmentary to make any reliable comparisons with other Pleistocene *Erinaceus* species.

Discussion. Records of hedgehog are uncommon from the Pleistocene and, where recorded, finds are invariably of a fragmentary nature, so our knowledge of the Pleistocene history of *Erinaceus* is poorly understood. Plio-Pleistocene hedgehog remains tend to be smaller than the living *E. europaeus*, and while *E. samsonowiczi* Sulimski from Weze (Sulimski 1959, 1962) has been described from good skull material and is clearly different from the living *E. europaeus*, other species such as *E. praeglacialis* Brunner and *E. lechei* Kormos are only known from fragmentary lower jaws. For the time being, therefore, identification of these remains is impossible beyond generic level until more material is available from both Westbury and other Pleistocene sites.

Family TALPIDAE Gray 1825
Talpa europaea Linnaeus 1758

1912 *Talpa europaea* L.; Miller, pp. 3–14, text-figs. 1, 2. (Diagnosis and synonomy of living sp.).

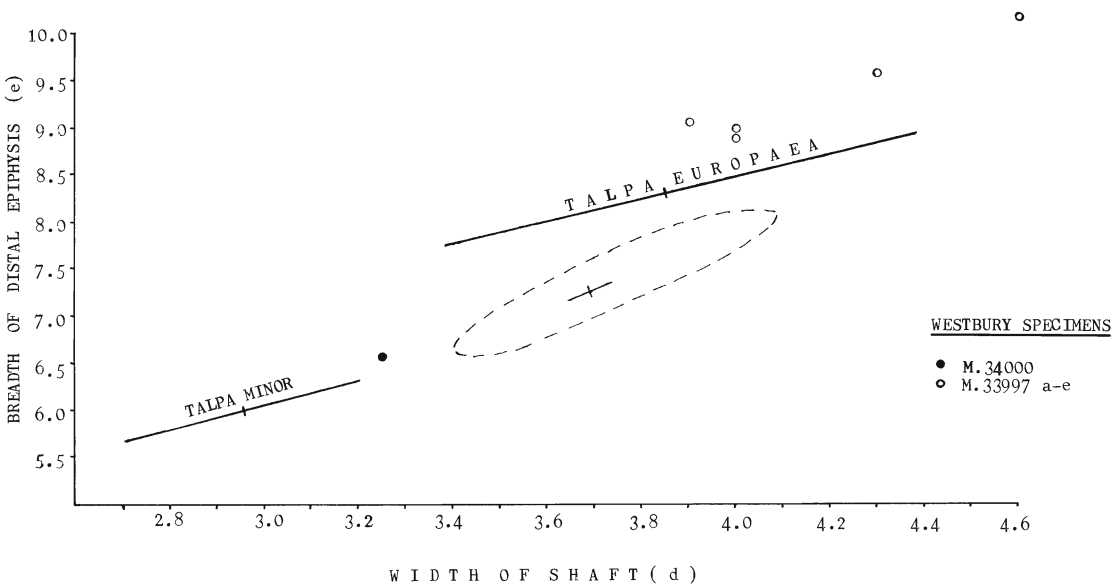
Material. Nine mandibles (M.33998a–i), one upper M2 (M.33998j), and numerous humeri (M.33997), all from Bed 10.

Description. The morphology of these remains is identical to the living *T. europaea*, and in size these remains closely compare with fossil and living representatives of this species (text-fig. 12).

TABLE 1. Measurements (in mm) of the lower tooth row M_1–M_3 in *Talpa* from Westbury and Hundsheim.

	Length M_1–M_3
Westbury M.33998*a*	6·55
Westbury M.33998*b*	6·25
Westbury M.33998*c*	6·40
Westbury M.33999 (*Talpa minor*)	5·50
T. europaea. Hundsheim (Rabeder 1972)	6·3–6·7 (m = 6·46)
T. minor. Hundsheim (Rabeder 1972)	5·5–6·1 (m = 5·58)

Discussion. Much of the earlier Pleistocene mole material has been attributed to *T. fossilis* Petenyi, a form morphologically very similar to *T. europaea*, but intermediate between it and *T. minor* in size. Recent workers (Koenigswald 1970; Rabeder 1972; Rzebik 1972) have questioned the validity of *T. fossilis*, and certainly an allied form, *T. praeglacialis* Kormos is synonomous with *T. europaea*. The Pleistocene *T. minor* Freudenberg is considerably smaller than *T. europaea*, and this species also appears to be present at Westbury, as indicated in the table above and in the measurements of the humeri (text-fig. 12). Both species of *Talpa* appear to be slightly larger than those described by Koenigswald (1970) from Petersbuch but, as text-fig. 12 shows, the separation between the two is as distinct, if not more so, than the Petersbuch material. *T. europaea* described by Stuart (1975) from West Runton is much smaller than the material from Petersbuch, and very considerably smaller than



TEXT-FIG. 12. Regression lines (*e* on *d*) plotting distal epiphysis breadth against shaft width of *Talpa* humeri from Petersbuch (Koenigswald 1970), with area of scatter and mean for West Runton *Talpa europaea* (hatched line) (Stuart 1975), and Westbury *Talpa* specimens (circles). Measurements in mm.

the Westbury *T. europaea*, so small in fact that the variation overlaps with *T. minor* (text-fig. 12). Pleistocene workers in Europe based the species *T. fossilis* on material intermediate in size between *T. minor* and *T. europaea*, and, as such, mole material from the Cromerian of West Runton clearly falls within the *T. fossilis* grouping (text-fig. 12). The clear distinction between the West Runton mole and the Westbury mole is an important feature taken up again later in this paper.

Both fossil and living representatives of *T. europaea* are widely distributed throughout Europe and Asia, so it is likely that the fossil populations occupied similarly wide ranges of habitat to living populations.

Talpa minor (Freudenberg 1914)

1914 *Talpa europaeus* var *minor* Freudenberg, p. 209, pl. 19, figs. 7, 32, 33, 35–37.
1972 *Talpa minor* Freudenberg; Rabeder, pp. 385–394, pls. 1–2, figs. 1–3. (Synonomy and diagnosis.)

Material. One fragmentary mandible (M.33999) and one humerus (M.34000), both from Bed 10.

Discussion. T. minor has been recorded from several Lower and Middle Pleistocene sites in central Europe, but has not been recorded from the British Isles before. Rabeder (1972) has suggested that *T. minor* is the ancestor of the living *T. hercegovinensis* Bolkay, and has even proposed that the latter name be given sub-specific rank as *T. minor hercegovinensis*. *T. minor* has recently been recognized from the Cromerian of Sugworth (Stuart 1980).

Further finds of mole from the British Museum (Natural History) excavations have included more finds of this small-mole species (A. Currant pers. comm.).

Desmana moschata Linnaeus 1758

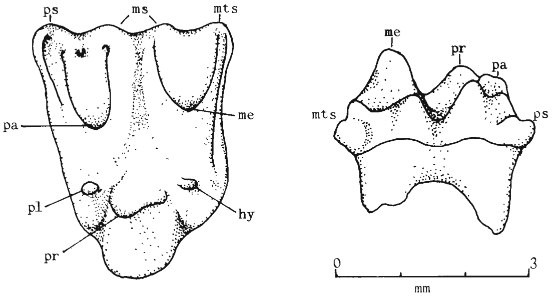
Text-fig. 13

1940 *Desmana moschata* L.; Schreuder, pp. 212–308, pl. VIII, figs. 1, 2, 5, 7, 8; pl. IX, figs. 1, 5, 6; pl. X, fig. 9; pl. XI, figs. 1, 10, 11, 17, 18, 21, 22, 25; and 31 text-figs. (Extensive review and diagnosis.)

Material. One fragmentary mandible (M.34002), 1 isolated lower M1 (M.34003f), 5 isolated upper molars (M.34003a–e), and 8 limb bones (M.34001), all from Bed 10.

Description. The dentition is of the typical insectivore pattern, while the upper molars are distinctive in that the mesostyle is divided into two separate cusps, which in occlusal view produces two V-shaped figures, unlike the single W-shape in *Talpa* (text-fig. 13). Other smaller differences allow distinction from *Talpa* and comparison with *Desmana* as described by Miller (1912). The measurements of the teeth (Table 2) are comparable to *D. moschata* and *D. thermalis*, but the latter can be excluded in the morphology of the teeth, in particular the absence of an outer cingulum in the lower M1, and the presence of a guard in the upper M1. Two other details, a cusp-like parastyle in the upper M2, and a remnant cingulum in upper M3, are not seen in the living *D. moschata*, but are described by Schreuder (1940) in the two fossil subspecies *D. moschata mosbachensis* and *D. moschata magna*. The Westbury remains are closely similar in morphology to the latter, except for a higher degree of development in the parastyles, and an extra cusplet in upper M2.

The mandible can be distinguished from *Talpa* by its relatively flat undersurface, and the limb-bones are very distinctive (Schreuder 1940).



TEXT-FIG. 13. Upper left M2 of *Desmana moschata* Pallas from Bed 19 (M.34003b) in occlusal and outer view. Abbreviations follow Schreuder (1940).

Discussion. The Westbury remains clearly belong to *D. moschata*, and appear to be intermediate in both size and morphology between the recent species and *D. moschata* from West Runton.

The presence of desman at Westbury is interesting as it is an aquatic insectivore, the living species (now a relict species restricted to south-eastern Russia) making its home in the banks of streams and rivers. The distribution of Pleistocene desmans given in Jánossy (1965*a*) demonstrates this dependence in showing localities are invariably on or near major rivers. At Westbury, however, Bed 10 in which the desman remains are found, appears to be a bird of prey deposit so these animals probably represent prey caught some distance from the site.

TABLE 2. Comparative measurements (in mm) of teeth in *Desmana*.

	Upper						Lower	
	M1		M2		M3		M1	
	L	B	L	B	L	B	L	B
Westbury M.34003a, b, d, f.	4·2	3·9	3·1	4·0	2·9	3·1	3·6	2·7
Westbury M.34003c, e.			3·0	4·0	3·0	3·0		
D. moschata. West Runton	3·5–4·0	3·2–3·8	2·7–3·0	3·5–4·0	—	—	3·2–3·5	2·5–2·7
D. moschata. Recent	4·3–4·7	3·6–4·3	3·4–3·6	4·3–4·6	3·2–3·6	3·4–3·9	3·5–4·0	2·8–3·1
D. thermalis. Pleistocene	4·2	3·4	2·8	3·7	2·8	2·9	3·6	2·7

Family SORICIDAE Gray 1821
Neomys cf. *N. newtoni* Hinton 1911

Text-fig. 17*c*.

Material. Eight fragmentary mandibles (M.34004a–h) all from Bed 10.

Description. The mandibles and teeth are of the typical shrew form, but are distinct from *Sorex* in the morphology of the condyle (text-fig. 17*c*) in which the superior and inferior facets are connected by a very slender interarticular bridge, which is characteristic of *Neomys*. The interarticular bridge is especially narrow in these specimens, the superior facet is only about two-thirds the size of the inferior (these are more nearly equal in *N. browni*, *N. fodiens*, and *N. anomalus*), and the inferior facet is slender. The measurements of the mandibles are given in Table 3.

Discussion. The morphology of the condyle indicates that these shrews belong to the *N. newtoni* group, first described by Hinton (1911) from West Runton. Hinton also described another species, *N. browni*, from Grays Thurrock, but the Westbury material shows a much more slender condyle, and in this respect is closely comparable with *N. newtoni*. The measurements of *Neomys* given above indicate that the height of the coronoid process is of little diagnostic value, but the length of the tooth row may be of some importance. The three species *N. newtoni-browni-fodiens* are probably interrelated, and do show a general increase in size and robustness, so the length of the tooth row suggests that the Westbury species may be 'advanced' in the *N. browni-fodiens* direction while still retaining the primitive *N. newtoni* condyle.

Neomys is an amphibious shrew, but as in the other cases of mammals from Bed 10 was probably brought in from outside the immediate area of the site.

TABLE 3. Comparative measurements (in mm) of the coronoid process height and tooth row length (M_1–M_3) in *Neomys*. Figures from Hinton (1911), Rabeder (1972) and Meulen (1973).

	Height Coronoid Process	Length M_1–M_3
Westbury M.34004a	—	4·35
Westbury M.34004b	4·2	—
Westbury M.34004c	4·1(e)	—
Westbury M.34004d	4·3	—
N. newtoni. West Runton	4·07	3·85
N. cf. *newtoni*. Monte Peglia	4·41, 4·62	3·93
N. browni. Grays	4·29	4·29
N. anomalus. Hundsheim	4·4–4·5	4·1–4·5
N. fodiens. U. Pleistocene–Recent	4·18–4·73	4·29–4·4

Sorex minutus Linnaeus 1766

1912 *Sorex minutus* L.; Miller, pp. 53–60, text-figs. 10, 11. (Diagnosis and synonomy of living sp.)

Material. Three fragmentary mandibles (M.34005a, b, c) from Bed 10.

Description. The mandibles closely compare with the typical *Sorex* morphology, except that the coronoid process is relatively more forwardly directed to the ramus than in *S. araneus*, and the remains are much smaller than *S. araneus* and *S. runtonensis*. Measurement of the mandibles are given in Table 4.

Discussion. These remains closely compare with living and fossil representatives of *S. minutus*. This species appears sporadically throughout the Pleistocene, from sites such as Weze, Poland (Sulimski 1959), in the Lower Pleistocene onwards, and appears to be very conservative in size and morphology. The living Pygmy Shrew has a preference for dry, well-covered ground, and is rarely found in closed woodland (Brink 1973).

TABLE 4. Comparative measurements (in mm) of the coronoid process height and tooth row length (M_1–M_3) in *Sorex minutus* L.

	Height Coronoid Process	Length M_1–M_3
Westbury M.34005a	2·8(e)	3·1
Westbury M.34005b	3·1(e)	—
Westbury M.34005c	—	2·6(e)
S. minutus. Stránská Skála (Rzebik 1972)	3·09	—
S. minutus. Petersbuch (Koenigswald 1970)	2·8–3·2	3·2
S. minutus. Husarenhof 4 (Koenigswald 1973*b*)	3·05–3·15	3·1
S. cf. *minutus*. Weze (Sulimski 1959)	2·9–3·3	2·8–3·2
S. cf. *minutus*. Hundsheim (Rabeder 1972)	2·75–2·9	2·8–3·0
S. minutus. Recent (Rabeder 1972/Hinton 1911)	3·0–3·35	3·13

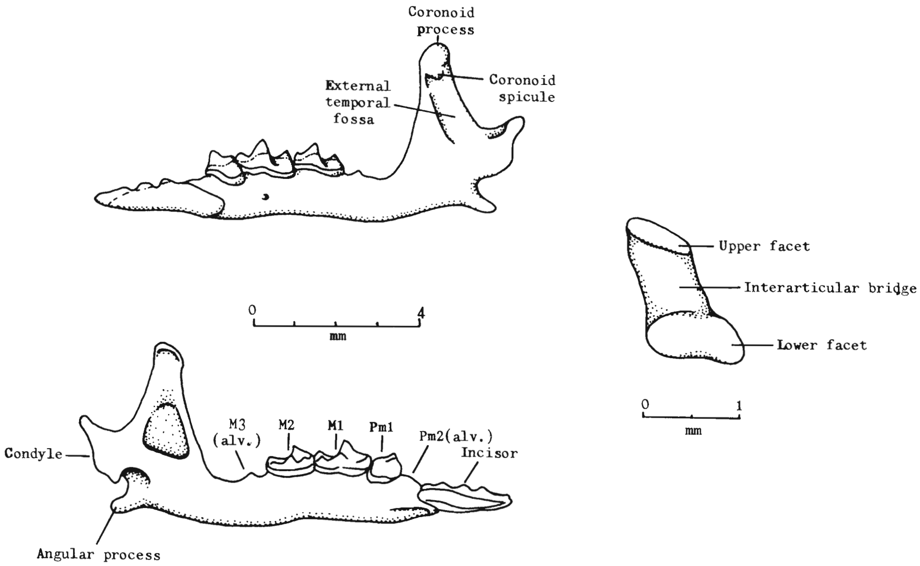
Sorex runtonensis Hinton 1911

Text-figs. 14, 17*a*

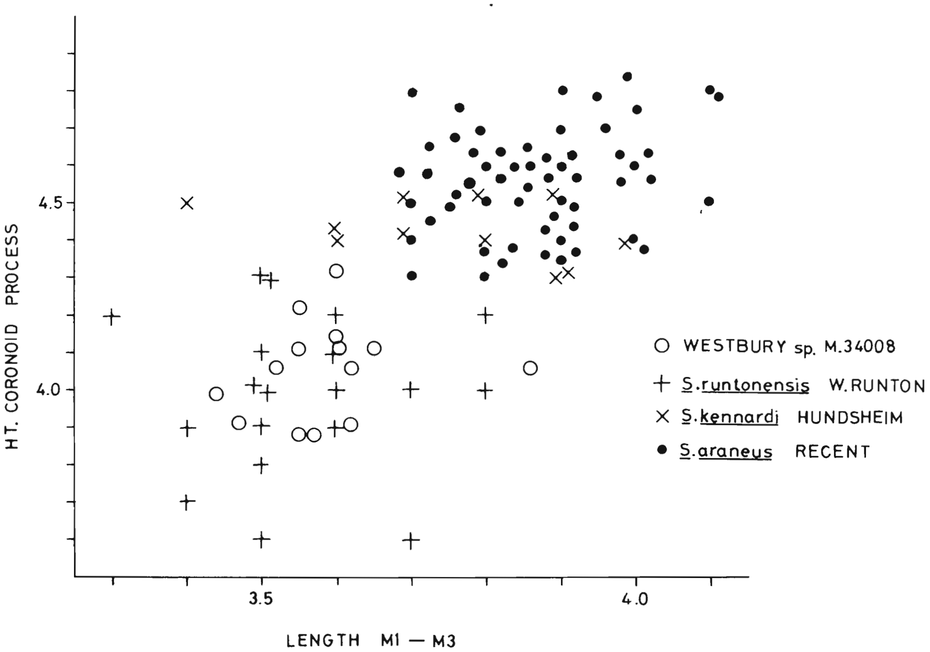
1911 *Sorex runtonensis* Hinton, p. 532, pl. 25, figs. 8, 9; text-fig. 8*a*.
1930 *Sorex araneoides* Heller, pp. 260–261, p. XV, fig. 4*a*–*b*; text-fig. 10.
1974 *Sorex* species A and B; Bishop, pp. 309, 311, 314.

Material. Very numerous fragmentary mandibles (M.34008) and maxillary fragments (M.34009) from Bed 10, and a small number of fragmentary mandibles from Bed 5.

Description. The morphology of these remains is almost identical to *S. araneus* L., except that the condyle in the mandible has a narrower interarticular bridge joining the inferior facet (text-fig. 14) and the coronoid process is more narrowly tapered. The remains are intermediate in size between *S. minutus* and *S. araneus*.



TEXT-FIG. 14. Left mandibular ramus of *Sorex runtonensis* Hinton from the East Basin below Bed 4 (M.33562), showing outer and inner views of the ramus, and posterior view of the condyle.



TEXT-FIG. 15. Graph of lower tooth row length (M1–M3) plotted against height of coronoid process in medium-sized *Sorex* species. Comparative figures from Rabeder (1972) and Jánossy (1969). Measurements in mm.

Discussion. The size of these remains and the morphology of the condyle are consistent with *S. runtonensis*, first described by Hinton (1911) from West Runton (text-fig. 14). The systematics of medium-sized shrews allied to the living *S. araneus* is very confused, and recent studies by Koenigswald (1970) and Meulen (1973) have stressed the wide variation in the morphology of the condyle, which has been used to create several species. The Westbury material shows a limited variation around the condyle form in text-fig. 14, with a common tendency of an inward- and downward-pointing lower facet relatively free on the inner side of the interarticular bridge. Two generalized shapes are common to medium-sized *Sorex* species, which are used in text-fig. 16 to separate finds attributed to six different species. The *S. runtonensis–S. araneus* group appears to be divisible on size (text-figs. 15, 16), but other groups are not so easily separated.

Like *S. savini*, *S. runtonensis* is a 'Cromerian' *sensu lato* element of mammalian faunas, and at sites of a later date remains attributed to *S. kennardi* or *S. araneus* are recorded. Until more work is done on the middle-sized fossil shrews, it is probably dangerous to place emphasis on this species as a key fossil.

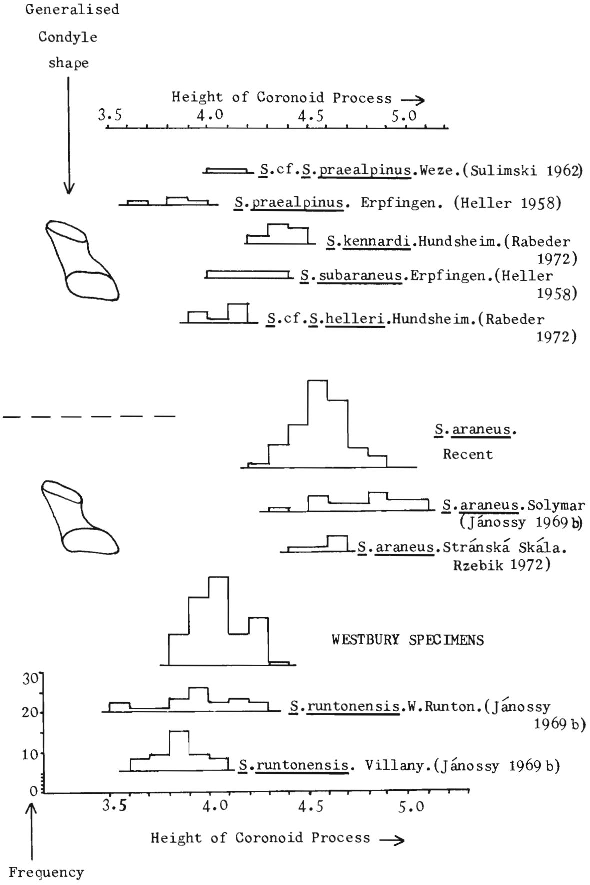
Sorex savini Hinton 1911

Text-fig. 17*b*.

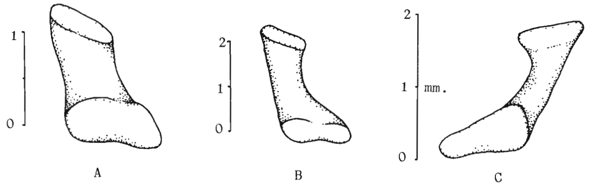
1911 *Sorex savini* Hinton, pp. 531–532, pl. 25, figs. 6, 7; text-fig. 7*a*.

Material. Ten fragmentary mandibles (M.34006a–j) and one lower incisor (M.34007), all from Bed 10.

Description. The mandibles are of the typical shrew form, but differ from *S. araneus* L. in their very large size, the robust condyle (text-fig. 17), the well-developed external temporal fossa in the coronoid process, and the tip of the coronoid process which is large and boss-like with a distinct coronoid spicule. Another distinctive feature is



TEXT FIG. 16. Histograms of the height (in mm) of the coronoid process in medium-sized *Sorex* species, grouped above and below according to the two common generalized condyle shapes.



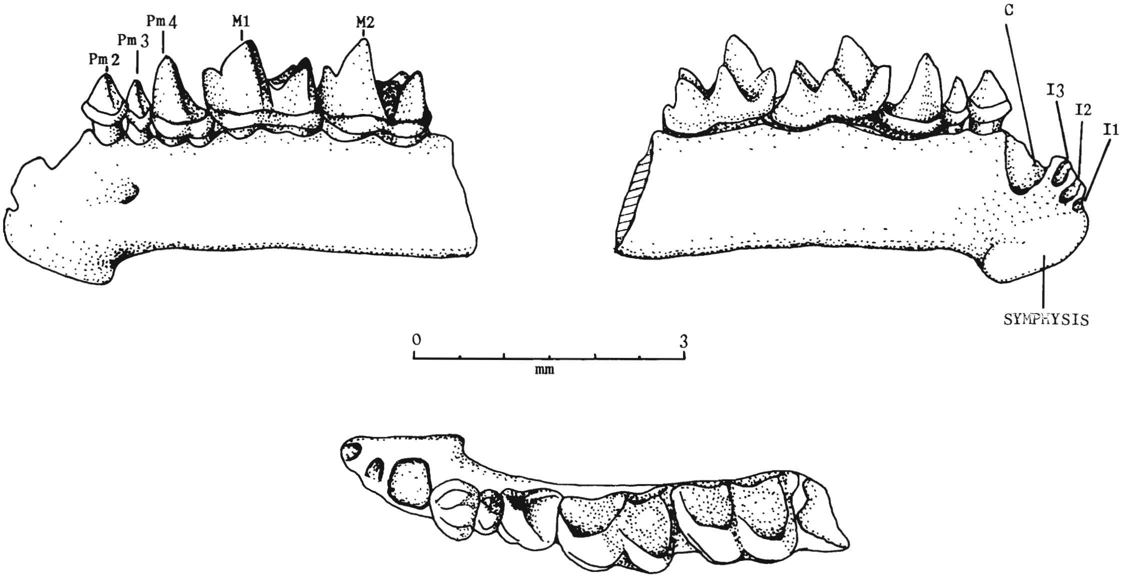
TEXT-FIG. 17. Condyle shapes in (A) *Sorex runtonensis* Hinton, (B) *S. savini* Hinton, and (C) *Neomys* cf. *newtoni* Hinton, from examples from Bed 10, Westbury.

TABLE 5. Comparative measurements (in mm) of the coronoid process height and tooth row length (M_1–M_3) in large *Sorex* species.

	Height coronoid process	Length M_1–M_3
Westbury M.34006a	5·4	—
Westbury M.34006b	5·7	—
Westbury M.34006c	—	4·3
Westbury M.34006d	5·4(e)	4·1(e)
Westbury M.34006e	5·4	—
Westbury M.34006f	—	4·3
Westbury M.34006g	—	4·2
S. savini. W. Runton (Hinton 1911)	5·61–5·72	4·07
S. savini. W. Runton (Jánossy 1969*b*)	5·3–5·9 ($n = 24$)	—
S. cf. *S. margaritodon.* Kormos, Petersbuch (Koenigswald 1970)	4·4–5·5	3·8–4·1
S. tasnadii. Kretzoi, Erpfingen (Heller 1958)	5·6–5·8	4·2–4·3
S. austriacus. Kormos, Hundsheim (Rabeder 1972)	5·7–6·4	4·2–4·6

that the teeth are stained an orange-yellow colour, unlike the red of other *Sorex* species, and this stain in the molars and premolars extends from the crown tips to the external cingulum. The incisor bears four denticles, which are also stained.

Discussion. This very large shrew is directly comparable to *S. savini* originally described by Hinton (1911) from West Runton. Other large species probably related to *S. savini*, and often referred to by European authors as the genus *Drepanosorex* Kretzoi, are *S. margaritodon* a smaller species, and *S. austriacus* which is larger and whose tooth crowns are only stained at the tips.



TEXT-FIG. 18. Left mandibular ramus of *Plecotus auritus* L. from ?Bed 5 (M.33561a), in outer, inner, and occlusal views.

The presence of *S. savini* is important as it has always been regarded as a 'Cromerian' *sensu lato* element of mammalian faunas. Koenigswald (1973*a*) regards it as a key fossil, the significance of which is discussed at the end of this paper.

Order CHIROPTERA Blumenbach 1779
Family VESPERTILIONIDAE Gray 1821
Plecotus auritus Linnaeus 1758

Text-fig. 18

1912 *Plecotus auritus* L.; Miller, pp. 256–262, text-fig. 45. (Diagnosis and synonomy of living sp.)
1972 *Plecotus auritus* L.; Rabeder, pp. 433–438. (Review of living and fossil sp.)

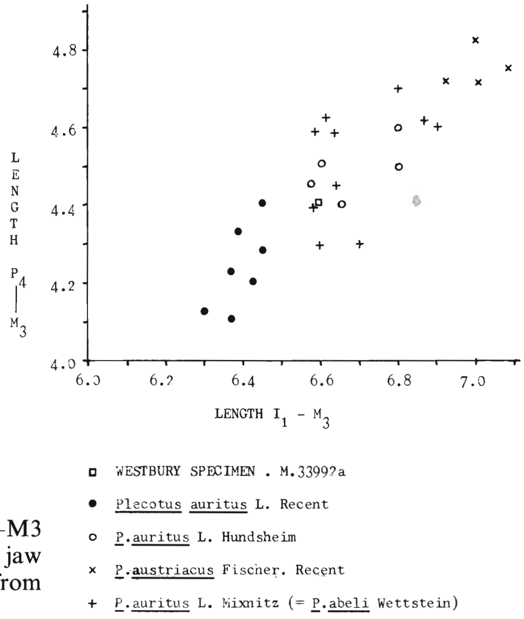
Material. Eight fragmentary mandibles, 3 from Bed 4 (M.33992a–c), and 5 from ?Bed 5 (M.35561a–e), and 1 fragment of maxilla with M1 and M2 (M.33993) from Bed 8.

Description. The mandible has the dental formula I3, C1, P3, M3, and the coronoid process is pointed. Lower P3 is oval in occlusal view, with its long axis perpendicular to the tooth row, and is about half the size of P2. P2 is subtriangular in occlusal view, and is about half the size of P4, which is quadrangular (text-fig. 18). All the premolars bear a well-developed cingulum. The lower molars are of the typical insectivore pattern, the only diagnostic feature being M3 where the posterior triangle is much narrower than the anterior. In the maxilla the posterior border of the antorbital foramen lies over the anterior of M1.

Most of the specimens recovered were too fragmentary to provide useful measurements, except M.33992a (text-fig. 18), in which the length of the tooth row could be estimated for inclusion in text-fig. 19.

Discussion. These chiropteran remains can be attributed to *Plecotus* by the dental formula, the morphology of the premolar teeth, and the position of the antorbital foramen. Text-fig. 19 shows that the Westbury species falls within the fossil *P. auritus* group.

P. auritus is recorded from many Pleistocene sites, and judging from the living species might be expected at this site, since *P. auritus* has a preference for hibernating in caves. Of possible further significance is that this species normally inhabits woodland areas.



TEXT-FIG. 19. Graph of the tooth row length I3–M3 plotted against P4–M1 (in mm) in the lower jaw of *Plecotus* (comparative measurements from Rabeder 1972).

Myotis cf. *emarginatus* Geoffroy 1806

Text-fig. 20*a*

1970 *Myotis nattereri* Kuhl; Heal, p. 136.

Material. One fragmentary mandible (M.33994) from Bed 5(?).

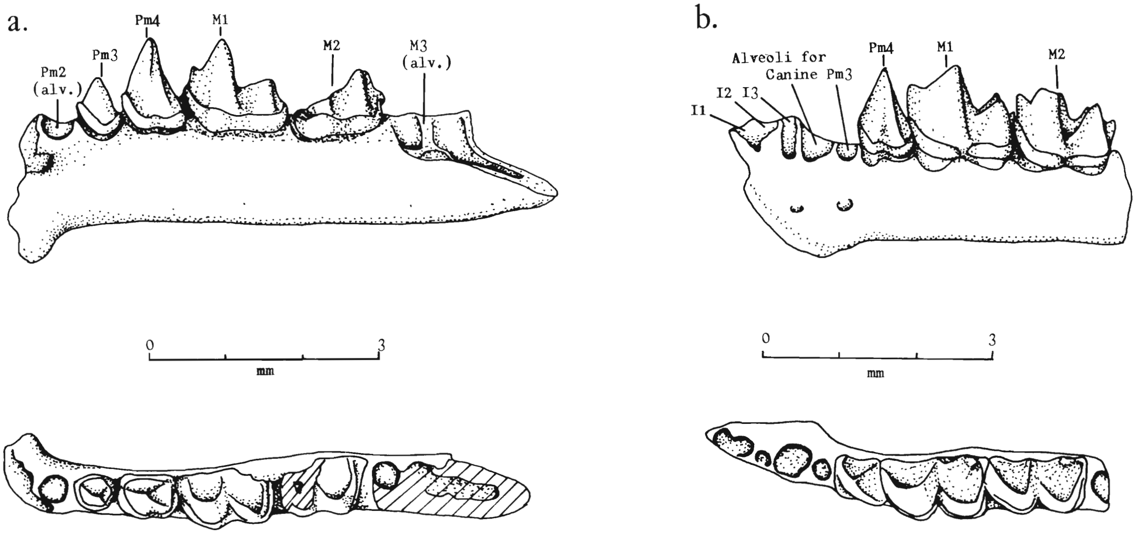
Description. Only P3, P4, M1, and M2 are preserved in the mandible (text-fig. 20*a*), but the P2 and the canine alveoli are present, and show that the premolar teeth are in a straight line and not crowded together. The crown tip of P4 rises just above the highest cusp of M1, and P4 is quadrangular, about twice the size of the round P3, and has a strong cingulum developing into a distinct antero-internal cusp.

TABLE 6. Comparative measurements (in mm) of the tooth row lengths C–M_3 and M_1–M_3 in *Myotis*.

	L. C–M_3	L. M_1–M_3
Westbury M.33994	6·3(e)	3·8(e)
M. emarginatus. Hundsheim (Rabeder 1972)	6·4	3·6, 3·8
M. emarginatus. Recent (Rabeder 1972)	6·7–6·9	3·8–4·1
M. nattereri. Stránská Skála (Kowalski 1972)	6·3–6·8	3·9–4·1
M. daubentoni. Stránská Skála (Kowalski 1972)	5·6, 5·8	3·5

Discussion. This chiropteran mandible can be diagnosed on the uncrowded straight premolar tooth row and the small round P3 which indicate *Myotis*. Of the many species of *Myotis* this mandible is closest in size to *M. emarginatus*, with *M. nattereri* and *M. daubentoni* the next nearest in size. The latter two species, however, have a more crowded premolar tooth row, and the P4 in *M. nattereri* has a lower cingulum and less pronounced antero-internal cusp.

M. emarginatus has not been recorded from the British Pleistocene before, so it is to be hoped that future finds can add weight to this record. The living species lives near trees and hibernates in caves.



TEXT-FIG. 20. (*a*) Left mandibular ramus of *Myotis* cf. *emarginatus* Geoffroy from ?Bed 5 (M.33994), in outer and occlusal views. (*b*) Left mandibular ramus of *Barbastella barbastellus* Schreber from ?Bed 5 (M.33995c), in outer and occlusal views.

Barbastella barbastellus Schreber 1774

Text-fig. 20*b*

1912 *Barbastella barbastellus* Schreber; Miller, pp. 263–268, text-fig. 46. (Diagnosis and synonomy of living sp.)
1972 *Barbastella barbastellus* Schreber; Rabeder, pp. 438–447. (Review of recent and fossil sp.)

Material. Three fragmentary mandibles (M.33995a, b, c) from Bed 3, Bed 4, and Bed 5(?).

Description. The mandible has the dental formula I3, C1, P2, M3. The first premolar is tightly packed between the canine and second premolar. The second premolar (P4 in text-fig. 20*b*) is of rhomboidal shape in occlusal view, with a strong cingulum and an antero-internal cusp. The tip of its cusp is nearly as high as the highest cusp of M1.

TABLE 7. Comparative measurements (in mm) of the tooth row lengths C–M_3 and M_1–M_3 in *Barbastella barbastellus* Schreber.

	L. C–M_3	L. M_1–M_3
Westbury M.33995a	5·3(e)	3·7(e)
Westbury M.33995b	—	3·9(e)
Westbury M.33995c	5·2(e)	—
B. barbastellus. Recent (Rabeder 1972)	5·0–6·1	3·5–3·7
B. barbastellus. Hundsheim (Rabeder 1972)	5·0–5·4	3·5–3·8

Discussion. The dental formula, the morphology of P4, and the size of these Chiroptera remains, closely compare with living and fossil representatives of *B. barbastellus*. The barbastelle has been recorded from many Middle and Upper Pleistocene sites in Europe, and like the other species of bats at Westbury has a preference for living in wooded regions, and hibernates in caves.

Order CARNIVORA Bowdich 1821

Family URSIDAE Gray 1825

Ursus deningeri Reichenau 1906

Plates 3, 4, figs. 1–6

1846 *Ursus spelaeus* Rosenmüller and Heinroth (*partim*); Owen, pp. 85, 89, 90, 107 (text-fig. 35*c*.)
1882 *Ursus* sp.; Newton, pp. 14, 15, pl. II, figs. 6–8.
1882 *Ursus spelaeus* Rosenmüller and Heinroth; Newton, pp. 6–15, pl. I, figs. 1–4; p. II, figs. 1–5.
1882 *Ursus ferox-fossilis*? Busk; Newton, pp. 12–15, pl. I, figs. 5, 5*a*.
1906 *Ursus deningeri* Reichenau, pp. 208–243, 246, 251–260, pl. I, fig. 1; pl. II; pl. III, fig. 1; pl. IV, figs. 1, 2; pl. V, figs. 1, 4; pl. VI, fig. 1; pl. VII, figs. 1–3; pl. VIII, figs. 1–3; pl. IX, figs. 1, 2, 5, 6, 9, 10, 14; pl. XII, fig. 2; pl. XIV, figs. 3, 4.
1906 *Ursus spelaeus* Rosenmüller and Heinroth; Reynolds, p. 7, pl. VI, figs. 6*a*, 6*c*.
1922 *Ursus savini* Andrews, pp. 204–207.
1926 *Ursus sussenbornensis* Soergel, pp. 115–156, pls. III–VI.
1938 *Ursus etruscus gombaszoegensis* Kretzoi, pp. 138–141, 146, pl. III, figs. 7–26.
1958 *Ursus arctos deningeri* Kurtén, pp. 72–75.
1959 *Ursus arctos deningeri* Kurtén, pp. 73–99, pls. LXII–LXIV.
1968 *Ursus deningeri* Reichenau; Schütt, pp. 5–120, pls. 1–6. (Review of species.)
1969*b* *Ursus deningeri* Reichenau; Kurtén, pp. 735–745, text-figs. 1, 4, 5, 6.
1970 *Ursus arctos* L.; Heal, p. 136.
1970 *Ursus spelaeus* Rosenmüller and Heinroth; Heal, p. 136.

Material. Three substantial facial portions of skulls bearing dentitions, two from Bed 3 (M.33552, M.33553) and one from Bed 4 (M.33530). Numerous fragmentary mandibles, over 1000 isolated teeth, and over 1000 postcranial bones, with stratified finds from all layers except Bed 1 (Table 44)

Description

Skull and mandible. The large crushing type cheek teeth, without well-developed cutting edges, the anteriorly placed carnassials, and dental furmula I$\frac{3-3}{3-3}$, C$\frac{1-1}{1-1}$, PM$\frac{4-4}{4-4}$, M$\frac{2-2}{3-3}$, are diagnostic of *Ursus*. In the skulls the profile of the forehead is of specific importance. In M.33552 the lateral profile of the forehead is angular, the approximate angle of the top of the nasal to the anterior of the frontal being about 130°, though in M.33530 this angle is probably less acute (the frontal is detached in this specimen, and a reconstruction is only approximate). In both specimens the width across the canines is slightly less than the depth of the skull in front of the orbit. Measurements of the fragmentary skulls are given in Table 8 and of the mandibles in Table 9.

Upper and lower incisors. The incisors do not appear to show any special morphological characters useful in determining the species, though are large and close to *U. spelaeus* in size.

Upper and lower canines. The canines also show no special differences from other bear species, except in size, which is again large. The canines are, however, useful in another respect, in that the width measured at the crown base and plotted on a histogram (text-fig. 21), shows the male-female difference as two size distributions.

Upper and lower premolars. The large fourth premolar is always present in both upper and lower dentitions, but the small single-cusped premolars 1 to 3 are shed to different degrees in bears, and their presence or absence has been used by many authors in differentiating between species. In the portions of skulls an alveolus for P3 is present in all three, while in 32 mandibles, 4 showed evidence of P3, 2 of P2, 1 of P1, and 26 showed no evidence of any premolars before P4 (Table 16). The upper P4 is of the typical *Ursus* form with three main cusps, and in the Westbury specimens the inner cusp is well developed, and an antero-internal cingulum runs from the base of this cusp in the main anterior cusp. The lower P4 is a single-cusped tooth, but bears a varying number of small accessory tubercles on the posterior and inner side of the crown.

Upper M1. The upper M1 is about rectangular in occlusal view, the outer and inner sides are bi-convex, and the posterior width is equal to or greater than the anterior width in 79% of the sample. The inner side of the crown bears a well-developed cingulum, and the cusps are in general rather brachydont compared with *U. arctos*. Of the two large outer cusps, the posterior is predominantly slightly higher than the anterior.

Upper M2. The anterior outer side of this tooth bears two main cusps, the largest being at the anterior corner of the tooth, and a third smaller cusp lies behind the second main cusp. The posterior portion of this tooth is very variable in morphology (Pl. 4), though on average tapers backwards and inwards and is fairly well tuberculated.

Lower M1. In occlusal view this tooth is elongated, and bears a relatively wide posterior heel which is separated from the anterior portion by a marked constriction. On the inner side of the posterior part of the heel is a large cusp (endoconid) usually with a small cusp developed on its anterior side.

Lower M2. In occlusal view this tooth has a well-marked median constriction, and the posterior portion is wider than the anterior in 90% of the sample. The tooth is rather narrower and more brachydont than specimens of *U. arctos* of the same length.

Lower M3. As in the heel of the upper M2, this tooth is very variable in morphology (Pl. 4), though on average has parallel sides and is tapered posteriorly, often with a slight posterior constriction forming a small talon, the whole surface well tuberculated. The tooth is very brachydont, with just a small antero-internal cusp.

Milk dentition. Of the deciduous dentition the milk canines were by far the most abundant (over 150 were found), but only a very small number of milk incisors and molars have been recovered. Their presence is of significance in indicating the presence of juveniles, but they are not of diagnostic value.

Ageing and pathology. The permanent teeth recovered represent individuals of all ages, from juveniles represented by open rooted germs, to senile animals represented by teeth almost worn to the roots. Unfortunately the author has not been able to study a large enough stratified sample to conduct an age analysis, though the unstratified and stratified material together shows the total sample to comprise about 50% adults and 50% juveniles. An unusual feature of many of the canines, not associated with wear patterns, is erosion around the base of the crown. The degree of erosion is variable, but is greatest around the outer side of the crown base, and in advanced cases of erosion the crown base is 'pinched' by the erosion to such a degree that some specimens have completely lost the tooth crown. While not uncommon in the canines, erosion of the crown base was rarely seen in other teeth, and where present was less severe and confined to the anterior dentition (incisors, P4 and M1).

TABLE 8. Measurements (in mm) of Westbury bear skulls compared with *Ursus deningeri*, *U. spelaeus*, and *U. arctos*

Skull (cm)	Length P4–M2	Palate width across M2	Snout width across canines	Length behind M2 to front of canine	Height at orbits	Diastema P4–C
Westbury M.33530 Bed 4 ♀	81	91	79(e)	140	—	39
Westbury M.33552 Bed 3 ♂	—	105(e)	105(e)	156	125	—
Westbury M.34128 (W. 3) ♂	91·5	96	87(e)	—	—	42
U. deningeri. Scharzfeld (Schütt 1968)	71–90	—	85–94	—	—	35–50
	81					*43*
U. deningeri. Mosbach (Schütt 1968)	73·5–101	98–110	79–112	—	132–142	38·5–56
	84		*92*			*50*
U. deningeri. Hundsheim (Schütt 1968)	77, 81	—	87, 90·5	—	131	28–39·5
U. deningeri. Bacton M.17918	—	98	—	152	—	39(e)
U. deningeri. Petralona (Kurtén 1977)	78(e)	95(e)	83(e)	—	—	—
U. spelaeus. Goffontaine (Cordy 1972)	78–101	96–130		168–198	131–159	38–50
	90·9	*112·8*	—	*183*	*147·5*	*44·7*
U. spelaeus. Swanscombe (Kurtén 1959)	87(e)	103	107	174(e)	162	51(e)
U. spelaeus. Mixnitz (Schütt 1968)	87–104	—	99–128	—	—	35–68
	95		*113*			*48*
U. arctos. Mixnitz (Schütt 1968)	62–78	—	66–84	—	—	21–35

TABLE 9. Measurements (in mm) of Westbury bear mandibles compared with *Ursus deningeri*, *U. spelaeus*, and *U. arctos*.

Mandibles (cm)	Total length Canine-Condyle	Diastema P4–C	Length M1–M3	Height before P4	Height between M2 and M3	Height of coronoid process
Westbury M.33531–33551						
O.R.	240–320	36–67	68.5–91	47·4–64	49–80	114, 124
n	7	24	25	24	26	2
Mean	280·7±9·03	51·5±2·16	78·4±1·14	52·3±1·14	61·6±1·64	
Standard deviation	23·89	7·47	5·70	5·57	8·35	
U. deningeri. Scharzfeld (Schütt 1968)	260–320	38–63	72–86	48–68	50–82	121–148
	280 (*n* = 10)	*50* (*n* = 24)	*81* (*n* = 16)	*56* (*n* = 26)	*61* (*n* = 24)	*133* (*n* = 3)
U. deningeri. Mosbach (Schütt 1968)	254–316	30–67	72–96	50–71	52–77	110–172
	285 (*n* = 18)	*52* (*n* = 30)	*79* (*n* = 33)	*57* (*n* = 37)	*62* (*n* = 33)	*134* (*n* = 12)
U. deningeri. Hundsheim (Schütt 1968)	288, 309	50, 47	78, 89	60, 64	70, 72	149, 179
U. spelaeus. Mixnitz (Schütt 1968)	276–353	54–67	75–96	62–82	56–85	135–204
U. arctos. Mixnitz (Schütt 1968)	205–254	30–44	61–72	39–51	37–54	103–142

TABLE 10. Measurements (in mm) of the Westbury bear cheek teeth compared with *Ursus deningeri*, *U. spelaeus*, and *U. arctos*. (mm)

	Upper M2		Upper M1			Upper P4	
	Length	Breadth	Length	Ant. breadth	Post. breadth	Length	Breadth
Westbury	33·6–51·0	18·9–25·0	23·8–32·3	14·9–21·7	16·0–22·0	16·4–21·7	11·1–15·9
(*n* = 56, 52, 51)	*42·40*	*21·25*	*26·22*	*18·54*	*18·93*	*19·00*	*13·39*
U. deningeri. Scharzfeld	34·9–49·0	18·0–24·3	22·3–30·1	15·3–22·1	16·0–22·1	16·0–22·2	11·0–17·5
(*n* = 86, 102, 78)	*42·8*	*21·6*	*26·7*	*18·7*	*19·1*	*18·8*	*13·9*
U. deningeri. Mosbach	36·7–49·4	18·4–24·0	22·6–29·8	15·5–21·0	16·0–21·8	16·0–21·0	10·9–15·3
(*n* = 39, 34, 28)	*40·9*	*20·8*	*25·4*	*17·9*	*18·2*	*18·8*	*12·9*
U. deningeri. Hundsheim	34·0–45·0	18·5–22·1	24·0–29·0	16·0–20·5	16·8–21·0	16·5–21·0	11·0–14·0
(*n* = 6/7, 10, 6)	*39·1*	*20·3*	*25·5*	*17·7*	*18·3*	*18·1*	*12·8*
U. spelaeus	40·3–54·2	—	24·9–32·5	—	—	17·2–23·7	—
(*n* = 105/6, 132/42, 83/7)	*45·1*	*22·6*	*28·9*	*19·7*	*19·6*	*20·3*	*14·1*
U. arctos	29·5–39·5	—	19·2–25·0	—	—	13·2–18·2	—
(*n* = 80, 76/8, 80)	*34·0*	*17·4*	*21·5*	*15·0*	*16·1*	*15·6*	*11·5*

Westbury B.M.N.H. Nos.
(unstrat. finds lumped)

Unstratified	Stratified
U. P4 M.33564	M.33801–1
M1 M.33565	M.33812–2
M2 M.33566	M.33828–3
L. P4 M.33567	M.33836–4
M1 M.33568	M.33841–4
M2 M.33569	M.33849–6
M3 M.33570	M.33866–9

Comparative figures from Schütt (1968)

	Lower M3		Lower M2			Lower M1		Lower P4	
	Length	Breadth	Length	Ant. breadth	Post. breadth	Length	Breadth	Length	Breadth
Westbury	18·0–29·2	14·9–21·4	23·7–33·1	13·4–19·1	14·6–20·6	23·9–30·5	10·6–15·5	11·9–17·3	7·4–10·6
(*n* = 129, 95, 46, 54)	*24·77*	*18·12*	*28·24*	*16·19*	*17·17*	*27·85*	*13·38*	*15·20*	*8·87*
U. deningeri. Scharzfeld	20·0–31·6	15·5–21·3	24·1–33·3	13·4–20·0	13·8–21·0	25·0–33·4	9·5–13·7	11·9–16·3	8·1–11·4
(*n* = 86, 130, 100, 37)	*25·1*	*18·4*	*28·8*	*17·2*	*17·6*	*28·9*	*11·5*	*14·2*	*9·4*
U. deningeri. Mosbach	19·9–29·6	15·4–20·9	24·6–31·0	14·0–18·4	14·0–20·4	23·5–31·0	11·7–15·0	13·1–17·2	7·9–10·0
(*n* = 34, 36, 26, 21)	*24·0*	*17·9*	*27·2*	*16·1*	*16·8*	*27·0*	*13·1*	*15·0*	*8·9*
U. deningeri. Hundsheim	23·0–25·0	16·4–19·0	26·0–32·0	15·0–18·0	15·5–19·2	27·5, 26·0, 26·5	12·5, 11·5, 13·0	16·0, 15·0	9·4, 8·4
(*n* = 4, 5, 3, 2)									
	24·2	*17·3*	*28·7*	*16·2*	*17·7*				
U. spelaeus	21·3–32·4	—	26·1–35·7	—	—	26·5–34·4	—	12·3–18·3	—
(*n* = 167/92, 219/245, 206, 153)	*27·3*	*19·1*	*30·4*	*17·7*	*18·4*	*30·3*	*14·6*	*15·5*	*10·4*
U. arctos	15·4–22·5	—	20·0–27·3	—	—	19·6–26·3	—	10·3–15·1	—
(*n* = 35/70, 69/73, 86, 85)	*19·3*	*14·6*	*23·6*	*14·1*	14·9	23·0	11·3	12·6	7·1

EXPLANATION OF PLATE 3

Palate of female *Ursus deningeri* (M.33530) from Bed 4. × 1. Alveoli for P3 can just be discerned immediately in front of P4 on either side.

TABLE 11. Measurements (in mm) of the cheek teeth of the Westbury *Ursus deningeri*, with standard deviations.

	Length				Breadth			
	n	O.R.	Mean	S.D.	*n*	O.R.	Mean	S.D.
P^4	51	16·4–21·7	19·00±0·17	1·18	50	11·1–15·9	13·39±0·13	0·92
M^1	52	23·8–32·3	26·22±0·21	1·50	a 50	14·9–21·7	18·54±0·18	1·29
					p 52	16·0–22·0	18·93±0·18	1·28
M^2	56	33·6–51·0	42·40±0·53	3·95	56	18·9–25·0	21·25±0·21	1·58
P_4	54	11·9–17·3	15·20±0·15	1·12	54	7·4–10·6	8·87±0·10	0·77
M_1	46	23·9–30·5	27·85±0·22	1·52	46	10·6–15·5	13·38±0·15	1·05
M_2	95	23·7–33·1	28·24±0·20	1·92	a 93	13·4–19·1	16·19±0·11	1·03
					p 94	14·6–20·6	17·17±0·13	1·25
M_3	129	18·0–29·2	24·77±0·21	2·35	129	14·9–21·4	18·12±0·12	1·41

TABLE 12. Numbers of bones of *Ursus* found to 1974 as stratified/unstratified finds

43/37	Vertebrae	83/91	Metepodials
3/5	Scapulae	86/98	Phalanges
5/17	Inomenates	4/9	Scapho-lunars
7/18	Humeri	12/18	Calcanea
10/6	Radii	4/22	Astragali
7/9	Ulnae	13/11	Patellae
13/10	Femora	33/32	Small bones of hand and foot
10/9	Tibiae	(25/47	Fragmentary mandibles)
6/2	Fibulae	(13/24	Skull fragments)

TABLE 13. Comparative measurements (in mm) of limb bones in *Ursus*.

	Humerus		Radius length	Ulna length	Femur	
	Length	Distal width			length	distal width
Westbury	385	—	320	400	374	83
	304(e)	—	255	—	—	102
	—	117	275	—	—	83
Mean	*344·5*	*117*	*283*	*400*	*374*	*89*
U. deningeri. Scharzfeld (Schütt 1968)	—	99–133	286–332	292–345	375–447	81–107
		111	*305*	*327*	*408*	*91*
U. deningeri. Mosbach (Schütt 1968)	330–370	100–134	316	306–390	340–452	78–110
	350	*113*		*332*	*390*	*90*
U. deningeri. Hundsheim (Schütt 1968)	343–364	103–105	289–290	320	384–409	82–89
	356	*104*	*289*		*393*	*84*
U. spelaeus (Zapfe 1946)	388–456	109–144	317–356	334–414	388–501	85–122
U. arctos (Zapfe 1946)	290–353	83–109	272–306	311–358	341–399	64–84

Postcranial bones. The number of stratified/unstratified postcranial bones recovered are given in Table 12. The majority of the postcranial bones do not exhibit any useful morphological features of diagnostic value, though size alone suggest a bear approaching *U. spelaeus* (Table 13). The proportions of the metapodials have been shown by Kurtén (1959) to be of diagnostic value, and measurements of the Westbury material is given in Tables 14 and 15.

TABLE 14. Measurements (in mm) of metacarpals and metatarsals of *Ursus* from Westbury, with standard deviations.

		Length			Mid-shaft width			Distal width		
	n	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.
MC I	4	55·6–65·0	60·75±1·20	3·99	10·7–13·7	12·1±0·66	1·32	16·2–19·8	18·7±0·83	1·66
MC II	6	65·4–85·9	74·3±2·79	6·82	14·0–17·2	15·0±0·49	1·21	21·3–25·7	22·8±0·65	1·58
MC III	6	71·7–85·0	77·3±2·82	6·9	12·8–18·4	15·3±0·89	2·19	20·1–27·1	23·7±0·98	2·41
MC IV	4	74·5–83·0	79·4±2·15	4·29	16·1–17·9	16·9±0·47	0·93	21·8–29·7	25·5±2·02	4·05
MC V	8	58·7–89·7	76·8±3·10	8·76	13·1–18·5	17·0±0·62	1·74	18·3–28·6	25·7±1·13	3·19
MT I	6	51·1–59·8	57·4±1·36	1·36	10·7–13·9	11·8±0·52	1·27	15·4–18·0	16·7±0·46	1·12
MT II	6	55·6–71·5	64·9±2·64	6·46	10·4–13·2	12·2±0·55	1·35	15·3–20·3	18·4±0·74	1·81
MT III	11	62·5–83·5	73·7±2·16	7·18	11·6–18·5	14·8±0·55	1·82	18·6–24·6	21·3±0·64	2·15
MT IV	8	78·0–98·8	85·0±2·86	8·08	13·0–17·2	14·8±0·46	1·30	18·8–25·6	22·0±0·93	2·45
MT V	5	85·0–92·1	87·5±1·79	3·99	12·5–17·0	14·9±0·75	1·69	21·2–18·0	23·8±1·32	2·95

TABLE 15. Index of the distal width of *Ursus* metacarpals amd metatarsals × 100 divided by their length. Figures from Kurtén (1959) and Schütt (1968).

	Westbury	*U. deningeri*			*U. spelaeus*	*U. arctos*
		Scharzfeld	Mosbach	Hundsheim	M.C. Odessa M.T. Salzofen	Grays
MC I	31	30	29	28	30	30
MC II	31	31	29	29	32	28
MC III	31	30	29	30	31	26
MC IV	32	31	33	30	—	—
MC V	33	34	33	33	28·4	29
MT I	29	31	28	30	—	—
MT II	28	30	28	29	30	28
MT III	29	27	26	25	29	25
MT IV	26	28	27	26	26	24
MT V	27	29	27	27	29	24

Discussion. Of the Pleistocene bears *U. etruscus* Cuvier, *U. deningeri* Reichenau, *U. spelaeus* Rosenmüller and Heinroth, and *U. arctos* L., with which the Westbury material can be compared, *U. etruscus* can be excluded by its much smaller size and its relatively large carnassial teeth. According to Kurtén (1969*a*) *U. etruscus* is the common ancestor to *U. arctos* and *U. spelaeus*, while *U. deningeri* appears to be an intermediate between *U. etruscus* and *U. spelaeus*, in a continuous evolving lineage of *U. etruscus-deningeri-spelaeus* spanning the Lower and Middle Pleistocene. Distinction of Upper

Pleistocene *U. spelaeus* and *U. arctos* is relatively easy especially because of the large size difference, but the distinction between *U. deningeri* and *U. spelaeus* must be made on an appraisal of various morphological features and measurements in order to be able to discriminate within a continuous range of populations.

The most notable features in the *U. deningeri–U. spelaeus* line are the gradual increase in size and the increase in heaviness of build as the *U. spelaeus* condition is reached. The problem in studying small numbers of remains is the great morphological and size variability within *Ursus* populations, but fortunately sites such as Westbury, Mosbach, Scharzfeld, Hundsheim, and many *U. spelaeus* localities in Europe have yielded large numbers of remains where the chances of preservation were high (N.B. within caves). In these cases comparisons can be very successfully made on a statistical basis, which without doubt allows the differentiation of *U. deningeri* and *U. spelaeus*. Apart from size differences shown in the accompanying tables and text-figures discussed later, the following features summarize the principal differences between *U. deningeri* and *U. spelaeus* (mainly based on Schütt 1968):

1. The skull of *U. spelaeus* has a strongly domed brow, which is less pronounced than *U. deningeri*.
2. The upper and lower P4 of *U. deningeri* tend to lack the small accessory cusps seen in *U. spelaeus*. Traces of premolars 1, 2, and 3 are very uncommon in the upper and lower jaws of *U. spelaeus*, but at least one of these premolars is more often present in *U. deningeri*.
3. In the upper M1 of *U. spelaeus* the paracone is generally higher than the metacone, while in *U. deningeri* they are generally about equal or the paracone is lower.
4. In the lower M1 of *U. deningeri* the endoconid region comprises three cusps descending in size from the posterior, while in *U. spelaeus* this region generally comprises two cusps of about equal size.
5. In the upper M2 and lower M3 of *U. spelaeus* the talon area is commonly highly developed, bearing a mass of small tubercles. In *U. deningeri* this condition tends to be less marked, and is often undeveloped such that these teeth bear a closer resemblance to *U. arctos*.
6. In the forelimb of *U. deningeri* metacarpal V is relatively larger than the rest of the metacarpals, but in *U. spelaeus* it is relatively smaller, the functional significance of which is reflected in differences in size of articular facets in the carpus (details in Schütt 1968). The metapodials as a whole are more stout in *U. spelaeus*.
7. In the hindlimb *U. spelaeus* exhibits a greater relative shortening of the tibia (compared against the femur) than in *U. deningeri*, and in *U. spelaeus* tibia torsion is greater (40–60° as opposed to 35–50° in *U. deningeri*).

The relatively domed forehead seen in the Westbury skull specimens is typical of *U. deningeri*, and approaches the condition in *U. spelaeus*. The few measurements available for the skulls (Table 8) are within the range of both *U. deningeri* and *U. spelaeus*, but average around the *U. deningeri* mean for Mosbach specimens. Measurements of the mandibles (Table 9) are also most closely comparable with *U. deningeri*. Within the diastema between the canine and fourth premolar, *U. arctos* nearly always bears two small premolars in the upper jaw and at least one in the lower jaw, *U. spelaeus* rarely retains any (Reynolds 1906; Koby 1952; Kurtén 1959), while in *U. deningeri* small premolars are usually absent in the lower jaw, but at least one in the lower jaw, *U. spelaeus* rarely retains any (Reynolds 1906; Koby 1952; Kurtén 1959), while in *U. deinigeri* small premolars are usually absent in the lower jaw, but at least one is common in the upper jaw (Andrews 1922; Kurtén 1958; Koby 1952; Schütt 1968; Laville, Prat and Thibault 1972).

As Schütt (1968) has observed, and as may be seen from Table 16, the presence of the anterior premolars is not a very reliable specific character. Without therefore placing too much weight on this character, it may be said that the moderately frequent incidence of anterior premolars in the Westbury sample adds weight to these remains belonging to *U. deningeri*.

The morphology and size of the cheek teeth offer the most useful diagnostic characters in identifying these remains. The features of most value, and measurements from Tables 10 and 11 are summed up as follows:

Upper P4—the consistently well-developed inner cusp and the absence of small accessory cusps contrasts with *U. spelaeus*, while the well developed antero-internal cingulum is a spelaeoid character.

TABLE 16. Incidence of first, second and third upper and lower premolars in *Ursus*.

Premolars 1-3	*U. deningeri* (Scharzfeld)	*U. deningeri* (Mosbach)	Westbury	*U. spelaeus*	*U. arctos*
U. None	89%	16%	—	Norm	Rare
P1	—	21%	—	Rare	Present
P2	—	5%	—	Rare	Occasional
P3	11%	79%	100%*	Occasional	Present
L. None	84½%	95½%	80%	Norm	Rare
P1	3%	—	3½%	Occasional	Present
P2	5½%	—	6½%	Occasional	Occasional
P3	7%	4%	13½%	Occasional	Occasional

* N.B. Based on three specimens only.

The size of this tooth is in range and mean value very close to *U. deningeri* from Mosbach and Scharzfeld (Table 10).

Upper M1—the relative brachydonty of this tooth, the well-developed inner cingulum, and the angular outline of the tooth, contrast with *U. arctos*, and are typical spelaeoid characters. The most important distinguishing feature is the relative breadth of the anterior and posterior lobe, which clearly separate these remains from both *U. spelaeus* and *U. arctos* (Table 17).

TABLE 17. Percentage occurrence in upper M1 of *Ursus* of the posterior width equal to, or greater than, the anterior width.

		N
U. arctos (Recent)	99%	78
U. arctos (U. Pleistocene)	94%	73
U. deningeri (Hundsheim)	80%	10
Westbury	79%	48
U. deningeri (Scharzfeld)	78%	101
U. deningeri (Mosbach)	71%	34
U. spelaeus (U. Pleistocene)	48%	162

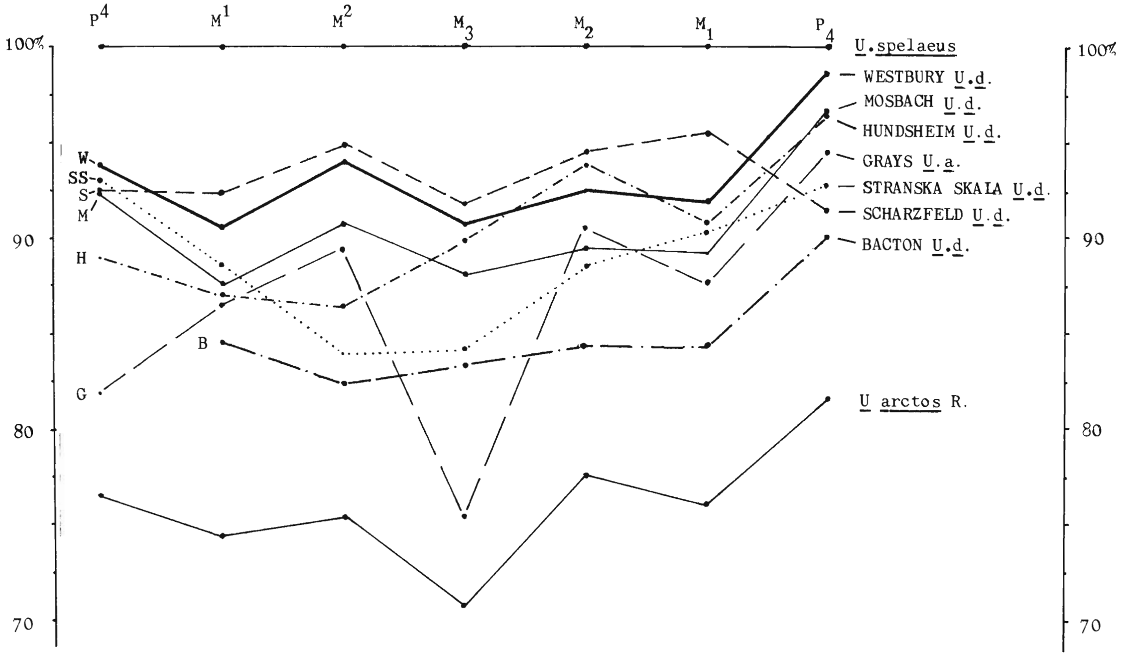
The dimensions of this tooth are again very close to, though slightly larger than, *U. deningeri* from Mosbach and Scharzfeld (Table 10).

Upper M2—the relative brachydonty of this tooth and the differentiation in height of the three anterior outer cusps are typical spelaeoid characters. The talon ranges in morphology between *U. arctos* and *U. spelaeus* (Pl. 4, figs. 1–3), but is on average of intermediate form. In size this tooth is close to *U. deningeri* from Scharzfeld, and with the latter lies between *U. spelaeus* and the Mosbach bear in size (Table 10).

Lower P4—this tooth approaches the spelaeoid condition in bearing small accessory tubercles next to the main cusp. The dimensions of this tooth are close to *U. deningeri* from Mosbach, but at the same time only slightly smaller than *U. spelaeus* (Table 10).

Lower M1—the morphology of the endoconid cusps contrasts with *U. spelaeus* where the endoconid comprises two cusps of about equal size. In size this tooth most clearly compares with *U. deningeri* from Mosbach (Table 10).

Lower M2—the relative brachydonty, narrowness, and marked median construction contrast with



TEXT-FIG. 21. Ratio diagram showing the relative mean lengths of the cheek teeth in *Ursus deningeri* and *U. arctos* against *U. spelaeus* (100%). Comparative measurements from Kurtén (1959, 1977), Musil (1972*b*), and Schütt (1968).

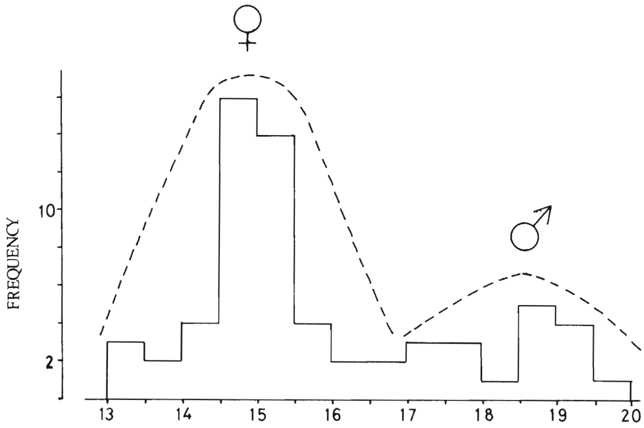
U. arctos, and are spelaeoid characters. In size this tooth is closest to *U. deningeri* from Scharzfeld (Table 10).

Lower M3—this tooth ranges in morphology between *U. arctos* and *U. spelaeus*, but is on average of an intermediate form, though tending towards the spelaeoid condition. In size this tooth is very close to *U. deningeri* from Scharzfeld (Table 10). The increase in size and tuberculation in this tooth is matched in the talon of upper M2 with which it occludes. Ehrenberg (1962) interprets this as an adaptation to cope with an increased herbivorous diet, reaching a maximum in Upper Pleistocene cave bears which have very large heavily tuberculated lower M3s and upper M2s. A graph plotting mean lengths of upper M2 against lower M3 (text-fig. 21) domonstrates the relationships of bears from various Pleistocene sites with regard to the marked size increase in these two teeth. The Westbury material falls within the *U. deningeri deningeri* group comprising the bears from Mosbach, Scharzfeld, and Petrolona B.

Metapodials—Kurtén (1959) has shown that the metapodials of the lineage *U. etruscus-deningeri-spelaeus* are relatively shorter and more robust than in *U. arctos*. Tables 14 and 15 show that the Westbury material is very close in dimensions to *U. deningeri* from Scharzfeld. Like the Scharzfeld bear, the larger metapodials representing the male bears overlap with the smaller *U. spelaeus* measurements which represent females.

Limb bones—complete limb bones are rare at most sites, so comparative measurements (Table 13) are based on very small samples, and sexual dimorphism can bias such figures where only males or only females are represented (e.g. the complete Westbury ulna, which is probably from a large male). The figures from the Westbury material nevertheless, approximate most closely to mean measurements for *U. deningeri*.

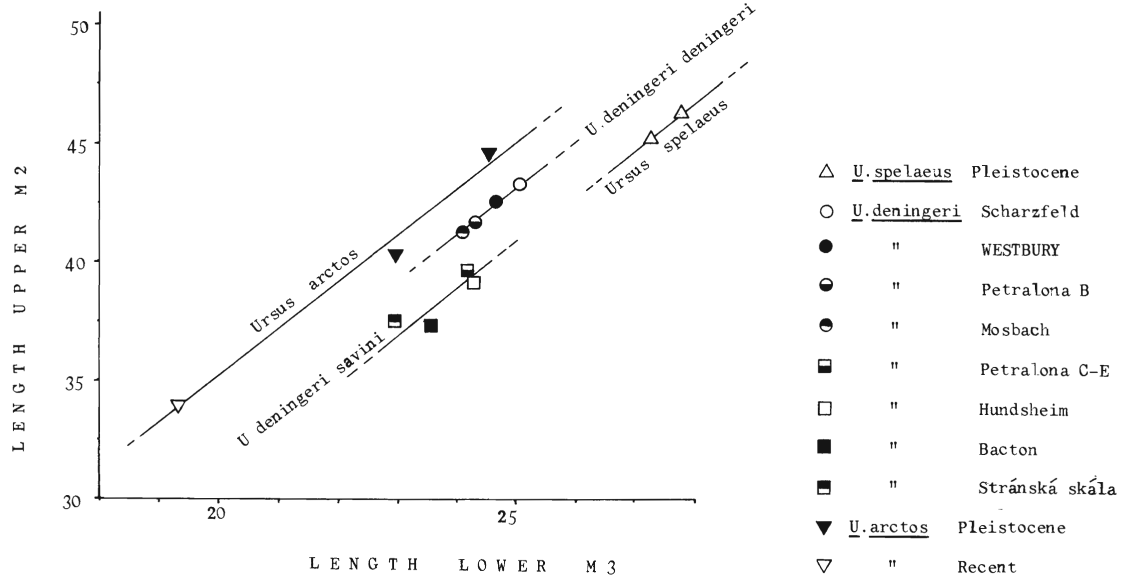
Stratified material—about 20% of the total bear sample is represented by stratified finds from all horizons except Bed 1, and Beds 3, 4, and 5 yielded the most numerous finds. The statistics and descriptions have, however, treated the sample as a whole, since, as the author will develop elsewhere in this paper, he believes that the fossil remains contained therein represent individuals that lived within a single temperate period. On analysis of the stratified sample alone, no significant differences were evident between samples from different horizons, while measurements of mixed stratified and unstratified material exhibit normal distributions (or show a bimodal male-female distribution in those elements showing sexual dimorphism) indicating a single, near contemporaneous, population.



TEXT-FIG. 22. Histogram of the width (in mm) of lower canines of *Ursus* from Westbury, showing a large female and small male distribution.

Summary

Text-fig. 23 shows the comparative mean values for the length of each of the cheek teeth in the Westbury bear and other samples, compared with a large sample of *U. spelaeus* described by Rode (1935) (measurements given in Schütt 1968) which is used as the 100% standard of comparison. This diagram sums up much of what has been said in discussing comparisons with other species. First, the Westbury bear can clearly be distinguished from *U. arctos* and *U. spelaeus*, and secondly can be closely compared with *U. deningeri* from both Mosbach and Scharzfeld, but contrasts somewhat with *U. deningeri* from Bacton and Hundsheim. The bears from Bacton and Hundsheim are referred by Kurtén (1969*b*) to the subspecies *U. deningeri savini*, while the Mosbach bear is referred to *U. deningeri deningeri*. The Westbury *U. deningeri* is somewhat advanced over the Mosbach bear in size, though as may be seen from text-fig. 23 it shows an exactly parallel relative difference to *U. spelaeus*, whereas *U. deningeri savini* shows a slightly different trend marked by a conservatism in the length of Upper M2. The Scharzfeld bear, with which the Westbury bear compares very closely, has, however, a relatively short lower P4, a peculiar trait to the Scharzfeld bear alone, but one which Schütt (1968) did not regard as sufficiently important to designate special subspecific status. Like *U. deningeri* from Scharzfeld, the Westbury bear appears to be ecologically like *U. spelaeus*, in that it inhabited a cave as a lair. The complete range of juvenile to senile specimens strongly suggests that Westbury provided an environment suitable for hibernation, in which the remains themselves may be interpreted as predominantly winter mortalities. Of the possible significance here too, is the large representation of females (75% of the populations), which occur in exactly the same proportion at Scharzfeld. The adaptation to the cave environment may be equated with the more severe cold periods of early Middle Pleistocene times onwards, and one would expect the female element of the population to



TEXT-FIG. 23. Graph showing the mean length of lower M3 plotted against mean length of upper M2 in *Ursus*. Measurements in mm.

be first to take up a relatively easily defended habitat offering safety to the young. By Upper Pleistocene times, males constitute the larger percentage of the population at many cave sites (e.g. Mixnitz).

The similarity of the Westbury bear with both the Mosbach and Scharzfeld bear is of significance in correlation. The Mosbach fauna as a whole is very similar to that of Westbury (see concluding part of this paper), and the similarity between the bears suggests they are nearly contemporaneous. The Mosbach main fauna is equated by most authors to a temperate period or interstadial of the Elster glaciation or, put another way, belongs to a temperate phase *following* the Cromerain *sensu stricto*. Unfortunately it is not easy to make useful comparisons with *U. deningeri* from the British 'Cromerian' since, although *U. deningeri* remains are certainly known from several of the Cromer Forest Bed localities, these localities are represented by horizons of different ages to which the remains cannot be attributed (Stuart 1974). The only well-documented fauna is from West Runton (Stuart 1975), from which unfortunately there is no statistically useful bear sample. Figures for *U. deningeri* from Bacton have been included (text-fig. 21) since more material is available from this site

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EXPLANATION OF PLATE 4

Figs. 1–3. Upper right M2's of *Ursus deningeri*, showing the extremes of variation in the morphology of crown shape and cusp pattern. × 1.

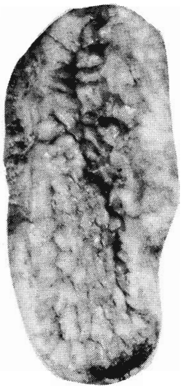
Figs. 4–6. Lower right M3's of *Ursus deningeri*, showing the extremes of variation in the morphology of crown shape and cusp pattern. Slightly > × 1.

Fig. 7. Upper left P3 of *Hyaena brevirostris* Aymard (M.33985) from Bed 1. Inner view. × 1.

Fig. 8. Lower right M1 of *Homotherium latidens* Owen (M.33703). Outer view. × 1.

Fig. 9. Upper left canine of *Homotherium latidens* Owen (M.33983) from Bed 4. Inner view. × 1.

PLATE 4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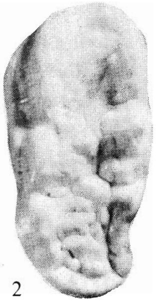
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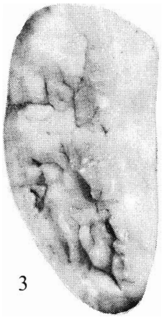
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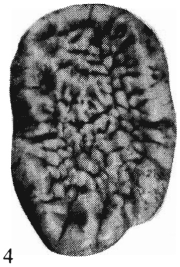
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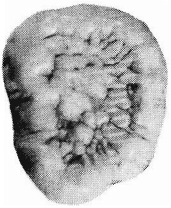
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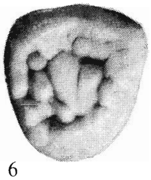
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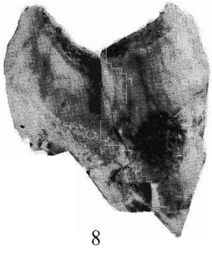
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BISHOP, Pleistocene mammals

than any other Forest Bed locality. The Bacton material probably comes from the Cromerian horizon (Zone IV, West 1980) which is most exposed to erosion, though Pastonian sediments are known to underly the shore level (West 1980), so a mixed assemblage may be represented though, whatever the case, the Westbury bear is a much closer relative to *U. spelaeus* than anything from Bacton.

The morphological and size differences seen between *U. deningeri* and *U. spelaeus* clearly suggest associated behavioural differences, further justifying the differentiation of the two species. *U. deningeri* was probably relatively active, occupying the habitat of its ancestor *U. etruscus.* and what was later to become the habitat of *U. arctos* in Europe. The onset of increasingly severe episodes of cold climate at the beginning of the Middle Pleistocene, and the strong competition from the very numerous carnivore groups must have been very strong selection pressures in the evolution of *U. deningeri–U. spelaeus*. By the Hoxnian/Holsteinian the species *U. spelaeus* can clearly be identified, and was probably rather stationary in habits, largely herbivorous, and relied heavily on caves for hibernation and rearing its young. *U. arctos* entered Europe at the same time and with the cave bear ranges through the remaining period of the Pleistocene, probably infilling to some extent the niche formerly occupied by *U. deningeri.*

In conclusion, the Westbury bear can be closely compared with the subspecies *U. deningeri deningeri* from Mosbach and Scharzfeld, and probably belongs to a population living in a temperate stage immediately antedating the Hoxnian/Holsteinian, when *U. spelaeus* appears.

Family HYAENIDAE Gray 1869
Hyaena brevirostris Aymard 1846

Plate 4, fig. 7

1972 *Hyaena brevirostris* Aymard; Kurtén pp. 113–117, text-figs. 1–4. (Synonomy.)
1974 *Hyaena brevirostris* Aymard; Schütt, pp. 75–80, pls. 4, 5. (Review and diagnosis.)

Material. One upper P3 from Bed 1 (M.33985).

Description. This tooth is of the typical robust, high-crowned, hyaenid type. In lateral view the crown is of isosceles-triangle-shape except that its posterior bears a rudimentary cusp arising from the cingulum about half-way up the crown (Pl. 4, fig. 7). From the structure on the inner side, the cingulum descends, and runs around the inner base of the crown, rising again at the antero-internal corner of the tooth into a triangular structure, from the top of which a ridge runs to the crown tip. The angle formed by the lateral outline of the cusp is about 58°.

TABLE 18. Comparative measurements (in mm) of the length and breadth of the upper P3 in *Hyaena*.

	Length	Breadth
Westbury *P3* M.33985	27(e)	17·5(e)
H. brevirostris (Kurtén and Poulianos 1977)	25·5–28·0	17·4–20·0
	26·9	*18·7*
H. brevirostris Val d'Arno (Kurtén 1956)	25·9–43·8	—
	27·5	
H. perrieri (Kurtén and Poulianos 1977)	22·3–25·8	13·6–18·1
	23·9	*16·5*
H. perrieri. Mosbach (Schütt 1971)	24·4–25·4	17·4–18·5
	25·0	*17·8*

Discussion. This tooth can be attributed to *Hyaena* on the basis of the antero-internal triangular structure developed in the cingulum, and by the fact that the tooth is more brachydont than the same tooth in *Crocuta*. The measurements of this tooth correspond with *H. brevirostris* Aymard, whereas the only other large *Hyaena* species, *H. perrieri* Croizet and Jobert, has a relatively shorter length in relation to breadth.

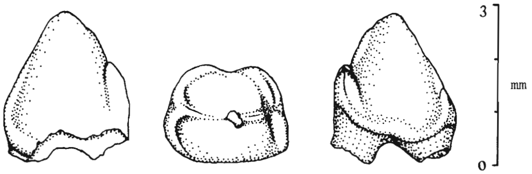
This record is of some significance since *H. brevirostris* appears to range up to the Cromerian *sensu stricto*, having been recorded from the Cromer Forest Bed (Bacton, Mundesley, Sidestrand), Süssenborn, Stránská Skála, and Gombaszog, but is not recorded from later sites such as Mosbach and Mauer.

Crocuta crocuta Erxleben 1777

Text-fig. 24

1846 *Hyaena spelaea* Goldfuss; Owen, pp. 138–160, text-figs. 54, 55, 57–61.
1902 *Hyaena crocuta* Erxleben; Reynolds, pp. 1–25, pls. 1–14. (Review and diagnosis.)
1971 *Crocuta crocuta praespelaea* Schütt, pp. 41–73, pls. 10, 11. (Review.)

Material. One lower left P3 from Bed 4 (M.33986), and unstratified, 1 lower left P3 (M.33726), 1 fragmentary lower left M1 (M.33724), 1 fragmentary upper left P3 (M.33725), and 2 right calcanea (M.33727-8).



TEXT-FIG. 24. Lower left P3 of *Crocuta crocuta* Erxleben (M.33726) in outer, inner, and occlusal views.

Description. The teeth are of the typical robust, high-crowned hyaenid type. The lower third premolar bears a cingulum at the inner base of the crown, which rises anteriorly to about one-third of the way up from the crown base, where it is met by an anterior ridge from the crown tip. To the posterior the cingulum rises and forms a rudimentary cingulum cusp, again about one-third of the way up from the crown base, and it is met by a ridge running down the posterior edge from the crown tip. The angle formed by the main cusp is about 55° in lateral profile (text-fig. 24).

TABLE 19. Comparative measurements (in mm) of the length and breadth of the lower P3 in *Crocuta* and *Hyaena*.

Lower P3	Length	Breadth
Westbury M.33986	24·0	16·4
Westbury M.33726	22·9	18·0(e)
C. crocuta. Mosbach (Schütt 1971)	23·0–24·8	15·5–18·8
	23·8	*17·3*
C. crocuta. Upper Pleistocene (Schütt 1971)	20·2–24·1	14·1–17·2
	22·5	*15·9*
H. perrieri. Mosbach (Schütt 1971)	21·4–22·5	14·5–15·8
	22·1	*15·3*

Discussion. The relatively high crowns of the premolars, the nature of the posterior cingulum cusp, and the size of these remains indicate that they belong to *C. crocuta* Erxleben.

The spotted Hyaena first appears at 'Cromerian' sites such as Süssenborn (Kurtén 1969*b*), Stránská Skála (Kurtén 1972), and West Runton (Stuart 1974), and in the Middle and Upper Pleistocene becomes a common element of cave faunas. Their comparative rarity at Westbury is consistent with the fauna being of early Middle Pleistocene age, when these animals were relatively thin on the ground.

Family FELIDAE Gray 1821

Homotherium latidens (Owen 1846)

Plate 4, figs. 8, 9

1846	*Machairodus latidens* Owen, pp. 179–183, text-figs. 69, 70.
1866	*Machairodus latidens* Owen; Dawkins and Sandford, pp. 184–194, pl. XXV, figs. 1–7.
1901	*Machairodus latidens* Owen; Boule, pp. 559–560, 562, 571–573, text-figs. 8, 9.
1966	*Homotherium*(= *Dinobastis*) *latidens* (Owen); Churcher, p. 273.
1970	*Homotherium* sp.; Heal, p. 136.

Material. One upper and 1 lower canine from Bed 4 (M.33983–4) and unstratified, 2 fragmentary upper canines (M.33700a, b), 1 upper incisor (M.33705), 1 fragmentary upper P4 (M.33702), 2 lower canines (M.33701a, b), and 1 lower M1 (M.33703).

Description. The upper canines are distinctive in being extremely laterally compressed and bear fine crenulations along the anterior and posterior edge of the blade (Pl. 4, fig. 9). The lower canines are, however, small and incisiform, with a protuberance at the antero-internal base of the crown, but again bear the very distinctive crenulated edges on the crown blades. The upper incisor (1 or 2) has a central recurved cusp, bearing a protuberance on either side of the crown base, and also has crenulated edges. The cheek teeth do not bear crenulated cutting edges, but follow the general felid pattern, except that they are much narrower and blade-like.

TABLE 20. Measurements (in mm) of the upper canines, lower M1, and upper P4 of *Homotherium*.

Upper canines		Ant./post. length at crown base	Width at crown base
Westbury M.33983, Bed 4		33·1	14·3
H. latidens. Kent's Cavern M. 14954		33·0	11·7
H. latidens. Kent's Cavern	(Dawkins and	30·0	—
H. latidens. Kent's Cavern	Sandford 1869)	33·9	13·2(e)
Lower M1		*Length*	*Width*
Westbury M.33703		27·0	11·4
Upper P4			
Westbury M.33702		—	10·2

Discussion. Crenulated and laterally compressed teeth of the feline type can be ascribed to the tribe Homotheriini, of which the only Pleistocene genus is *Homotherium.* There are two widely recognized species from the Pleistocene, *H. sainzelli* Aymard and *H. latidens* Owen, and a rather poorly known species, *H. moravicum* Woldrich, recorded from Stránská Skála (Thenius 1972) and Voigstedt (Thenius 1965). *H. sainzelli* is a relatively large cat, which characteristically has upper canines in which the blade length of the crown is long compared with the anterior-posterior length of the crown base (ant./post. length averages 43% of crown length). *H. moravicum* also appears to have canines of this type. In *H. latidens* the blade length is relatively short (ant./post. length averages 50% of crown length), and the whole canine is more recurved in comparison with *H. sainzelli.* The Westbury specimen (M.33983) compares with *H. latidens* in these characteristics, and its size and the size of the other *Homotherium* remains suggest all belong to this species.

The presence of sabre-toothed cats in the British Pleistocene has long been of interest, especially since Owen's description of the remains discovered by McEnery from Kent's Cavern (Owen 1846). As well as the Kent's Cavern finds, *H. sainzelli* is recorded from Dove Holes, Derbyshire (Dawkins 1903;

Spencer and Melville, 1974), and *H. latidens* from Creswell Crags, Derbyshire (Kurtén 1968; Stuart 1974). The finds from Dove Holes do not pose any problems, since *H. sainzelli* typically occurs in the Lower Pleistocene, and the Dove Holes fauna as a whole is consistent with this early date (Spencer and Melville 1974; Stuart 1974; Sutcliffe 1976). The records from Kent's Cavern and Creswell are more problematic since their faunas appear to belong to the Devensian. At Creswell there are considerable doubts about the authenticity of the find and until fresh evidence comes to light, this record is best ignored. At Kent's Cavern it is possible that the *Homotherium* remains came from a basal breccia associated with an earlier fauna including *Pitymys gregaloides* and *Arvicola cantiana* (Campbell and Sampson 1971), and unless fresh excavations can be made and new material discovered, there will always be some doubt about the range of *Homotherium* in Britain, despite Oakley's fluorine analyses (Oakley 1969) which the present writer regards as of doubtful value having used the same analyses on Westbury material. Westbury provides at least a locality for which there is a definite stratigraphic record for this species.

Felis (*Lynx*) sp.

Material. One distal end of a humerus (M.33935) from Bed 1, and one distal end of a tibia (M.33936) from Bed 3.

Description. The distal end of the humerus shows the typical felid supracondylar foramen, the coronoid fossa comprises two shallow concavities, and in size is very close to *Felis* (*Lynx*) (greatest width = 38 mm, cf. *Felis lynx*, Beeston Tor, Derbyshire M.13143 = 39 mm).

The distal end of the tibia is similarly indistinguishable from the living lynx.

Discussion. These remains might belong to any of the three lynx species known from the Pleistocene, namely *F. issiodorensis* Croizet and Jobert, *F. pardina* Oken, or *F. lynx* L. All three were probably dependent on woodland like the living lynxes, so its presence may be a useful paleoecological indicator, especially the record from Bed 1.

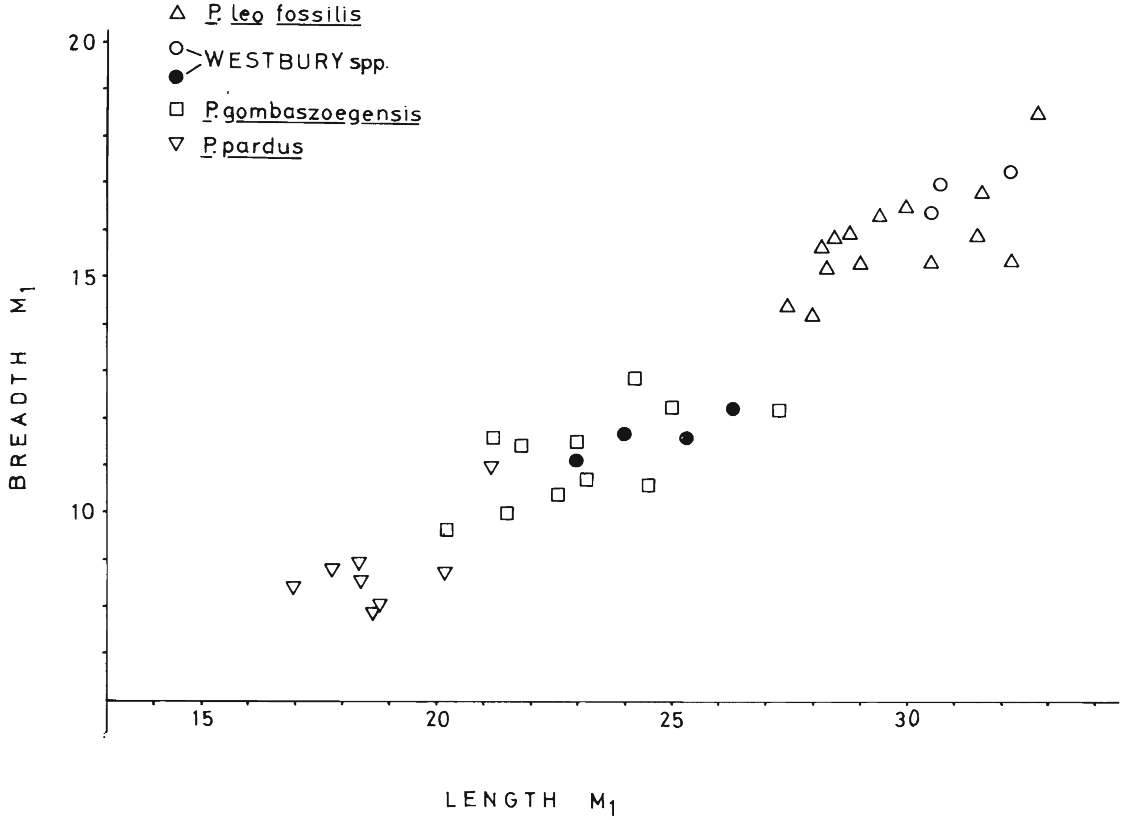
Panthera gombaszoegensis (Kretzoi 1938)

1938 *Leo gombaszoegensis* Kretzoi, pp. 100–104, 112, pl. I, figs. 1–7.
1969 *Panthera gombaszoegensis* (Kretzoi); Hemmer and Schütt, pp. 90–101, pls 1–3. (Synonomy.)
1971 *Panthera gombaszoegensis* (Kretzoi); Hemmer, pp. 701–711. (Diagnosis and additional synonomy.)
1974 *Felis gombaszoegensis* (Kretzoi); Bishop, pp. 309, 310, 313, pl. 24C.

Material. Two fragmentary mandibles (M.33678–9), 1 fragment of maxilla with P4 (M.33680), 2 isolated lower P3 (M.33968–9) from Bed 3, 2 lower P4 from Bed 3 (M.33971–2), 1 lower P4 from Bed 4 (M.33970), and 1 unstratified lower P4 (M.33682), 4 unstratified lower M1 (M.33683–6), 1 unstratified upper P3 (M.33680), 1 upper P4 from Bed 3 (M.33974), and 1 unstratified upper P4 (M.33681), 5 unstratified upper canines (M.33687a–c), 1 unstratified lower canine (M.33687f). Numerous isolated foot bones and fragmentary limb bones, stratified and unstratified.

Description. The general morphology and size of these remains compare closely with the living *P. leo*, but small differences in morphology are evident, and there are great differences in size compared with fossil *P. leo*. The most obvious morphological differences are the relatively higher crowns of the canines which reach up to 50% of the entire length of the tooth, the relatively flat profile of the undersurface of the mandible which is more typical of the tiger than the lion, and the thickening of the upper and inner side of the mandible ramus. The size of these remains is most distinctive (Tables 21, 22, text-fig. 25).

Discussion. The morphology and size of these remains closely compare with *P. gombaszoegensis* Kretzoi, originally described from Gombaszog, Hungary (Kretzoi 1938). The systematics of Pleistocene felids of this type have received much attention recently particularly by Hemmer and Schütt (1969, 1970) and Hemmer (1971*a*, *b*. 1972), and from these studies *P. gombaszoegensis* (= *P. toscana* Schaub) appears to be a 'good' species. As may be seen from Table 21 and text-fig. 25, the Middle Pleistocene lion is a much larger animal, so large in fact that it is very easily recognized visually in fossil samples. At the smaller end of the scale lies the leopard *P. pardus*, for which there are few Pleistocene records, but amongst the few fossils known, Hemmer (1971*a*) attributed the Stránská



TEXT-FIG. 25. Graph showing the length of lower M1 plotted against breadth in European Pleistocene *Panthera*. Measurements in mm.

TABLE 21. Comparative measurements (in mm) of *Panthera* mandibles.

Felid mandibles	Height jaw before P3	Height jaw behind M1	Diastema P3-C	Length P3-M1	Length P3	Length P4	Length M1
Westbury M.33678	41·6	41·7	15·0	61·5	17(e)	23·4	24·0
Westbury M.33679	38(e)	42(e)	—	59(e)	16(e)	21·6	23·0
P. gombaszoegensis Mosbach (Hemmer 1972)	38·5	40·5	16(e)	62	—	—	24·2+
P. onca. Pleistocene, N. America (Kurtén 1973)	38–45	37·3–46·0	—	56–62	13·7–18·1	20·6–25·0	21·1–26·1
P. pardus. Mauer (Schütt 1969)	28	31	19	48	12·8	17·3	18·4
P. leo spelaea. Gailenreuth (Dietrich 1968)	51–62	56–62	—	72–82	17·3–20·6	25·8–30·7	28·3–32·2
P. leo Recent (Dietrich 1968)	41	48	30·5	71	16·4	24·8	28·8

TABLE 22. Measurements (in mm) of teeth of *Panthera gombaszoegensis* from Westbury compared with Pleistocene jaguars (*P. onca*) from N. America (from Kurtén 1973).

	P^3		P^4		M^1		P_3		P_4		Ur. Canine		Lr. Canine	
	L	B	L	B	L	B	L	B	L	B	L	B	L	B
Westbury	17·3	8·2	23·4	11·4	24·0	11·7	21·7	10·7	29·7	—	20·7	16·5	19·9	14·7
	16·8	7·5	21·6	10·3	23·0	11·1			33·0	18·5	18·5	15·0		
			—	11·3	25·3	11·6					21·3	15·7		
			22·2	10·2	—	12·3					22·5	18·2		
			23·7	11·3	26·3	12·2					24·1	19·3		
			—	10·6										
O.R.	17·3, 16·8	8·2, 7·5	21·6–23·7	10·2–11·4	23·0–26·3	11·1–12·3			29·7, 33·0		18·5–24·1	15–19·3		
Mean			22·72	10·85	24·65	11·78	21·7	10·7		18·5	21·4	16·9	19·9	14·7
P. onca. Pleistocene. N. America (Kurtén 1973)	13·7–18·1	7·9–8·9	20·6–25·0	10·0–13·0	21·1–26·1	11·0–12·9	19·3–22·3	9·6–11·8	28·4–33·5	15·8–16·7	19·5–21·5	16·1–18·8	19·6–21·7	15·6–17·2

Skála material to *P. pardus* and stated that it showed affinities with the Pleistocene North American jaguars. *P. gombaszoegensis* lies between the leopard and lion in size, grouping in size with the jaguar *P. onca* (Table 22), and Hemmer (1971*b*) regards *P. gombaszoegensis* as a primitive jaguar. Kurtén (1973) believes it possible that early forms of *P. gombaszoegensis* and the Blancan-Irvingtonian jaguars of North America were once members of a circumpolar population broken up by local extinction in the Old World. In Africa, Dietrich (1968) has attributed remains from the Lower Pleistocene of the Serengeti to *P. gombaszoegensis*, while a similar cat from Choukoutien described by Zdansky (1924) as *P. palaeosinensis* is regarded by Hemmer (1971*b*) as ancestral to the tiger *P. tigris*. It seems likely that a widely distributed Lower Pleistocene form of *P. gombaszoegensis* was the ancestral stock to leopards, jaguars, lions, and tigers. In Europe *P. gombaszoegensis* ranges into the early Middle Pleistocene, and is found associated with other large cats (Table 23).

TABLE 23. Association of *Panthera* species at various European early Middle Pleistocene sites.

	P. gombaszoegensis	*P. leo fossilis*	*P. pardus*
Petralona	+	+	–
Hundsheim	+	–	–
Süssenborn	+	–	–
Gombaszog	+	–	+
Stránská Skála	+	?	+
Mosbach	+	+	–
Mauer	–	+	+
Scharzfeld	–	+	?
Voigstedt	–	–	+
Westbury	+	+	–

This is the first record of this cat in Britain, although a single tooth from the Red Crag described by Owen (1846) as *P. pardoides*, may well represent a member of the early representatives of *P. gombaszoegensis*. *P. gombaszoegensis* is probably a useful key fossil since it makes its last appearance in Europe in the early Middle Pleistocene.

Panthera leo fossilis (Reichenau 1906)

1906 *Leo fossilis* Reichenau, pp. 189–313, pl. IX, fig. 7; pl. X, fig. 1.
1969 *Panthera leo fossilis* (Richenau); Schütt, pp. 192–220, pl. 23, figs. 1–3. (Review and diagnosis.)
1970 *Felis leo* L.; Heal, p. 136.
1978 *Panthera leo fossilis* (Reichenau); Schütt and Hemmer, pp. 228–255. (Review.)

Material. Two lower M1 (M.33974, M.33975) and 1 first phalange from Bed 5, 1 canine and 1 fragmentary metapodial from Bed 4. Unstratified finds comprise 2 lower P4 (M.33661–2), 2 lower M1 (M.33663, M.33664), 1 upper P3 (M.33665), 3 fragmentary upper P4 (M.33666–8), 2 canines (M.33659–60), 1 astragalus (M.33669), one 2nd phalange (M.33670), and 1 fragmentary ecto-cuneiform (M.33671).

Description. The morphology of these remains is identical to the living *P. leo* and to lion remains described by Dawkins (1868) from the British Pleistocene. The most notable feature of the Westbury remains is their enormous size (Table 24, text-fig. 25).

Discussion. The lion entered Europe in the early Middle Pleistocene (Cromerian *sensu lato*), and these records indicate an enormous cat, probably the largest felid that ever existed (Kurtén 1968). Later finds represent a slightly smaller animal often found in cave deposits, and formerly referred to the species *P. spelaea* Goldfuss. Recent studies of European Pleistocene lions by Schütt (1969) and Schütt and Hemmer (1978), have demonstrated that two subspecies may be recognized, *P. leo fossilis* (Reichenau) from the early Middle Pleistocene, and *P. leo spelaea* (Goldfuss) from the Middle and

TABLE 24. Comparative measurements (in mm) of isolated teeth in *Panthera leo*.

Isolated teeth	Lower				Upper		
	P4		M1		P3		P4
	L	B	L	B	L	B	L
Westbury	30·1	15·1	32·2	17·3	27·7	13·3	40(e)
M.33661–66, 33975	—	14·4	30·5	16·4	—	—	—
			30·7	17·0			
			m. *31·13*	*16·9*			
P. leo fossilis	27·1–32·8	11·8–14·9	27·8–32·9	15·3–18·6	23·8–29·3	14·5–19·2	36·4–45·1
(Schütt and Hemmer 1978)	*29·2*	*13·1*	*29·8*	*16·4*	*26·7*	*16·2*	*39·9*
P. leo spelaea	21·9–29·7	10·0–12·4	26·4–31·7	13·5–16·2	26·0–26·5	13·5–14·2	33·8–42·4
(Shcütt and Hemmer 1978)	*26·9*	*10·9*	*28·9*	*14·7*	*26·2*	*13·9*	*38·4*

	Ant./post. length	Breadth	Crown height
Westbury, Ur. canine M.33660	28·5	20·0	—
Lr. canine M.33659	30·5	22·1	56(e)

Upper Pleistocene. The Westbury material directly compares with the larger *P. leo fossilis* as may be seen in Table 24 and text-fig. 25. As has been discussed above, *P. leo fossilis* replaced *P. gombaszoegensis* in the early Middle Pleistocene, and at a few sites (including Westbury) are found together.

Family MUSTELIDAE Swainson 1835

Mustela erminea Linnaeus 1758

Text-fig. 27

1912 *Mustela erminea* L.; Miller, pp. 385–398, text-fig. 81. (Diagnosis and synonomy of living sp.)
1970 *Mustela* sp.; Heal, p. 136.
1974 *Mustela* cf. *palerminea* Petenyi; Bishop, p. 309.

Material. Fifteen fragmentary mandibles (M.33988a–o) and assorted isolated teeth from Bed 10, and an entire mandible and associated postcranial elements from Bed 3 (M.33987).

Description. These remains are indistinguishable in morphology from the living stoat *M. erminea* L., and the weasel *M. nivalis* L. These two species, despite a marked sexual dimorphism, can be distinguished by size, and measurements of the length of lower M1 are set out in text-fig. 26 showing both species are present. The mandible from Bed 3 (M.33987), which is complete except it is missing the incisors, allows comparison with figures given by Miller (1912).

Discussion. Early Pleistocene forerunners of the stoat and weasel are *M. palerminea* Petenyi and *M. praenivalis* Kormos, which like the living stoat and weasel may be distinguished by their difference in size. The length of M1 in the Westbury mandible (M.33987) falls in the middle of the male distribution of the weasel group in text-fig. 26 and, as seen above, compares in size with the smallest living

TABLE 25. Comparative measurements (in mm) of the mandible and M_1 of *Mustela erminea* L. Figures for Recent form from Miller (1912), and *M. palerminea* from Kormos (1934).

	Total Length mandible	Length mandibular tooth row	Length M_1
Westbury M.33987, Bed 3	24(e)	14·5(e)	4·9
Westbury Bed 10. O.R.	—	—	3·94–4·96
Westbury Bed 10. Mean	—	—	4·53
M. erminea. L. Recent (Europe).	23·8–30·0	14·0–17·2	—
M. palerminea. Kormos. Villány. O.R.	—	—	4·40–5·55
M. palerminea. Kormos. Villány. Mean.	—	—	5·10

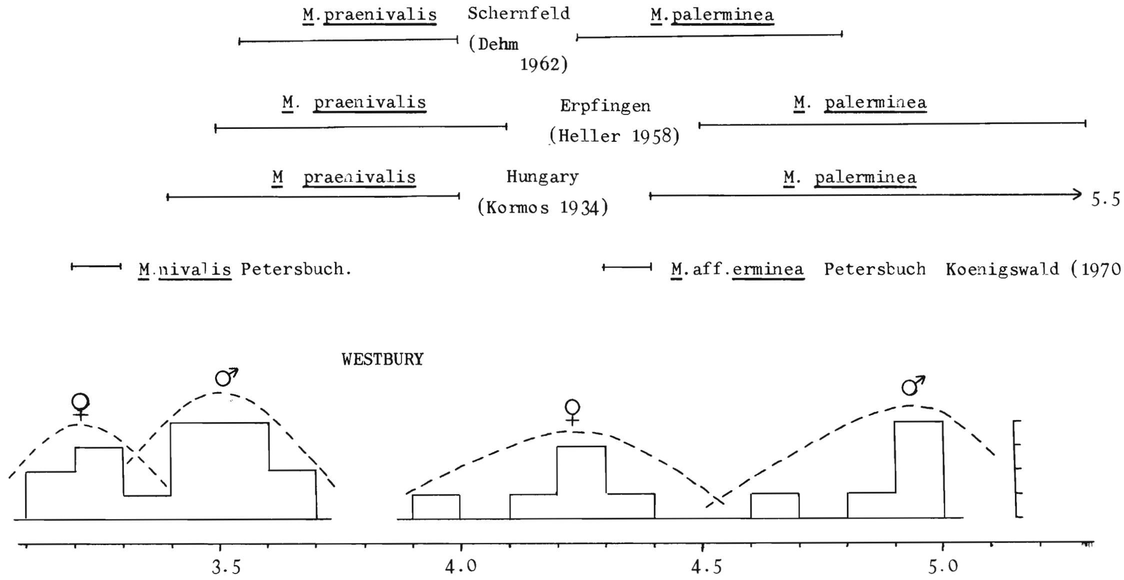
European representatives (from Norway and Sweden). Since the Westbury sample falls between *M. palerminea* and *M. erminea* in size, and since it shows no morphological differences to the latter, it is ascribed to *M. erminea.*

The stoat is essentially a woodland form, though the majority of remains come from Bed 10, and in the context of this being a bird-of-prey deposit, these remains may have been brought in from another area.

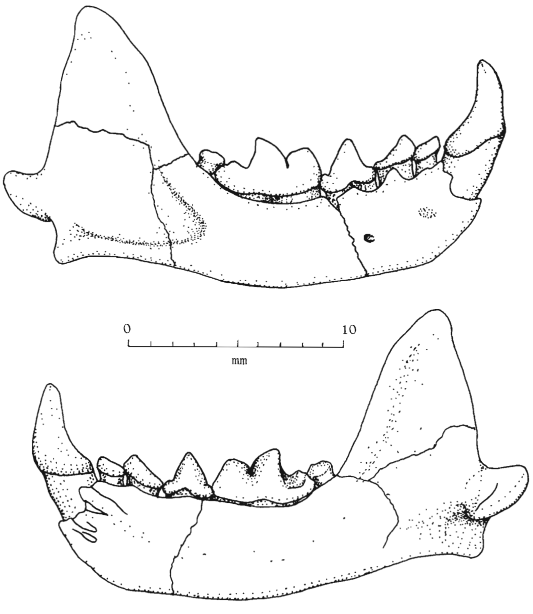
Mustela nivalis Linnaeus 1766

1912 *Mustela nivalis* L.; Miller, pp. 401–412, text-fig. 82. (Diagnosis and synonomy of living sp.)
1970 *Mustela* sp.; Heal, p. 136.
1974 *Mustela* cf. *praenivalis* Kormos; Bishop, p. 309.

Material. Fourteen fragmentary mandibles (M.33990a–n), one lower M1 (M.33991a), and four upper P4 (M.33991b–e), all from Bed 10.



TEXT-FIG. 26. Histograms and ranges in length (in mm) of lower M1 in early Middle Pleistocene stoats and weasels. Histograms of the Westbury specimens exhibit clear sexual dimorphism.



TEXT-FIG. 27. Right mandible of *Mustela erminea* L. from Bed 3 (M.33987), in outer and inner views.

Description. These remains are indistinguishable in morphology from the living *M. erminea* and *M. nivalis* but, as described above and shown in text-fig. 26, they form the smaller size group to *M. erminea*, and are intermediate in size between the early Pleistocene *M. praenivalis* and the living *M. nivalis*.

Discussion. These remains are attributed to *M. nivalis* on the basis of their size. The living species is more dependent on forest than *M. erminea*, but again all these remains are from Bed 10, so may have been brought in some distance from their natural habitat.

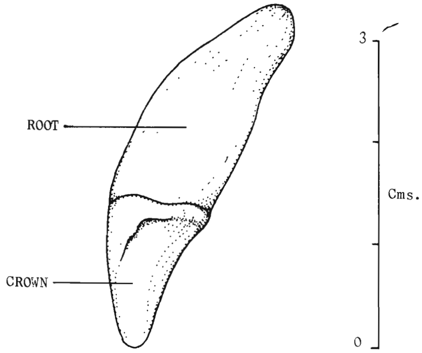
Gulo gulo Linnaeus 1758

Text-fig. 28

1912 *Gulo gulo* L.; Miller, pp. 434-440, text-figs. 88-91. (Diagnosis and synonomy of living sp.)
1974 *Gulo* sp.; Bishop, p. 309.

Material. One upper right canine from Bed 3 (M.33934).

Description. The stout and blunt nature of this canine exclude it from the Felidae and Canidae, while its rounded robust body, short crown, and its size are directly comparable to the living glutton *G. gulo* L. (text-fig. 28).



TEXT-FIG. 28. Upper right canine of *Gulo gulo* L. from Bed 3 (M.33934). Inner view (scale in cm).

TABLE 26. Comparative measurements (in mm) of the upper canine of *Gulo gulo* L.

	Ant. Post. L.	Width at Crown base	Max length
Westbury M.33934	9·4	7·5	37·6
G. gulo. Tornewton (Kurtén 1973)	9·9–12·2	7·7–9·4	—
	10·7	*8·2*	

Discussion. The earliest record of Glutton from the European Pleistocene is *G. schlosseri* Kormos, a small form from the early Middle Pleistocene of Hungary. The small size appears to be the only marked distinguishing character of this species, while larger specimens are known from Stránská Skála, the Cromer Forest Bed (Mundesley), and Mosbach, all of which are probably referable to *G. gulo*. The Westbury specimen represents an animal rather smaller than the Tornewton glutton, and in this respect may compare with the smaller specimens from the Forest Bed and Mosbach (no canines are described from these sites to allow direct comparison). Clearly, little emphasis can be put on size comparisons based on this single canine.

Early Middle Pleistocene glutton remains are found associated with warm faunas, but later in the Pleistocene the glutton is a 'cold' element of faunas, and today it occupies boreal zones. The presence of glutton at Westbury does not necessarily therefore bear any paleoclimatic implication.

Family CANIDAE Gray 1821
Canis lupus mosbachensis Soergel 1925

Plate 5, figs. 1–2

1925 *Canis lupus mosbachensis* Soergel, pp. 414–416.
1954 *Canis lupus mosbachenis* Soergel; Thenius, pp. 231–250, 280–283, text-figs. 1–11. (Synonomy and diagnosis.)
1970 *Canis lupus* L.; Heal, p. 136.
1972*a* *Canis lupus mosbachensis* Soergel; Musil, pp. 77–85, 97–106, pl. III, figs. 3–8; pl. IV, figs. 1–9; pl. V, figs. 1–5.
1974 *Canis lupus mosbachensis* Soergel; Schütt, pp. 72–74. (Review.)

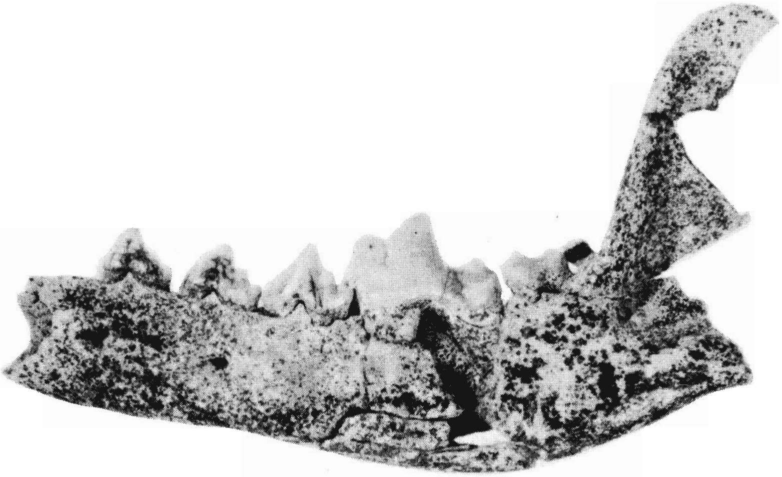
Material. Five mandibles from Bed 3 (M. 33937–40, M.33942), numerous isolated teeth and fragmentary postcranial bones predominantly from Beds 3, 4, and 5, and about 100 unstratified isolated teeth and fragmentary bones.

Description. The mandibular tooth row (excluding the incisors) bears one canine, four premolars, and three molars, the anterior tooth row being of a trenchant type, and the posterior of a crushing type. In the lower M1 there is a small but distinct metaconid on the posterior inner side of the protoconid, and the heel of the tooth bears a large hypoconid and smaller entoconid. M2 bears three cusps. These teeth are closely comparable with the wolf *Canis lupus*, except that in the mandible the premolar tooth row is less crowded such that only P4 and M1 overlap, and that the teeth and mandible as a whole are much smaller than *C. lupus* (Tables 27, 28). The upper dentition and the postcranial bones are also closely comparable with *C. lupus*, but are again much smaller than both the living and Upper Pleistocene wolf.

EXPLANATION OF PLATE 5

Figs. 1–2. Outer and occlusal views of left mandible of *Canis lupus mosbachensis* Soergel from Bed 3 (M.33940). × $\frac{4}{5}$.
Figs. 3–4. Outer and occlusal views of left mandible of *Xenocyon lycanoides* Kretzoi from Bed 3 (M.33965). × $\frac{4}{5}$. Note in Fig. 4 the lack of the posterior inner cusp in P3 (cf. Fig. 2).

1



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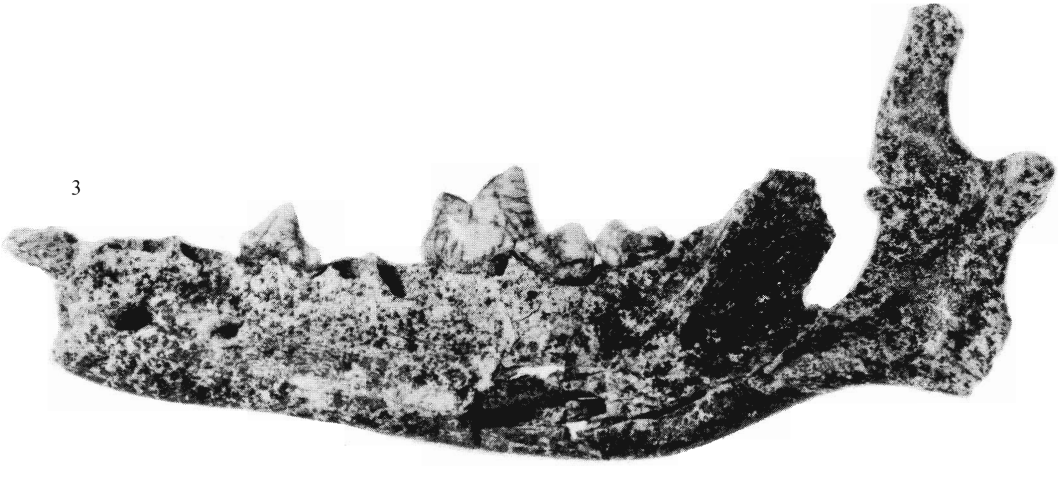


4

BISHOP, Pleistocene mammals

TABLE 27. Comparative measurements (in mm) of small canid mandibles.

Mandibles	Length P1–P2	Canine		P1		P2		Height Jaw	P3		P4		Height Jaw	M1		M2		Height Jaw	M3	
		L	B	L	B	L	B		L	B	L	B		L	B	L	B		L	B
Westbury M.33640	—	—	—	—	—	—	—	17·8	10·2	4·2	11·6	5·1	21(e)	21·5	8·0	—	—	—	—	—
Westbury M.33937	—	—	—	—	—	—	—	19·5	—	—	13·4	6·4	22	22·8	9·3	10·1	8·2	24	—	—
Westbury M.33940	72	—	—	—	—	12·5	5·8	21·5	14·2	6·0	15·1	7·0	23	25·6	10·7	10·7	8·4	28·1	5·0	4·4
Westbury Univ. Bristol Colln.	82	11·2	6·9	(5·3)	—	11·1	5·5	—	13·7	—	15·0	—	—	—	—	9·2	7·0	—	—	—
C. lupus mosbachensis Mosbach (Mottl 1941)	—	—	—	5·6–5·9	4·5	10·1–11·6	5·2–5·8	—	11·5–13·9	5·2–6·3	12·2–16·4	6·5–7·0	23·4–26·3	22·4–24·7	9·5–10	10·0–11	7·2–8·0	—	5·0	4·0
C. lupus mosbachensis	—	10·2	6·5	—	—	—	—	—	12·5	5·3	14·5	6·7	22	—	—	—	—	22·1	—	—
Hundsheim (Thenius 1954)	—	—	—	—	—	—	—	19·6	11·8	4·9	—	—	23·5	23·9	8·8	10·1	7·0	25·0	—	—
Cuon priscus Hundsheim (Thenius 1954)	—	11·6	7·7	—	—	8·9	5·2	23·5	10·7	5·0	14·0	6·8	26·2	23·3	9·8	8·9	6·9	—	—	—

TABLE 28. Comparative measurements (in mm) of isolated teeth in *Canis lupus*.

Upper	Canine		P1		P2		P3		P4		M1		M2	
	L	B	L	B	L	B	L	B	L	B	L	B	L	B
Westbury O.R.	9·1–11·9	5·3–7·7	4·8	3·1	12·4–13·6	4·6–6·1	13·7–15·1	4·9–6·4	19·5–23·0	8·9–12·0	12·1–14·4	15·0–18·5	7·7–9·3	12–12·8
n	10	10	1	1	3	6	4	5	5	5	10	9	4	3
Mean	10·78 ± 0·31	6·78 ± 0·20			12·93 ± 0·35	5·22 ± 0·21	14·3 ± 0·30	5·7 ± 0·33	21·34 ± 0·69	10·38 ± 0·50	13·22 ± 0·22	16·58 ± 0·36	8·48 ± 0·33	12·37 ± 0·23
S.D.	0·97	0·64			0·61	0·51	0·61	0·74	1·55	1·13	0·69	1·07	0·67	0·40
C. l. mosbachensis Hundsheim (Thenius 1954)	10·7–11·8	6·3–6·8	—	—	12·6	5·0	13·7	6·0	21·1	11·1–11·8	13·3–13·6	16·3–18·3	7·9	10·6
C. l. mosbachensis Gombaszog (Kretzoi 1938)	—	—	—	—	—	—	14·8	5·8	21·3–21·6	10–11·0	15·2	18·2	8·2	11·0
C. l. mosbachensis Wurzburg (Schütt 1974)	10(e)	—	7·0	—	12·5	—	14·5	—	24·0	—	15·0	19·0	9·0	13·0

Lower	Canine		P1		P2		P3		P4		M1		M2	
	L	B	L	B	L	B	L	B	L	B	L	B	L	B
Westbury O.R.	10·6–12·9	6·4–7·9	5·3	—	10·2–12·5	5·2–5·8	12·4–14·2	4·2–6·2	11·6–15·5	5·1–7·0	21·5–25·7	8·0–10·7	9·0–11·0	6·7–8·4
n	11	13	1	—	4	4	6	4	9	8	7	12	7	6
Mean	11·55 ± 0·22	7·23 ± 0·13			11·55 ± 0·55	5·53 ± 0·12	12·83 ± 0·61	5·48 ± 0·45	14·01 ± 0·43	6·70 ± 0·45	23·64 ± 2·65	9·15 ± 0·22	10·13 ± 0·26	7·63 ± 0·28
S.D.	0·73	0·45			1·10	0·25	1·50	0·90	1·28	1·28	1·52	0·76	0·68	0·68
C. l. mosbachensis Mosbach (Mottl 1941)	—	—	5·6–5·9	4·5	10·1–11·6	5·2–5·8	11·5–13·9	5·2–6·3	12·2–16·4	6·5–7·0	22·4–24·7	9·5–10·0	10·0–11·0	7·2–8·0
C. l. mosbachensis Hundsheim (Thenius 1954)	10·2–11·5	6·5–7·2	—	—	—	—	10·8–12·5	4·9–5·3	12·5–14·5	6·5–6·7	23·9–24·0	8·8–9·2	10·1–10·9	7·0–7·7
C. lupus. U. Pleistocene (Lehman 1954)	—	—	—	—	11·7–14·5 *13·1*	—	13·0–17·0 *14·5*	—	15·0–19·0 *16·6*	—	26·5–34·0 *29·9*	—	10–13·5 *11·8*	—

Discussion. The morphology of these remains shows closest comparison with *C. lupus*, while the dhole *Cuon* can be excluded on the morphology of lower M1 and M2, and presence of M3, and the foxes *Vulpes* and *Alopex* can be excluded by their much smaller size and their higher canines. The small size of the Westbury material agrees exactly with the early Middle Pleistocene representative of the wolf *C. lupus mosbachensis* Soergel (Tables 27, 28). Torre (1974) has shown that this subspecies is more closely related to *C. lupus* than the small Villafranchian species *C. etruscus* Major and *C. arnensus* Del Campana, and considers it an intermediate between *C. etruscus* and *C. lupus*.

This subspecies has been recorded from most of the early Middle Pleistocene sites including the Cromerian of West Runton, but is replaced in post Cromerian *s.l.* faunas by the larger true wolf. It is interesting to note that the disappearance of *C. lupus mosbachensis* and replacement by the large *C. lupus* also saw the disappearance of the dhole *Xenocyon*. This canid, which was a contemporary of *C. lupus mosbachensis* and is present at Westbury, was the same size as the large *C. lupus* and even had dental characteristics closer to the wolf than to *Cuon*. The disappearance of this large wolf-sized canid after the Cromerian *s.l.*, may therefore be related to the successful expansion of the large *C. lupus* in the Middle Pleistocene.

Xenocyon lycaonoides Kretzoi 1938

Plate 5, figs. 3–4

1933	*Canis lupus* L.; Kormos, pp. 22–25.
1934	*Canus lupus* L.; Stehlik, pp. 30–32
1938	*Xenocyon lycaonoides* Kretzoi, pp. 132–134, pl. III, fig. 4.
1938	*Canis gigas* Kretzoi, p. 128, pl. II, fig. 10.
1941	*Xenocyon gigas* (Kretzoi); Kretzoi, pp. 112–115, pl. V, fig. 1.
1942	*Canis spelaeoides* Kretzoi, p. 349.
1954	*Cuon dubius stehlini* Thenius, pp. 275, 276, 283, text-fig. 33*a*.
1961	*Cuon dubius stehlini* Thenius; Kahlke, p. 504, pl. 4, fig. 3.
1972	*Xenocyon spelaeoides* Musil, pp. 85–88, 97–106, pl. I, figs. 1–4; pl. II, figs. 1–5; pl. III, figs. 1–2.
1973	*Xenocyon lycaonoides* Kretzoi; Schütt, pp. 49–53, 56–58, 62–74, pl. 1–3. (Review and diagnosis.)
1974	*Xenocyon lycaonoides* Kretzoi; Schütt, pp. 64–72, pls. 1, 2. (Review and diagnosis.)

Material. One metapodial from Bed 4 (M.33932). From Bed 3, 1 left mandible (M.33965), 1 fragmentary right mandible (M.33966), 1 fragmentary upper P4 (M.33528), 1 proximal end of tibia (M.33967), and 1 proximal phalange (M.33931). From Bed 5, 1 canine (M.33933), and unstratified 1 upper canine (M.33653), 1 lower canine (M.33657), 1 astragalus (M.33654), 1 fragment of metepodial (M.33655), and 1 distal fragment of tibia (M33656).

Description. In the mandibular tooth row (excluding the incisors) there is evidence for one canine, four premolars, and three molars, and together with its size is superficially similar to *Canis lupus* (Pl. 5). The fossa masseterica, however, extends under M2 which excludes both *Canis* and *Cuon*. The lower M1 and M2 are distinctive in that M1 has a very reduced meteconid and a centrally placed hypoconid in the heel, with a reduced entoconid on the lingual side, and M2 has a well-developed central anterior cusp and a rudimentary cusp to the posterior. These dental features are typical of the cusp reduction seen in dholes, and are easily distinguished from *C. lupus*. The premolar tooth row is relatively closely packed, unlike *Cuon* and the lower P3 bears a single cusp without any posterior cusps, unlike *Canis*, *Lycaon*, or *Cuon*. These remains can be further separated from *Cuon* by the incurved posterior border of the coronoid process immediately above the condyle and the presence of lower M3, which are seen in *Canis*, *Lycaon*, and *Xenocyon*, and by the relatively large size of M2, which is shorter in *Cuon*.

The measurements of the teeth and mandibles are given in Table 29, which show the close comparison of these remains to the primitive dhole *Xenocyon*. The postcranial remains can be easily recognized here by their much greater size compared with *C. lupus mosbachensis*.

Discussion. The presence of the lower M3, the dhole-like development of the lower M1 and M2, the single cusped nature of lower P3, the incurved posterior border of the coronoid process, and the forwardly placed fossa messaterica are diagnostic of the early Pleistocene genus *Xenocyon*.

TABLE 29. Comparative measurements (in mm) of dhole and wolf mandibles.

Dhole mandibles	Condyle to front canine	P1–M2	Mandible height behind			P3		P4		M1		M2		M3
			P2	P4	M2	L	B	L	B	L	B	L	B	
Westbury M.33965	178(e)	92	26·4	29·0	34·0	13·7	6·1	—	—	28·5	10·6	12·3	8·3	Alveolus
Westbury M.33966	—	—	—	34·5	—	—	—	—	9·5	29·6	12·1	—	—	—
X. lycaonoides. Wurzburg (Schütt 1974)	—	—	29·0	—	—	14·3	—	17·5	—	29(e)	—	—	—	—
X cf. *lycaonoides*. Mosbach (Schütt 1973)	—	—	—	33·5	34·5	—	—	17·0	8·6	29·0	11·0	—	—	Alveolus
Cuon priscus (Schütt 1973)	—	76+	21·5	22+	27·5	—	—	—	—	25·1	9·3	10·1	7·6	Absent
Cuon cf. *priscus*. Mosbach (Schütt 1973)	165e	82·5	25·5	28·5	29·0	12·1	5·6	14·9	7·5	25·9	10·1	9·6	7·8	Absent
Cuon priscus. Hundsheim (Thenius 1954). Holotype	—	—	23·5	26·4	27·5	10·7	5·0	14·0	6·8	23·3	9·8	8·9	6·9	Absent
Canis lupus mosbachensis. Westbury M.33940	—	72	21·5	23·0	28·1	14·2	6·0	15·1	7·0	25·6	10·7	10·7	8·4	Present

Measurements given in Table 29 clearly indicate that these remains can be compared with the early Middle Pleistocene *X. lycaonoides* Kretzoi (synonyms: *Canis gigas* Kretzoi 1938, *X. gigas* Kretzoi 1941, *Canis spelaeoides* Kretzoi 1942, *Cuon dubius stehlini* Thenius 1954). Schütt (1973, 1974) has reviewed the systematics of Lower and Middle Pleistocene dholes, and suggests (Schütt 1974) that the Lower Pleistocene *X. dubius* from China was ancestral to *X. lycaonoides*, *Mesecyon*, *Cynotherium*, and possibly to *Cuon priscus*, but not to *Lycaon*. Thenius (1954) regarded *Canis* as the ancestor of *Lycaon*, and Schütt (1974) goes further in suggesting *Canis africanus* from Olduvai as this ancestor. Thus *Xenocyon* and *Canis* may have had a close common ancestry, the former giving rise to *Cuon*, while representatives of the genus died out in the early Middle Pleistocene, and the latter giving rise to *Lycaon*, while the genus became widely represented by *Canis lupus* and other related canids.

X. lycaonoides is only known for the Cromerian *s.l.* of Mosbach (Schütt 1973), Rosieres (Stehlin 1912), and Eastern European sites (Gombaszog, Stránská Skála, Nagyharsany and Betfia), so its presence at Westbury is an important new record in the British Pleistocene. The living dhole *Cuon alpinus* is widely distributed across Asia, where it inhabits forests, and according to Ognev (1962), hunts deer, goats and sheep in small packs of five to ten individuals. The large size of *Xenocyon*, and its sporadic occurrence, suggests that it may not have hunted in packs like the living dhole or wolf, but was probably a powerful enough animal to have tackled its prey alone or perhaps in pairs. Relatively large numbers of the wolf *Canis lupus mosbachensis* are found at Westbury and other contemporary sites, and it had almost certainly attained an advanced social organisation which included pack hunting. It is therefore not surprising that this thinly distributed dhole should disappear, its biotope being taken over by the more successful *Canis lupus* and *Cuon alpinus*.

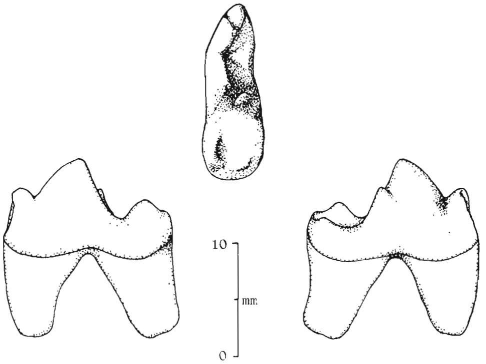
Vulpes cf. *vulpes* Linnaeus 1758

Text-fig. 29

1970 *Vulpes vulpes* L.; Heal, p. 136.
1974 *Vulpes* sp.; Bishop, p. 309.

Material. One distal end of a humerus (M.33964) from Bed 4, and one lower M1 (M.33658) from Bed 5(?).

Description. The morphology of the lower M1 (text-fig. 29) is clearly of canid form, and its very small size indicates that it belongs to a fox (*Vulpes* or *Alopex*). The heel of the tooth is as wide as the anterior portion, which is the case in *Vulpes*, whereas *Alopex* has a more narrow heel (Miller 1912). The humerus fragment is indistinguishable from that of *Vulpes*, though is a small specimen (width distal end = 18·5).



TEXT-FIG. 29. Lower left M1 of *Vulpes* cf. *vulpes* L. from ?Bed 5 (M.33658), in outer, inner, and occlusal views.

TABLE 30. Comparative measurements (in mm) of the lower M1 of *Vulpes*.

		Length	Breadth	*n* =
Westbury Lower M1 Bed 5? M33658		15·0	5·7	(1)
V. vulpes. Tornewton (Kurtén 1977)	$\bar{M}$ =	15·46	6·04	(47·58)
V. preglacialis. Hungary (Kurtén 1977)	$\bar{M}$ =	13·86	5·35	(14)
V. praecorsac. Hungary (Kurtén 1977)	$\bar{M}$ =	12·27	4·80	(3)

Discussion. Fox remains are rare from the early Middle Pleistocene, the earlier species *V. praeglacialis*, *V. praecorsac*, being small forms, while the larger *V. vulpes* becomes common from Middle Pleistocene times onwards. The Westbury remains are comparable with the Red Fox, *V. vulpes*, but are too few at present to substantiate this species being present.

Order PERISSODACTYLA Owen 1848
Family EQUIDAE Gray 1821
Equus caballus mosbachensis (Reichenau 1915)

1915 *Equus mosbachensis* Reichenau, pp. 46–99, pl. I, figs. 1–5; pl. II, figs. 1–4; pl. III, figs. 2–8; pl IV, figs. 2, 6, 7; pl. VIII, figs. 3, 4; pl. IX, fig. 11; pl. X, figs. 1–3; pl. XI, figs. 3–5; pl. XII, figs. 2, 4–7, 9, 10; pl. XIII, figs. 1, 2; pl. XIV, figs. 1–3, 5–7, 9–11, 15–18.
1948 *Equus caballus* L.; Pirlot, pp. 1118–1132.
1966 *Equus caballus mosbachensis* (Reichenau) = *robustus* (Pomel); Azzaroli, pp. 5–6, pl. I.
1974 *Equus mosbachensis* Reichenau; Bishop, pp. 309, 311, 313, 314.

Material. One lower premolar (4?) from Bed 4 (M.33730), 1 lower M2 from Bed 5 (M.33731), 1 upper M3 from Bed 5 (M.33772), and 1 incisor from Bed 10 (M. 33732). Unstratified finds comprise 4 isolated upper molars (M.33736–9), 1 upper P2 (M.33735), 1 upper canine (M.33740), 1 lower P3 (M.33741), 2 lower molars (M.33742–3), 1 fragmentary distal metapodial (M.33733), and 1 fragmentary second phalange (M.33734).

Description. The teeth are of the typical equid form being hypsodont, with a complex selenodont enamel pattern, and individual teeth of the upper and lower tooth rows show few differences from one another, apart from the anterior and posterior members (P2 and M3). Useful characters in the lower teeth drawn attention to by Hopwood (1936) are the shape of the enamel infold on the inner side of the tooth (between metastylid and metaconid), and the depth of the enamel infold on the outer side of the premolars (between hypoconid and protoconid). In zebrine horses the inner fold is distinctly V-shaped, while in caballine horses it is U-shaped, and in the premolars the outer fold is shallow in zebrine horses, but deep in caballine horses. All the Westbury lower teeth appear to belong to the caballine group. The only other distinctive feature of these remains is their very large size.

TABLE 31. Measurements (in mm) of the length and breadth of *Equus* teeth from Westbury.

	Length	Breadth
Westbury Upper M1/2 M.33738	35	29
Westbury Upper M3 M.33772	40	30
Westbury Upper P3? M.33736	35	31
Westbury Lower P3 M.33741	32	22
Westbury Lower P4? M.33730	38	22
Westbury Lower M1 M.33742	29·5	17·5
Westbury Lower M2 M.33731	35	17·5

Discussion. Of the many Pleistocene species of horses named, especially by von Reichenau (1915), many have been reviewed and rationalized, in particular by Azzaroli (1966) and Musil (1969), and the following Middle Pleistocene caballine and zebrine species appear to be valid (n.b. *E. stenonis* is not included):

Caballine Group	*Zebrine Group*
E. caballus mosbachensis Reichenau	*E. sussenbornensis* Wust
E. caballus plicidens Owen	*E. robustus* Pomel

E. caballus mosbachensis can be recognized by its great size, and so the Westbury material is assigned to this subspecies. Pirlot (1948) recognized both *E. caballus* (*mosbachensis*) and *E. robustus* from most of the Cromer Forest Bed localities, but *E. robustus* and *E. sussenbornensis* disappear from Europe after the Cromerian *s.s.*, and smaller forms of *E. caballus* replace *E. caballus mosbachensis* from the Middle Pleistocene onwards.

Family RHINOCEROTIDAE Owen 1845
Dicerorhinus etruscus (Falconer 1859)

Plate 6, figs. 1, 2.

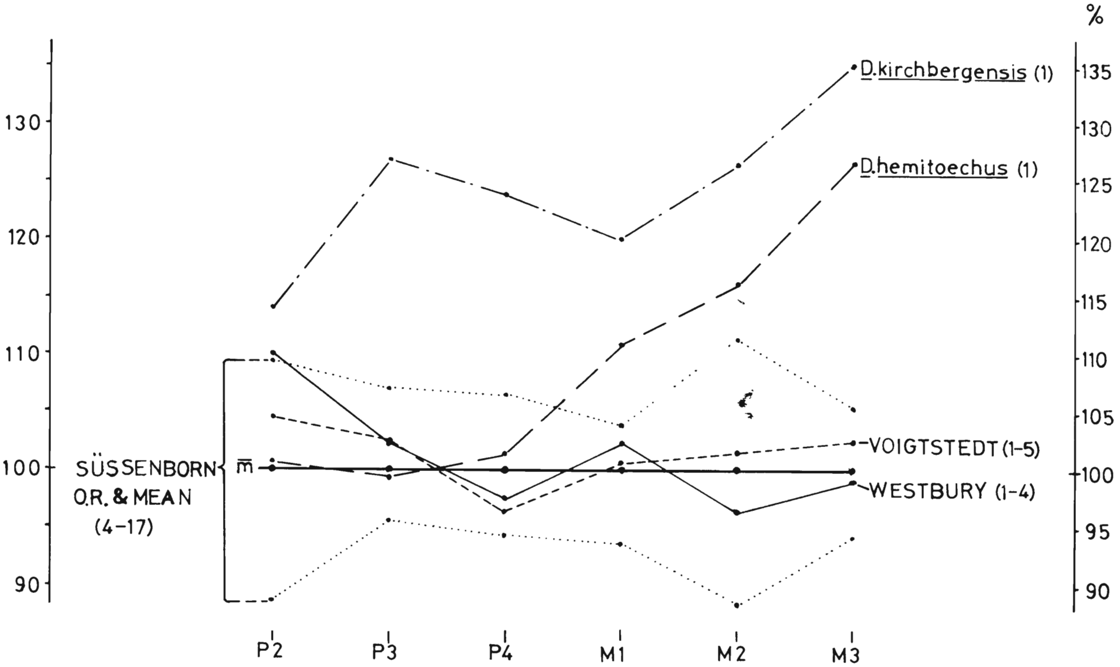
1868 *Rhinoceros etruscus* Falconer, pp. 309, 310, 354–368, pl. XXV, figs. 5–7; pl. XXVI, figs. 1–3; pl. XXVII, figs. 1–5; pl. XXVIII, figs. 1–5; pl. XXIX.
1868 *Rhinoceros etruscus* Falconer; Dawkins, pp. 207–218, pl. VII, figs. 1–3; pl. VIII, figs. 1–5.
1965 *Dicerorhinus etruscus* (Falconer); Kahlke, pp. 454–513, pl. XXIV; pl. XXV, figs. 1–3; pls. XXVI–XXVIII, pl. XXIX, figs. 1, 2; pl. XXX, figs. 1–4; pl. XXXI, figs. 1, 2; text-figs. 1–35.
1969 *Dicerorhinus etruscus* (Falconer); Kahlke, pp. 667–707, pl. XLVI, figs. 1, 2; pl. XLVII, figs. 1, 2; pl. XLVIII, figs. 1–3; pl. XLIX, figs. 1–5; text-figs. 1–28.

Material. One substantial upper dentition (M.33773) with left P2–M2 and right P2–P4 probably from a horizon equivalent to Bed 5, 1 fragmentary portion of palate with left P3 and P4, and right P3 (Bristol City Museum, Acn. no. 124/1969) from Bed 5, a fragmentary and crushed upper right dentition including M1, M2, and M3 (M.33729) from Bed 5, 1 fragmentary lower molar (M.33775) from Bed 1, tooth fragments from Bed 1 (M.33776), 1 fragment of upper molar from Bed 10, and unstratified 1 scaphoid bone (M.33774).

Description. The very large brachydont crushing teeth, with relatively simple enamel folds are characteristic of the Rhinocerotidae. The most important distinguishing features of the upper dentition are the well-developed cingulum on the inner side of the crowns (this is especially well marked in the premolars); the well-developed anterior guard which is an anterior development of the cingulum; the relative brachydonty of the crowns and hence abruptly tapering inner lobes; the square outline of the posterior valley in the premolars; the relatively high position of the inner valley above the cingulum; and the wide valley entrance in M3 (M.33729) which further into the tooth is truncated by a simple combing plate, in turn isolating a circular portion of the inner valley. These morphological features described by Falconer (1868) and Dawkins (1868) are diagnostic of *D. etruscus* Falconer, and allow distinction from the other Pleistocene species *D. megarhinus*, *D. kirchbergensis*, *D. hemitoechus*, and *Coelodonta antiquitatis*. Measurements of these remains given in Table 32 and text-fig. 30 substantiate this identification.

Discussion. In text-fig. 30 the Westbury mean values for the tooth widths are compared against *D. etruscus* from Süssenborn, mean values for which form the 100% basis for comparison, and its degree of variation is also plotted. As may be seen, the Westbury material lies within the variation of the Süssenborn *D. etruscus* and close to its mean value, apart from P2, which is in any case very variable, within the species.

D. etruscus is known from many Lower and early Middle Pleistocene sites, and has always been regarded as important as a key fossil indicating an early age, since it is thought to have become extinct by the Elsterian (?Anglian) glaciation. It is also important since it is associated with open deciduous forest. *D. etruscus* is replaced by *D. kirchbergensis* and *D. hemitoechus* in the Middle Pleistocene in response to the changing vegetational belts (Loose 1975).



TEXT-FIG. 30. Ratio diagram of the breadth of *Dicerorhinus* upper dentitions compared against *D. etruscus* from Süssenborn (100%, with variation between dotted lines).

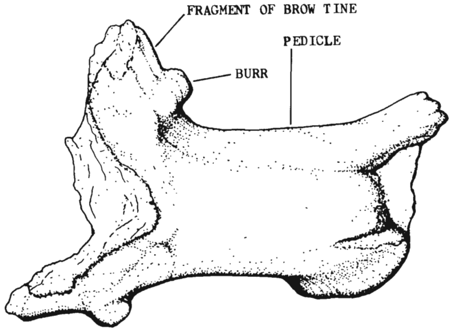
Order ARTIODACTYLA Owen 1848
Family CERVIDAE Gray 1821
Cervus cf. *elaphus* Linnaeus 1758

Text-fig. 31

1970 *Cervus elaphus* L.; Heal, p. 136.

Material. One fragmentary mandible (M.33791), 1 fragmentary antler attached to a fragment of skull (M.33797), 3 incisors (M.33790a–c), 5 lower premolars (M.33789 a–e), 12 lower molars (M.33788a–l), 7 upper molars (M.33756a–g), 3 astragali (M.33794a–c), 3 metapodials (M.33792a–c), 9 fragmentary small bones of forelimb (M.33795) and hindlimb (M.33796), all unstratified. One lower molar (M.33720) and 1 tine fragment from Bed 3, 1 lower M3 (M.33721) and 1 vertebra (M.33719) from Bed 4, and 1 upper molar (M.33722) and 1 lower molar (M.33723) from Bed 5.

Description. The antler fragment (text-fig. 31) comprises a portion of frontal bone from which a robust round pedicle arises and is encircled by a burr. The antler beam clearly ran along the line of the pedicle, but there is



TEXT-FIG. 31. Fragmentary antler and pedicle of *Cervus* cf. *elaphus* L. (M.33797). Three-quarters natural size.

TABLE 32. Comparative measurements (in mm) of the upper dentitions of *Dicerorhinus*.

Upper Dentition *Dicerorhinus*		P2		P3		P4		M1		M2		M3		P2–P4
		L	B	L	B	L	B	L	B	L	B	L	B	
Westbury M.33773	R	30	41	35	50	35	53	—	—	—	—	—	—	108
	L	29	42	35	53	36	54	46	58	44	57	—	—	104
Westbury Bristol City	R	—	—	39	52	—	—	—	—	—	—	—	—	—
Westbury Museum 124/1969	L	—	—	38	50	42	56	—	—	—	—	—	—	111(e)
Westbury M.33729		—	—	—	—	—	—	46(e)	—	46(e)	55·5	46	50	—
D. etruscus. C.F.B.M.19501		26	34	31	47	36	52	43	53	47	56	44	50	99
Trimmingham M.19492		31	40	38	52	41	59	46	59	48	62	48	53	111
D. etruscus. Voigtstedt (Kahlke 1965)		29·6–31·1	38·8–40·2	35·7–48·6	46·4–55·5	—	—	48·2–45·5	55·2–58·8	46·1–53·2	57·2–61·8	45·8–51·8	50·0–53·5	—
		30·35	*39·5*	*39·4*	*51·5*	38·0	54·2	*46·85*	*57·0*	*50·4*	*59·48*	*48·8*	*51·75*	—
D. etruscus. Sussenborn (Kahlke 1969)		27·2–33·5	33·5–41·3	36·8–49·6	49·7–53·8	40·2–45·1	53·2–60·0	46·8–51·0	53·1–58·9	43·3–54·3	51·8–65·2	50·8–56·7	47·6–53·2	107·4
		32·1	*37·7*	*39·9*	*50·15*	*42·3*	*56·2*	*48·25*	*56·6*	*49·7*	*58·47*	*53·5*	*50·5*	
D. hemitoechus. M.36620 Selsey		32	38	38	50	42	57	47	63	53	68	52	64	112
D. kirchbergensis. M.22020 Grays		37	43	41	64	51	70	48	68	63	74	58	68	123

evidence for a tine (the brow tine) arising anteriorly immediately above the burr. The size and morphology of this fragment are typical of *C. elaphus*.

The rest of these remains are identical to the living Red Deer, *C. elaphus*, in both morphology and size.

Discussion. The diagnosis of fossil deer remains is invariably based on the study of the antlers, which is why some emphasis is placed on the fragment described above.

C. elaphus is a common constituent of Middle and Upper Pleistocene faunas, appearing for the first time in the early Middle Pleistocene. Azzaroli (1953) reported *Cervus* c.f. *C. elaphus* from many of the Forest Bed localities, but like the Westbury material, was described from poor specimens.

Dama sp.

Material. One fragmentary lower M3 (M.33799), 1 upper M3 (M.33798), and 1 fragmentary molar (M.33800), from Bed 1, 1 astragalus (M.33761) from Bed 4, and 1 lower incisor (M.33760) from Bed 10.

Description. The molar teeth bear the typical cervid selenodont pattern. The upper M3 is more brachydont than *Cervus*, and bears on the inner side at the base of the crown between the two main lobes a rudimentary protuberance. In the lower M3 the third prism is broken off, but no protuberance or pillar is evident between the two main lobes. The third tooth from Bed 1 is too fragmentary to identify, but it clearly belonged to a cervid of the same size.

TABLE 33. Comparative measurements (in mm) of the lower and upper M3 of *Dama*.

	Length two ant. lobes	*Ant. breadth*
Westbury Lower M3 M.33799	17·0	11·4
Cervid cf. *D. nestii nestii*. East Runton. M.6261	15·5	10·8
Cervid cf. *D. nestii nestii*. East Runton. M.6283	18·0	10·5
D. clactonia (juvenile). Swanscombe. M.16956	18·1	11·7
D. dama. Recent. Dumfries. B.M.N.H.	16·3	10·6
Praedama sussenbornensis. Süssenborn (Kahlke 1969*c*)	—	16·5
	Length	*Breadth*
Westbury Upper M3 M.33798	17·0(e)	16·5
D. clactoniana M.16349. M. Pleistocene	21·4	23·0
D. dama. Recent. Dumfries. B.M.N.H.	16·3	16·3
P. sussenbornensis. Süssenborn (Kahlke 1969*c*)	26·0	25·5

The incisor and astragalus are indistinguishable from the living *D. dama* L. The astragalus of *Dama* is easily distinguished from the other comparably small cervid *Capreolus*, by being relatively narrow in relation to its greatest length.

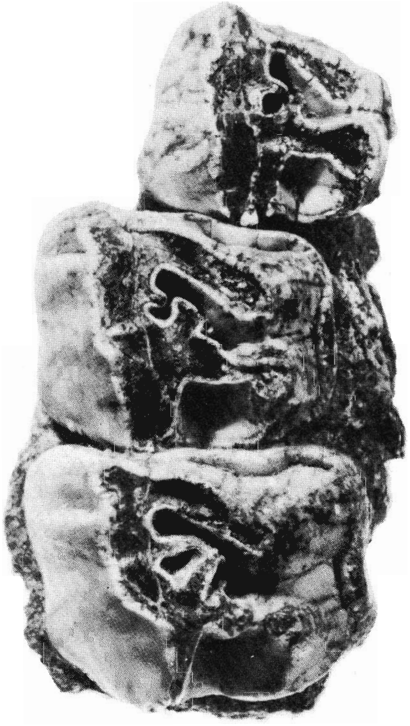
Discussion. All these remains compare closely with the living *D. dama* L., but there is clearly not enough material to allow specific identification. The fallow deer of the Hoxnian interglacial, *D. clactoniana* (Falconer), was about 20% larger than the living *D. dama*, and so the Westbury material can probably be excluded from this species. The pre-Hoxnian history of *Dama* is unclear, however.

EXPLANATION OF PLATE 6

Fig. 1. Fragmentary upper dentition of *Dicerorhinus etruscus* Falconer (M.33773), collected from a fallen block (possibly Bed 5?). $\times \frac{6}{7}$. Represented are left P2–P4, M1–M2 and right P2–P4.

Fig. 2. Upper right M3 of *Dicerorhinus etruscus* Falconer (M.33729) from Bed 5. $\times \frac{6}{7}$.

1



2

Azzaroli (1953) described a deer from East Runton (?Pastonian) comparable to *D. nestii nestii*, and a deer from West Runton (Cromerian *s.s.*) comparable to *D. clactoniana*. The former is comparable in size to the living *D. dama* and therefore comparable to the Westbury material, but early Middle Pleistocene *Dama* is so imperfectly known, and the material here so poor, that no closer comparison is possible at present.

TABLE 34. Comparative measurements (in mm) of the astragalus of *Dama*.

	Lateral length	Median length	Distal width
Astragalus			
Westbury. Astragalus. M.33761	38	36	25
D. clactoniana. Clacton. M.19894	47	44	29
D. clactoniana. Swanscombe (Sutcliffe 1960)	38–44 (M̄ = 40)	—	—
D. cf. *D. dama*. Joint Mitnor (Sutcliffe 1960)	30–39 (M̄ = 33)	—	—
D. dama. Recent. Dumfries. B.M.N.H.	40	38	26

Family BOVIDAE Gray 1821

Bovinae cf. *Bison schoetensacki* Frendenberg 1910

1974 *Bison* sp. (small); Bishop, pp. 309, 310, 312.

Material. Seventeen isolated molars and premolars (M.34910–18, M.34920–5, M.34748, M.34907) and twenty-five tooth fragments from Bed 1.

Description. The cheek teeth show the characteristic bovine selenodont grinding surfaces and hypsodont crowns, and in the molars there is a well-developed accessory column between the two main lobes. The upper molars tend to be almost square in occlusal outline, relatively uniform in length and breadth up and down the crown, and do not have particularly compressed outer lobes or strong outer ribs, which precludes these remains from *Leptobos* (Pilgrim 1939; Schreuder 1945). The morphology of the teeth closely compares with *Bos* and *Bison*, which are inseparable on tooth morphology alone.

TABLE 35. Comparative measurements (in mm) of the upper and lower M3 of *Bos* and *Bison* (taken at crown base).

	Upper M3		Lower M3	
	L	B	L	B
Westbury. Bed 1	27	26	37·5	17·5
Westbury. Bed 1	30	26	—	—
Westbury. Beds 3–10	31–35	25·5–30	43–49·5	17–21
Bos primigenius (Freudenberg 1914)	—	—	45	17
Bison priscus (Freudenberg 1914)	—	—	45·5	23
B. priscus (Degerbøl and Iversen 1945)	37·3	30·7	—	—
B. schoetensacki Voigstedt (Fischer 1965)	29–32·3	21–26·5	39·3–46	16–17·5
B. schoetensacki Mauer (Fischer 1965)	31	27	—	—

Discussion. *Bos* and *Bison* are represented by three species in the Middle Pleistocene, *Bison schoetensacki* Freudenberg, *Bison priscus* Bojanus, and *Bos primigenius*. Middle Pleistocene representatives of *Bison priscus* and *Bos primigenius* are very large, while *Bison schoentensacki* is relatively small, and the Westbury material from Bed 1 certainly seems to represent a bovid comparable to *Bison schoetensacki* in size. *Bison schoetensacki* is recorded from many Cromerian *s.l.* sites including Süssenborn (Flerov 1969), Voigstedt (Fischer 1965), and Stránská Skála (Flerov and Reshetov 1972), and appears to be associated with open forest.

Bison cf. *priscus* Bojanus 1827

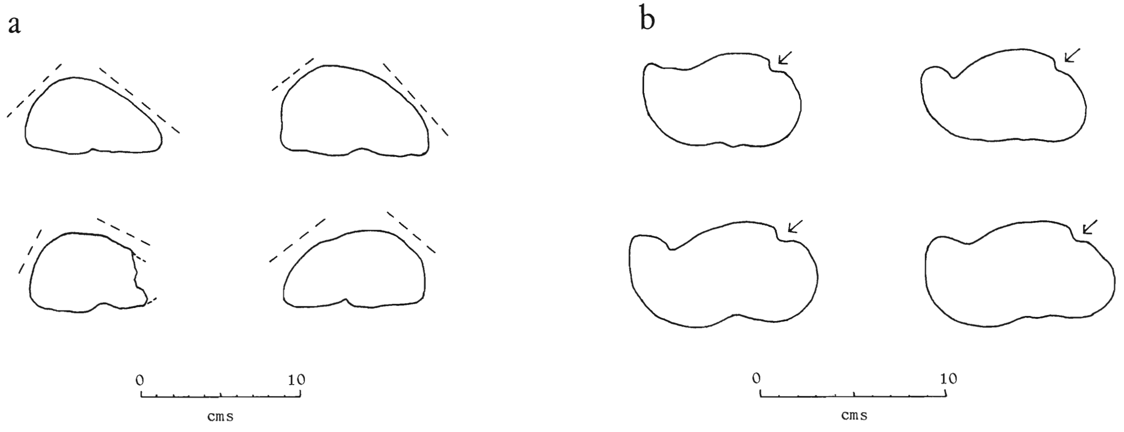
Text-fig. 32

1970 *Bos* sp.; Heal, p. 136.
1974 *Bison* sp. (large); Bishop, pp. 309, 314.

Material. From Bed 3 1 upper molar, 1 distal end of humerus, 1 fragmentary inominate, 1 trapezoid, 1 fragmentary jugal; from Bed 4 1 lower molar, 1 upper P3, 3 phalanges, 1 fragmentary radius, 1 proximal end of a humerus, 2 incisors, 1 radius; from Bed 5 2 lower molars, 1 upper P3, 1 phalange, 1 unciform; from Bed 8 1 upper molar; and a number of uncorrelated stratified finds, including 2 large vertebrae from the base of the eastern section (M.33778a, b). Unstratified remains comprise 7 incisors (M.33744a–g), 3 lower P3 (M.33746a–c), 1 lower P4 (M.33747), 7 lower molars (1 and 2) (M.33748a–g), 5 lower M3 (M.33749a–e), 9 upper P2 (M.33750a–i), 5 upper P3 (M.33751a–e), 9 upper P4 (M.33752a–i), 10 upper molars (1 and 2) (M.33753a–j), 18 upper M3 (M.33754a–r), 8 vertebrae (M.33755a–n), 4 humeri (3 fragmentary) (M.33756a–d), 2 fragmentary (M.33757a, b) and 1 entire (M.33757c) radius-ulna, 6 metacarpals (M.33758a–g), 8 astragali (M.33759a–h), and 55 fragmentary and small bones of the limb extremities (M.33762–71).

Description. The cheek teeth show the characteristic bovine selenodont grinding surfaces and hypsodont crowns, are very large in size, and their morphology is indistinguishable from the teeth of *Bos* and *Bison*.

Although no horn cores are available, these remains do include postcranial bones of systematic value in identifying this large bovine. Schertz (1936), Reynolds (1909), and Olsen (1960) have shown that the metacarpals of *Bos* and *Bison* can be distinguished upon the shape of the proximal articulation surface, and the profile of the distal end of the metacarpal. In the former, the articulation surface of *Bison* has more tapered lateral corners than *Bos*, giving it a rounded trapezium shape. In the latter, the width of the symphysial area above the articular condyles is about the same width as the most distal width across the condyles in *Bison*, but in *Bos* the symphysial width tends to be narrower. Text-fig. 32*a* shows the outlines of four Westbury specimens where the articulation surface is preserved, and all show the typical *Bison* shape.



TEXT-FIG. 32. (*a*) Outlines of proximal articulation surfaces of Westbury bovid metacarpals. (*b*) Outlines of lateral profiles of Westbury bovid astragali.

TABLE 36. Measurements (in mm) of the metacarpals of *Bison* from Westbury.

Metacarpals	Greatest Length	Width or Symphysis	Width across Condyles
Westbury M.33758a	254	87	91
Westbury M.33758b	267	96	98
Westbury M.33758c	266	—	—
Westbury M.33758e	—	89	90
Westbury M.33758f	—	85	88

The measurements above show that the symphysial width is within 4 mm of condylar width, which compares with the variation in *Bison* recorded by Reynolds (1909), and while a less reliable feature than the shape of the proximal articulation surfaces, supports the attribution of these remains to *Bison*.

Schertz (1936) draws attention to a notch in the lateral side of the astragalus, which is shallow in *Bos* but well developed in *Bison*. Text-fig. 32*b* shows the outlines of the latereal profiles of the best-preserved Westbury specimens, which are all comparable with *Bison*.

Finally, the well-preserved sixth cervical vertebra (M.33778a) is characteristic of *Bison* in bearing a neural spine and large ventral transverse processes, all of which are much smaller in *Bos*.

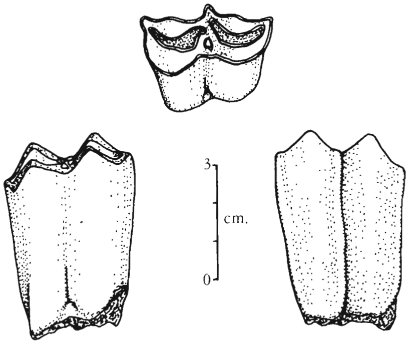
Discussion. All the postcranial elements of diagnostic value indicate *Bison* rather than *Bos*, while the size of the remains is comparable with *Bison priscus* and *Bos primigenius*, but considerably larger than *Bison schoetensacki*. Since both of the latter can be excluded, these remains are compared with *Bison priscus*. *Bison priscus* appears in Europe for the first time in the early Middle Pleistocene, being recorded from Hundsheim and Mosbach, while *Bison schoetensacki* appears to be the common bovine of the Cromerian *s.l.* (Flerov 1969).

Caprinae cf. *Soergelia elizabethae* Schaub 1951

Text-fig. 33

Material. One upper left M2 (M.33783), found at a horizon probably equivalent of Bed 5.

Description. The molar is hypsodont, has a selenodont enamel pattern, but unlike the Bovinae is relatively broad at the base and laterally compressed at the top (text-fig. 33). Unlike the Bovinae also, there is no pillar betwen the two main lobes, and the outer side of the crown bears three strong ribs between which the enamel is only very weakly folded. Between the two enamel crescents within the crown, there is a distinct small round enamel islet. These features and the very large size of the tooth indicate that it may belong to either *Megalovis*, *Praeovibos*, *Ovibos*, or *Soergelia*. The tooth differs from *Ovibos* and *Praeovibos* but compares with *Soergelia* in that its base is relatively wide compared with its length, and it has well-developed anterior and posterior outer ribs which project anteriorly and posteriorly, whereas in *Ovibos* they are weaker and they project outwardly, such that the anterior and posterior sides are nearly parallel. The size appears to be the only other diagnostic feature, and in this respect the tooth is identical to *Soergelia* in all aspects.



TEXT-FIG. 33. Upper left M2 of a large Caprine cf. *Soergelia elizabethae* Soergel (M.33783). Scale in cm.

TABLE 37. Comparative measurements (in mm) of the upper M2 of *Soergelia* and *Ovibos* (taken at crown base).

Upper M2	Length	Breadth (at crown base)
Westbury M.33783	27·5	25·5
S. elizabethae. Süssenborn (Kahlke 1969*b*). Holotype.	27·1	25·7
S. elizabethae. Süssenborn (Kahlke 1969*b*)	24·8	25·3
S. elizabethae. Süssenborn (Kahlke 1969*b*)	26·0	—
O. moschatus. Süssenborn (Kahlke 1969*a*)	26·3	22·8
O. moschatus. Süssenborn (Kahlke 1969*a*)	25·8	22·9

Discussion. This tooth is almost identical to the upper M2 of the holotype of *S. elizabethae* (figured by Kahlke 1969*b*) in both size and morphology. Kahlke (1969*b*) cited only four records of this genus in Europe, ranging from east Germany to Romania, and all apparently contemporaneous. He regarded this giant 'goat' as essentially a central Asiatic element, which advanced far into the west towards the Elsterian glacial epoch. Associated with *D. etruscus*, it appears to be a valuable key fossil. This is the first record of this species (and genus) in the British Pleistocene and, in association with *D. etruscus*, is strong evidence for the associated fauna being of pre-Elsterian (?Anglian) age.

Ovis or *Capra* sp.

Material. One fragmentary lower M3 (M.33784) from Bed 3.

Description. The molar is very hypsodont and laterally compressed, and it has a selenodont enamel pattern. It comprises two lobes (the third is broken off), of which the interior one bears a columnar projection, truncated interiorly giving it a rectangular profile. There is no accessory pillar or cement between the lobes. The estimated length of this tooth is 23 mm, and its breadth is 10 mm.

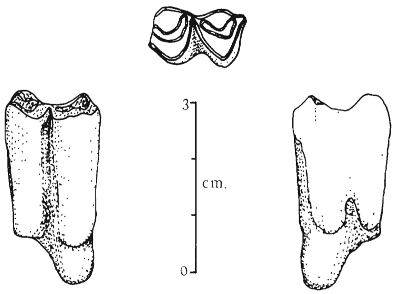
Discussion. This tooth is indistinguishable in morphology and size from *Ovis* and *Capra.* Records of Pleistocene sheep and goat are rare, and identification is only reliable where skull material is available. From the early Middle Pleistocene a horn core and frontal are known from the Cromer Forest Bed of Overstrand, described under the name *O. savini* Newton, and sporadic finds of *Ovis* or *Capra* are known from Tarkö, Uppony 1, Hundsheim and Grotte de l'Église (Jánossy 1969*b*; Laville *et al.* 1972; Kurtén 1968).

Hemitragus sp.

Text-fig. 34

Material. One lower left M2 (M.33785).

Description. The tooth is hypsodont, has a selenodont enamel pattern, and is relatively more broad than *Capra* or *Ovis.* The inner side of the crown is more strongly folded than *Capra/Ovis*, while the outer side of the crown comprises two lobes which are more robust and pointed than *Capra/Ovis*, and there is no accessory column between the lobes (text-fig. 34). Although the anterior and posterior borders of the tooth are broken, part of a



TEXT-FIG. 34. Lower left M2 of *Hemitragus* sp. (M.33785). Scale in cm.

TABLE 38. Comparative measurements (in mm) of the upper M2 in *Hemitragus*.

Upper M2	Length	Breadth
Westbury M.33785	18(e)	10·1
H. jemlahicus. Hundsheim (Daxner 1968)	19(e)	10(e)
H. jemlahicus. Hundsheim (Freudenberg 1914)	18(e)	—

posterior inner rib is present. In morphology the tooth closely compares with the living *Hemitragus*, and is a little larger than the living *H. jemlahicus* H. Smith.

Discussion. Hemitragus makes sporadic appearances in Europe during the early Middle Pleistocene and the Upper Pleistocene, and its record here is the first in the British Pleistocene. It has been recorded from Hundsheim (Freudenberg 1914; Daxner 1968) and from La Grotte de l'Église (Laville *et al.* 1972), both of early Middle Pleistocene age, and is possibly a useful key fossil in the Middle Pleistocene context though, like *Soergelia*, is unfortunately only known from a small number of finds. It is, however, likely that *Hemitragus* inhabited high ground, and is thus unrecorded from many lowland open sites, but might be expected to occur in an area such as the Mendips in Middle Pleistocene times.

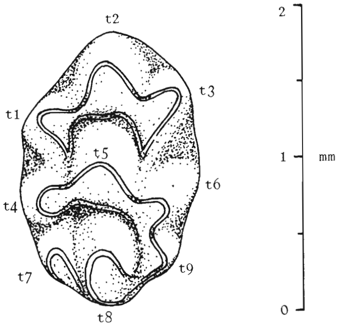
Order RODENTIA Bowdich 1921
Family MURIDAE Gray 1821
Apodemus sylvaticus (Linnaeus 1758)

Text-fig. 35

1912 *Appodemus sylvaticus* L.; Miller, pp. 797–823, text-figs. 165, 166. (Diagnosis and synonomy of living sp.)
1976 *Apodemus sylvaticus* L.; Sutcliffe and Kowalski, pp. 81–83. (Synonomy.)

Material. One mandible from Bed 10 (M.34011a), 2 unstratified mandibles (M.34011b, c), and 1 upper M1 (M.34012) from the western basin sequence.

Description. The mandibles are of the typical murid type, but the cheek teeth are distinctive in being brachydont, rooted, and tuberculate. Upper M1 bears three longitudinal rows of cusps (text-fig. 35), those of the inner row slightly smaller than those of the outer row. These cusps, which under Schaub's nomenclature (Schaub 1938) numbered t9, 8, 7, 4, 5, and 6, from a girdle-like ring. The most reduced cusp is t7, and this is level with t8 and t9. The first lower molar of M.34011b has six paired tubercles, but is too worn to show the structure of the anterior loop. The second lower molar has four paired tubercles, and a medium posterior tubercle.



TEXT-FIG. 35. Upper right M1 of *Apodemus sylvaticus* L. (M.34012) from the West Basin Complex. Cusp designation follows Schaub (1938). Occlusal view.

TABLE 39. Comparative measurements (in mm) of teeth in *Apodemus* and *Parapodemus*.

	Lower M1		Lower M2		Upper M1	
	L	B	L	B	L	B
Westbury M.34011b	1·5	0·95				
Westbury M.34011c			1·05	1·05		
Westbury M.34012					1·85	1·20
P. coronensis (Kowalski 1956)	1·4–1·7	0·8–1·0	—	—	—	—
P. coronensis (Dehm 1962)	1·4	0·9	—	—	1·65	1·03
A. cf. alsomyoides (Dehm 1962)	2·05	1·15	—	—	2·17	1·3
A. alsomyoides (Schaub 1938)	2·0	1·2–1·25	—	—	—	—
A. sylvaticus (Koenigswald 1970)	1·4–1·9 ($n = 174$)	—	—	—	—	—
A. sylvaticus (Koenigswald 1972)	1·7, 1·8	—	1·0 (*A.* sp.)	—	1·75	1·15

Discussion. These remains are indistinguishable from the living field mouse *A. sylvaticus* L. A close ancestor of *Apodemus* from the early Pleistocene of Europe is *Parapodemus coronensis* Schaub, but this does not develop the girdle-like ring of wear in the upper M1 seen in *Apodemus*, and the remains from Westbury are too small to belong to the Pleistocene species *A. alsomjoides* Schaub (Table 39).

Remains of *A. sylvaticus* are common from the early Middle Pleistocene onwards in Europe, and this species is recorded from the Cromerian *s.s.* of West Runton (Stuart 1974) and Sugworth (Stuart 1980). The living species is closely associated with woodland.

Family CRICETIDAE Rochebrune 1833
Lemmus lemmus (Linnaeus 1785)

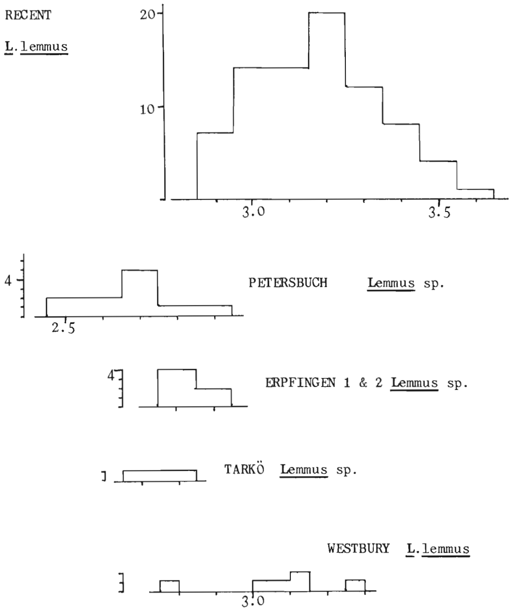
Text-fig. 37*a*

1912	*Lemmus lemmus* (L.); Miller, pp. 615–623, text-figs. 122, 123. (Diagnosis and synonomy of living sp.)
1974	*Lemmus* sp.; Bishop, pp. 309, 314.
1976	*Lemmus lemmus* (L.); Sutcliffe and Kowalski, pp. 90–92. (Synonomy.)

Material. One lower M3 from Bed 5 (M.34013a), and from Bed 10, 5 fragmentary mandibles (M.34013b–f) and 1 upper M3 (M.34013g).

Description. The mandibles are of the typical cricetid type, though relatively large, and the cheek teeth are rootless, prismatic, and flat crowned. The enamel of the molars is equally thick on the concave and convex sides of the re-entrant angles, but is frequently lacking from the tips of the salient angles and is then at the points of the re-entrant angles, and the re-entrant folds have cement inside. The lower M1 comprises a posterior loop, three closed triangles, and a narrow pointed anterior loop (text-fig. 37*a*). The lingual infolds are generally much deeper than the labial infolds in the lower molars, and vice versa in the upper molars.

Discussion. The morphology of these remains is indistinguishable from the recent *L. lemmus* (L.), which has the very characteristic tooth morphology described above. Remains of *Lemmus* are first recorded in the middle Villefranchian (Sutcliffe and Kowalski 1976), and up to the Middle Pleistocene *Lemmus* is associated with temperate faunas. In the Upper Pleistocene, however, *Lemmus* is a typical element of cold faunas, and the living *L. lemmus* has a boreal distribution. Early Pleistocene remains are represented by a small species of *Lemmus*, but in the early Middle Pleistocene



TEXT-FIG. 36. Histograms of the length (in mm) of lower M1 in *Lemmus*. Comparative measurements from Koenigswald (1970).

the size appears to fluctuate, and approaches the size of the living *L. lemmus*. The Westbury material (text-fig. 36) is large, and closely compares with the living species, but its range of size variation does overlap with early Middle Pleistocene material from Tarkö, Erpfingen, and Petersbuch (Koenigswald 1970).

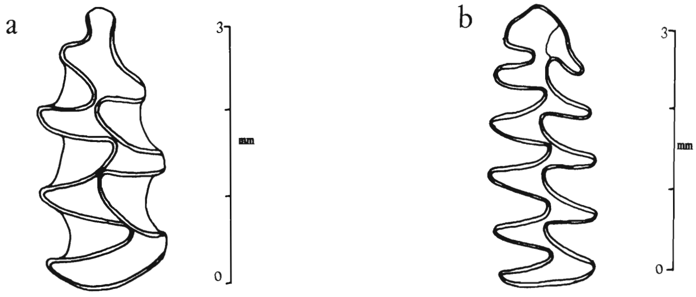
Dicrostonyx torquatus (Pallas 1779)

Text-fig. 37*b*

1974 *Dicrostonyx* sp.; Bishop, pp. 309, 314.
1976 *Dicrostonyx torquatus* (Pallas); Sutcliffe and Kowalski, pp. 87–90. (Synonomy.)

Material. One lower right M1 (M.34014) from Bed 10.

Description. The tooth is prismatic, rootless, flat crowned, and there is no cement in the re-entrant folds. The tooth comprises a posterior loop, seven closed triangles, and a simple anterior loop (text-fig. 37*b*). The enamel of the concave sides of the salient angles is thicker than that of the convex sides, and is very thin or absent at the tips of the salient angles which have a truncated appearance.



TEXT-FIG. 37. (*a*) Lower right M1 of *Lemmus lemmus* L. (M.34013b) from Bed 10. Occlusal view. (*b*) Lower right M1 of *Dicrostonyx* torquatus Pallas (M.34014) from Bed 10. Occlusal view.

TABLE 40. Comparative measurements (in mm) of lower M1 of *Dicrostonyx*.

Lower M1	Length
Westbury M.34014	3·35
Dicrostonyx sp. M. Pleistocene (Heller and Brunnacker 1966)	3·4–3·8 ($n = 4$) *3·63*

Discussion. The morphology of this tooth is indistinguishable from that of the living *D. torquatus* (Pallas), which has the very characteristic tooth morphology described above. Hinton (1910, 1926) distinguished two British Pleistocene species, *D. gulielmi* Sandford and *D. henseli* Hinton, but these are now regarded as synonyms of *D. torquatus* (Jánossy 1963; Sutcliffe and Kowalski 1976). Another species, *D. simplicior* has been described by Fejfar (1966) from two early Middle Pleistocene localities in Poland and Czechoslovakia, but the material is similar to *D. torquatus*, and considering the wide variation of the large sample of *Dicrostonyx* described by Jánossy (1963), can probably also be considered a synonym of *D. torquatus*. The earliest record of *Dicrostonyx* in Europe is probably the record from Brielle (Netherlands) of late Lower Pleistocene age (Meulen and Zagwijn 1974). *Dicrostonyx*, like *Lemmus*, is associated with a cold climate in Upper Pleistocene times but, again like *Lemmus*, appears in temperate faunas in the early Middle Pleistocene. It does, however, appear to have had a less broad climatic tolerance than *Lemmus* and can be associated at many sites with a steppe element or with ensuing cold climatic conditions.

Clethrionomys glareolus (Schreber 1780)

Text-fig. 38*a*

1912 *Evotomys glareolus* (Schreber); Miller, pp. 626–644, text-figs. 124, 125. (Diagnosis and synonomy of living sp.)
1976 *Clethrionomys glareolus* (Schreber); Sutcliffe and Kowalski, pp. 92–94. (Synonomy.)

Material. One lower M1 from Bed 5 (M.34022a), 1 lower M2 from Bed 5 (M.34022b), and 1 lower M3 from Bed 10 (M.34022c).

Description. The teeth are prismatic, flat crowned, have closed roots, have cement in the re-entrant folds, and the salient angles are rounded at their tips, rather than being pointed. The enamel is relatively thick throughout the tooth. In the lower M1 there is a posterior loop, four narrowly confluent triangles and a fifth triangle broadly confluent with a simple anterior loop (text-fig. 38*a*), and the tooth is 2·4 mm long.

Discussion. The morphology of these teeth is indistinguishable from and characteristic of *C. glareolus* (Schreber). The Bank Vole is a common element of faunas from early Middle Pleistocene times onwards, and in Britain is recorded from the Cromerian *s.s.* of West Runton (Stuart 1974) and Sugworth (Stuart 1980). The Sugworth remains indicate a smaller animal than at Westbury (length M_1 1·94–2·14).

The Bank Vole is a typical element of forest faunas.

Pliomys episcopalis Méhely 1914

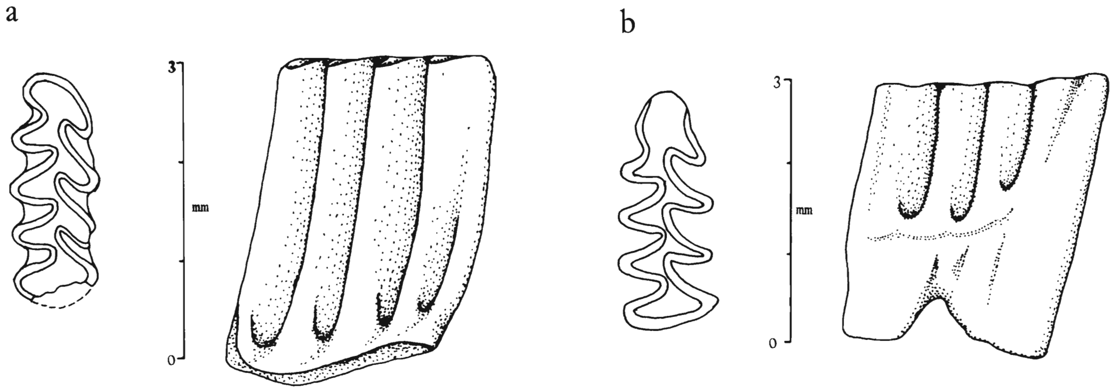
Text-fig. 38*b*

1914 *Pliomys episcopalis* Méhely, pp. 195–203, pls. 4–5.
1976 *Pliomys episcopalis* Méhely; Sutcliffe and Kowalski, p. 95.
1980 *Pliomys episcopalis* Méhely; Stuart, pp. 87, 88, 91, 95, 97, text-fig. 3G, H.

Material. One lower M1 from Bed 10 (M.34021).

Description. The tooth is prismatic, flat crowned, has closed roots, has no cement in the re-entrant folds, and the salient angles are rounded at their tips. The enamel is thicker on the concave (anterior) sides of the salient angles. The tooth comprises a posterior loop, four closed triangles, and a fifth triangle confluent with a simple anterior loop (text-fig. 38*b*). The lower M1 from Westbury (M.34021) measures 2·65 mm long.

Discussion. This tooth superficially resembles *Clethrionomys*, but has no cement in the re-entrant folds, has closed triangles, has differentially thickened enamel, and is larger than *Clethrionomys*. The only genus to which this tooth can be compared is *Pliomys*, and its size, robust nature, and simple anterior loop indicate that it belongs to *P. episcopalis* Mehely and not *P. lenki* Heller, which is larger, of slimmer construction, and has a more complex anterior loop (text-fig. 38*b*).



TEXT-FIG. 38. (*a*) Lower right M1 of *Clethrionomys glareolus* Shreber (M.34022a) from Bed 5. Occlusal and outer views. (*b*) Lower right M1 of *Pliomys episcopalis* Méhely (M.34021) from Bed 10. Occlusal and outer views.

This is the first record of this species and genus in Britain, but in Europe *P. episcopalis* is recorded from many Cromerian *s.l.* sites, including Mossbach, Mauer, Tarkö, Hundsheim, Erpfingen, Villany, Beremend, and Koneprusy. *P. episcopalis* may have survived until the Holsteinian in Italy (Sutcliffe and Kowalski 1976), though *P. lenki* replaces this species elsewhere after the Elsterian. Jánossy (1965) and Fejfar (1972) regard *P. episcopalis* as belonging to a forest habitat, but it is also commonly found as an element of the steppe fauna (Sutcliffe and Kowalski 1976). Stuart (1980) has recently described this species from the Cromerian (Zone III) of Sugworth, Oxfordshire, but as shown in text-fig. 39 the remains represent much smaller individuals than the Westbury specimen.

Mimomys savini Hinton 1910

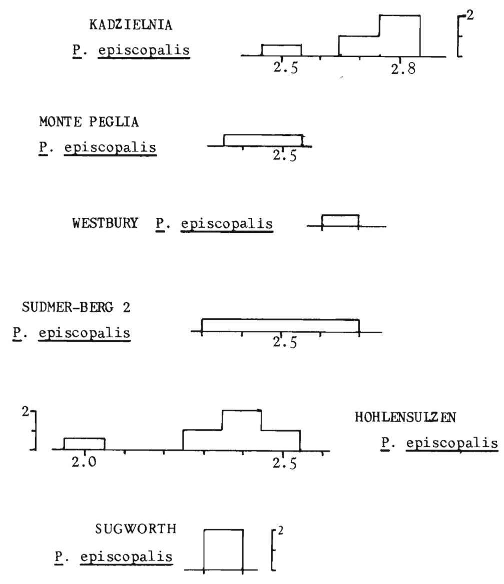
Text-fig. 40*a*

1910 *Mimomys savini* Hinton, p. 491.
1976 *Mimomys savini* Hinton; Sutcliffe and Kowalski, pp. 98–99. (Synonomy.)

Material. One left lower M1 (M.34018) from Bed 1.

Description. The teeth are prismatic, flat crowned, have closed roots, and have cement in the re-entrant folds. The enamel is thicker on the convex (posterior) sides of the salient angles. In the lower M1 (M.34018) the posterior loop has broken away, but preserved are three closed triangles, and an *Arvicola*-shaped anterior loop (text-fig. 40*a*). This tooth is relatively large, and can be estimated to have been no smaller than 3·3 mm and no larger than 3·5 mm (text-fig. 41). The tooth crown is high in this specimen, but the roots appear to be poorly formed.

Discussion. The morphology of the lower M1 and its large size are closely similar to *Arvicola cantiana* Hinton, but the presence of closed roots indicates this tooth belongs to *M. savini* Hinton, which is believed to be the ancestor of *A. cantiana* (Koenigswald 1973*a*; Sutcliffe and Kowalski 1976).

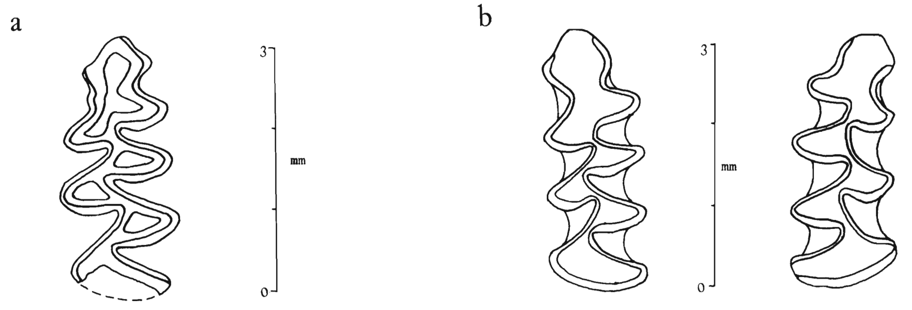


TEXT-FIG. 39. Histograms of the length (in mm) of lower M1 in *Pliomys episcopalis*. Comparative measurements from Kowalski (1958), Meulen (1973), Koenigswald (1972), and Storch, Franzen, and Malec (1973).

M. savini is the typical large vole of the Cromerian *s.s.* of West Runton (Stuart 1974, 1975) and of many European sites including Voigstedt and Süssenborn. Since *Mimomys* is ancestral to *Arvicola*, and so easily differentiated from *Arvicola*, it is an important key fossil. Koenigswald (1973*a*) has drawn attention to faunal assemblages containing either *Mimomys* or *Arvicola*, and on the strength of the presence or absence of these plus other small mammals recognized three faunal groups in the Middle Pleistocene:

(a) *M. savini* fauna, e.g. West Runton, Voigstedt, Süssenborn.
(b) *Arvicola* fauna, group 1, e.g. Mosbach, Mauer, Hundsheim.
(c) *Arvicola* fauna, group 2 (*Sorex savini*, *S. runtonensis*, *Pliomys* absent), e.g. Swanscombe, Petersbuch, Uppony 1.

While Koenigswald's original scheme can be altered in small details in the light of new finds, the implication remains that these faunal groups belong to different temperate stages. Thus the presence of *M. savini* suggests that the fauna from Bed 1 can be correlated with sites no later than the Cromerian *s.s.*, while the rest of the Westbury fauna which is associated with *Arvicola* is of a later date (see section on correlation).



TEXT-FIG. 40. (*a*) Lower left M1 of *Mimomys savini* Hinton (M.34018) from Bed 1 (young individual). Occlusal view. (*b*) Left and right lower M1 of *Arvicola cantiana* Hinton (M.34015) from Bed 10. Occlusal views.

Mimomys was almost certainly an amphibious vole, occupying a similar habitat to the living water vole *A. terrestris* (L.). The presence of *Mimomys* in Bed 1 is therefore consistent with the presence of the beaver *Castor fiber* in the same deposit which is so dependent on water.

An interesting feature of this particular specimen is the late-developing roots, a characteristic feature of the late *Mimomys* populations.

Arvicola cantiana (Hinton 1910)

Text-fig. 40*b*

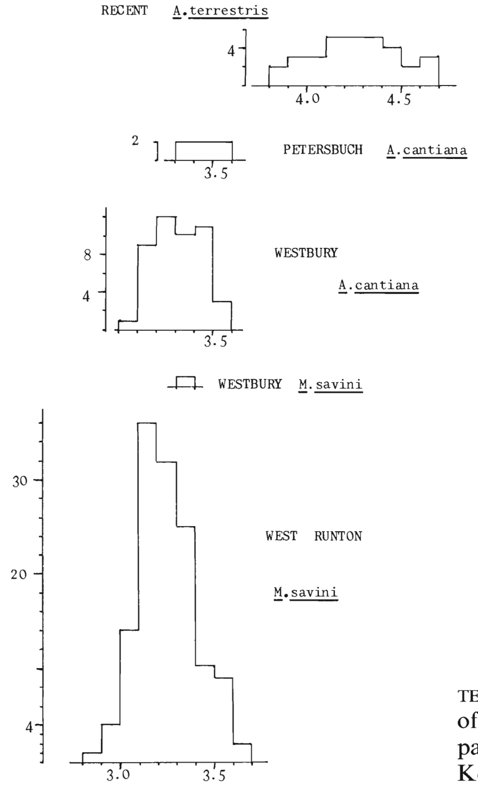
1910 *Mimomys cantianus* Hinton, p. 491.
1970 *Arvicola cantiana* (Hinton); Koenigswald, pp. 418–420, text-figs. 13–18.
1976 *Arvicola cantiana* (Hinton); Sutcliffe and Kowalski, pp. 100–103. (Synonomy.)

Material. Eight mandibles (M.34015), 40 isolated lower M1's (M.34016), and numerous isolated upper and lower molars (M.34017), all from Bed 10, and at least 19 isolated molars from the lateral equivalent of Bed 5.

Description. The mandibles are of the typical cricetid type, though relatively large, and the cheek teeth are rootless, prismatic, flat crowned, and have cement in the re-entrant folds. The lower M1 comprises a posterior loop, three closed triangles, and a relatively large anterior loop (text-fig. 40*b*). The enamel is thicker on the convex side of the salient angles.

Discussion. The large size (text-fig. 41) and the morphology of the teeth are typical of *Arvicola*, while the differentiation of the enamel indicates these remains belong to *A. cantiana* Hinton, and not *A. terrestris* where the enamel is thicker on the concave sides, or the intermediate forms where the enamel is about of equal thickness.

Koenigswald (1970, 1972, 1973*a*) has reviewed and revised the systematics of *Arvicola*, and has demonstrated its probable evolutionary lineage from *Mimomys savini*, to *A. cantiana*, to an



TEXT-FIG. 41. Histograms of the length (in mm) of lower M1 in *Arvicola* and *Mimomys*. Comparative measurements from Stuart (1975) and Koenigswald (1970).

intermediate *A. cantiana/terrestris*, to the living *A. terrestris*. Sutcliffe and Kowalski (1976) have adopted Koenigswald's *Mimomys–Arvicola* faunal groups (Koenigswald 1973*a*) which are based on this lineage, and have used them within their stage classification of the British Pleistocene.

As has been discussed in the previous section under *Mimomys*, the presence of *M. savini* in Bed 1 suggests the fauna from this horizon is earlier than the fauna from the rest of the Westbury sequence, which is associated with *Arvicola*. Stuart and West (1976) have suggested that the transition from *Mimomys* to *Arvicola* took place in Britain within the Cromerian *s.s.*, between Zones III and IV, based on the presence of *M. savini* at the Cromerian Zone III site of Sugworth (Briggs *et al.* 1975) and on the presence of *A. cantiana* at Ostend, Norfolk, which these authors ascribe to the Cromerian Zone IV. There is, however, evidence that the faunas of the Siliceous Member (Bed 1) and the Calcareous Member (Beds 2–10) belong to different temperate stages, and that the fauna of the Calcareous Member does not belong to the Cromerian *s.s.* A discussion of the correlation and age of these faunas is given at the end of this paper.

Microtus (*Allophaiomys*) sp.

Text-fig. 42*a*

Material. One left (M.33563a) and one right (M.33563b) lower M1 from Bed 1.

Description. The teeth are rootless, prismatic, flat crowned, and have cement in the re-entrant folds. The lower M1 comprises a posterior loop, three closed triangles, a fourth and fifth triangle either confluent or closed, and a very simple anterior loop which is either narrowly confluent or closed posteriorly (text-fig. 42*a*). The innermost point of the third outer salient angle lies opposite the same point in the fourth inner salient angle instead of behind it as in most *Microtus* species.

Discussion. The morphology and size of these teeth are comparable with *Microtus*, but the simple third outer and fourth inner salient angles at about equal positions along the tooth are characteristic of *M.* (*Allophaiomys*) and of *Pitymys*. The latter, however, has a much more complex anterior loop comprising one or two additional salient angles, whereas *M.* (*Allophaiomys*) has a simple rounded anterior loop with a faint indication of salient angles developing at either side, which is the case with the Westbury specimens. The Westbury specimens also agree with this subgenus in that the fourth and fifth triangles, and the anterior loop, are confluent to a variable degree. In size these remains closely agree with material described by Meulen (1973):

TABLE 41. Comparative measurements (in mm) of the lower M1 of *Microtus* (*Allophaiomys*). Figures from Meulen (1973).

	Length lower M1		
	Mean	Range	N
Westbury M.33563a		2·6(e)	1
Westbury M.33563b		2·4(e)	1
M. (*Allophaiomys*) *pliocaenicus*. Betfia 2	2·65	2·3–3·0	96
M. (*Allophaiomys*) sp. A. Monte Peglia	2·58	2·3–2·9	104
M. (*Allophaiomys*) sp. B. Monte Peglia	2·74	2·4–3·1	81

Many modern authors including Meulen (1973) regard *Allophaiomys* as a subgenus of *Microtus*, and in this instance the present writer follows this view. Meulen (1973) through an extensive biometrical study of fossil *Microtus* material, came to the conclusion that his *M.* (*Allophaiomys*) sp. A from Monte Peglia was the ancestor of *Pitymus gregaloides* and *P. arvaloides*, and his *M.* (*Allophaiomys*) sp. B was the ancestor of the true *Microtus* lineage. This suggests that these remains may antedate the Cromerian of West Runton, since both *Pitymys* and *Microtus* are present there. This record is, however, the first of this subgenus in the British Pleistocene, and it is only described from a small number of European sites, so it is very difficult to determine its range. This is made even more difficult by the fact that at least five species of *M.* (*Allophaiomys*) have been described from the early Middle Pleistocene, and material referred to *P. arvaloides*, *P. hintoni* Kretzoi, and various species of *Microtus*, in some cases probably belong to *M.* (*Allophaiomys*).

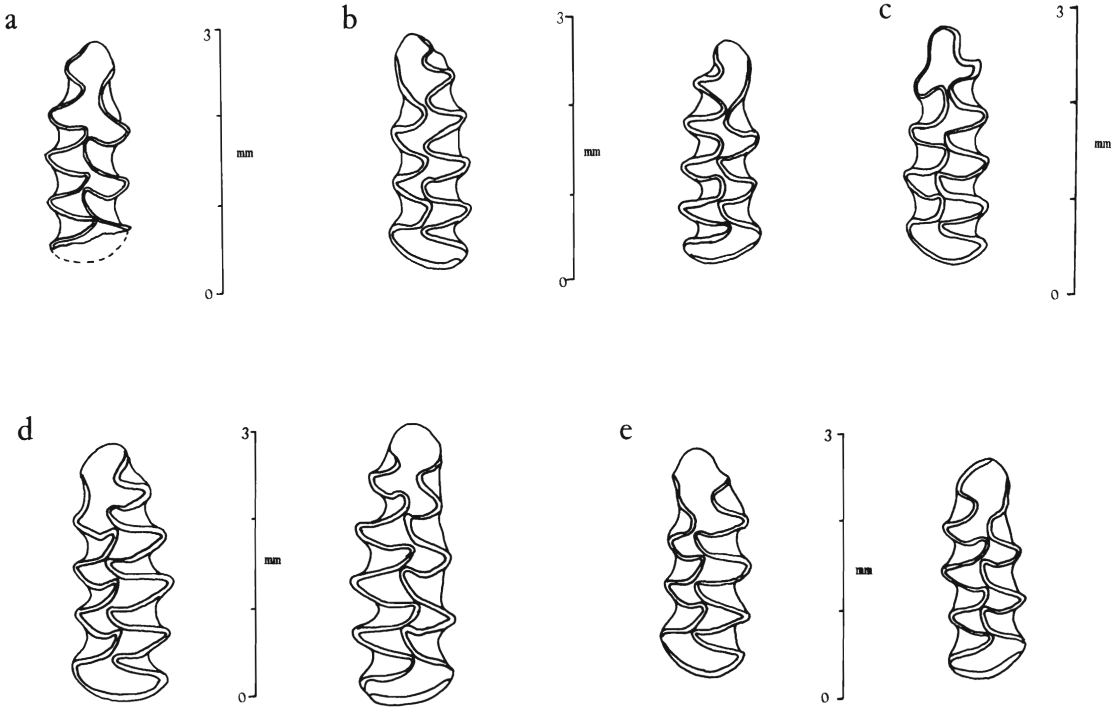
Pitymys gregaloides Hinton 1923

Text-fig. 42*b*

1923 *Pitymys gregaloides* Hinton, pp. 541, 542.
1976 *Pitymys gregaloides* Hinton; Sutcliffe and Kowalski, p. 107. (Synonomy.)

Material. Over 800 mandibles and isolated teeth from Bed 10 (M.34079). Over 50 isolated molars from Bed 5, and 3 isolated lower M1's from Bed 8.

Description. The mandibles are of the typical cricetid type, and the cheek teeth are rootless, prismatic, flat-crowned, and have cement in the re-entrant folds. The lower M1 comprises a posterior loop, three closed triangles, a confluent fourth and fifth triangle, and an elongated anterior loop bearing a salient angle on the inner side (text-fig. 42*b*).



TEXT-FIG. 42. (*a*) Lower right M1 of *Microtus* (*Allophaiomys*) sp. (M.33563b) from Bed 1. Occlusal view (posterior loop broken). (*b*) Lower left and right M1 of *Pitymys gregaloides* Hinton (M.34079) from Bed 10. Occlusal views. (*c*) Lower left M1 of *Pitymys arvaloides* Hinton (M.34020a) from Bed 10. Occlusal view. (*d*) Lower left and right M1 of *Microtus* cf. *arvalis* Pallas (M.34023) from Bed 10. Occlusal views. (*e*) Lower left and right M1 of *Microtus* cf. *oeconomus* Pallas (M.34024) from Bed 10. Occlusal views.

Discussion. The characteristic features of these remains are the confluent fourth and fifth triangles of lower M1 which indicate *Pitymys*, and the shape of the anterior loop which is characteristic of *P. gregaloides* Hinton. These remains are slightly larger in size to *P. gregaloides* from other early Middle Pleistocene sites (text-fig. 43).

The status of the genus *Pitymys* is not generally agreed upon, many Recent mammalogists regarding it as a subgenus of *Microtus*, though Sutcliffe and Kowalski (1976) chose to retain the name at generic rank. For convenience the genus *Pitymys* is referred to here, and the species dealt with here may be equated with *Microtus* (*Pitymys*) *gregaloides* of other authors (N.B. Meulen 1973).

Hinton (1923) recognized two species of *Pitymys* from the upper Freshwater Bed of West Runton, *P. gregaloides* and *P. arvaloides*, which he distinguished upon the shape of the anterior loop. Stuart (1975), however, believes only one species can be recognized, since although both 'gregaloides' and 'arvaloides' anterior loop shapes were present, there were intermediate forms, and measurements did not appear to indicate more than one species. At Westbury, however, while both forms can be recognized they occur together in very different proportions, as may be seen from the following examples:

TABLE 42. Frequency of finds of *Pitymys* forms in Beds 10 and 8 at Westbury.

Type of anterior loop	Number of finds	
	Bed 10	Bed 8
P. gregaloides	750	3
'Intermediate'	40	—
P. arvaloides	2	7

Meulen (1973) has made a detailed study of *Pitymys*, and recognized the validity of two fossil *Pitymys* species, which although they have intermediate morphotypes and cannot be distinguished by length measurement of M1 alone, could be diagnosed by a statistical analysis of the anterior loop. *P. gregaloides* from Westbury is larger than the Cromerian *s.l.* material from eastern Europe and from the Cromerian *s.s.* material from West Runton (text-fig. 43). It is also larger than the *P. arvaloides* material from Westbury, and, as such, a relative size difference between *P. gregaloides* and *P. arvaloides* cannot be used as a diagnostic character as suggested by Meulen (1973).

It should be noted that a small percentage of lower M1's have closed fourth and fifth triangles, but a 'gregaloides' type of anterior loop, and in this respect resemble *Microtus gregalis* (Pallas). These specimens, however, have precisely the same mean length as the larger *P. gregaloides* sample, and are almost certainly morphotypes of *P. gregaloides* where the fourth and fifth triangles have not opened to one another.

P. gregaloides has only been described from Cromerian *s.l.* sites, but is also known from Kent's Cavern (Hinton 1926), where it probably came from the Basal Breccia which is probably of pre-Hoxnian age and contemporary with Westbury.

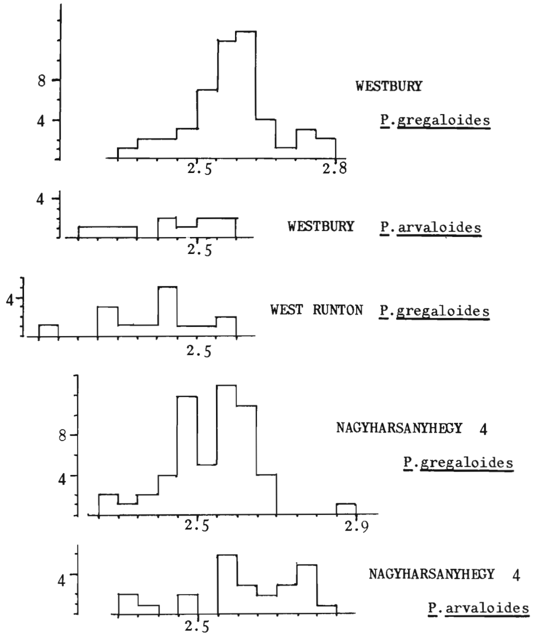
Pitymys arvaloides Hinton 1923

Text-fig. 42*c*

1923 *Pitymys arvaloides* Hinton, pp. 541, 542.
1976 *Pitymys arvaloides* Hinton; Sutcliffe and Kowalski, pp. 105, 106. (Synonomy.)

Material. Two lower M1's from Bed 10 (M.34020) and seven lower M1's from Bed 8 (M.34029).

Description. The teeth are rootless, prismatic, flat-crowned, and have cement in the re-entrant folds. The lower M1 comprises a posterior loop, three closed triangles, a confluent fourth and fifth triangle, and an anterior loop corresponding to the shape of that in *Microtus arvalis* (text-fig. 42*c*).



TEXT-FIG. 43. Histograms of the length (in mm) of lower M1 in *Pitymys*. Comparative measurements from Stuart (1975) and Meulen (1973).

Discussion. The confluent fourth and fifth triangles are characteristic of this tooth, and indicate *Pitymys*, and the shape of the anterior loop is characteristic of *P. arvaloides* Hinton. These remains are slightly smaller than *P. arvaloides* from other early Middle Pleistocne sites (text-fig. 43).

A number of points have already been discussed in the previous section on *Pitymys*, but as Sutcliffe and Kowalski (1976) point out, if *Pitymys* is a subgenus of *Microtus* then *P. arvaloides* is a taxonomic homonym and must be replaced by *M.* (*Pitymys*) *arvaloides* Kretzoi 1958, and this name is used in the literature where *Pitymys* is regarded as a subgenus (N.B. Meulen 1973). The generic interrelationship of *P. gregaloides*, *P. arvaloides, and Microtus* is unclear as has been pointed out, so both *Pitymys* species are recorded here since these species are well known to palaeontologists, and to use any other names may cause confusion.

P. arvaloides is recorded from numerous Cromerian *s.l.* localities, and in Britain survives into the Hoxnian interglacial (Sutcliffe and Kowalski 1976).

Microtus cf. *arvalis* (Pallas 1779)

Text-fig. 42*d*

1970 *Microtus arvalis* Pallas; Heal, p. 136.
1974 *Microtus arvalis* group; Bishop, pp. 309, 311, 314.
1976 *Microtus arvalinus* Hinton; Sutcliffe and Kowalski, pp. 61, 108, 109, 122, 124.

Material. Over 100 isolated teeth and mandibles from Bed 10 (M.34023) and 4 isolated lower M1's from Bed 8 (M.34027), 15 isolated lower M1's from Bed 5, and 1 lower M1 from Bed 4.

Description. The mandible is of the typical cricetid type, and the cheek teeth are rootless, prismatic, flat-crowned, and have cement in the re-entrant folds. The lower M1 comprises a posterior loop, five closed triangles, and a large anterior loop bearing a distinct salient angle on both sides (text-fig. 42*d*). All the upper M2's examined comprised a posterior loop and three closed triangles, and none bore an accessory loop.

Discussion. The morphology of these teeth and in particular the presence of five closed triangles indicates these remains belong to *Microtus*, while the morphology of the anterior loop is characteristic of *M. arvalis* (Pallas) and *M. agrestis* (L.). Since none of the upper M2's bear the accessory loop present in *M. agrestis*, these remains are compared with *M. arvalis*. The remains from Westbury are considerably larger than *M.* cf. *M. arvalis* from West Runton and Sugworth, and are slightly larger than Recent *M. arvalis/agrestis* (text-fig. 44).

Microtus cf. *oeconomus* (Pallas 1776)

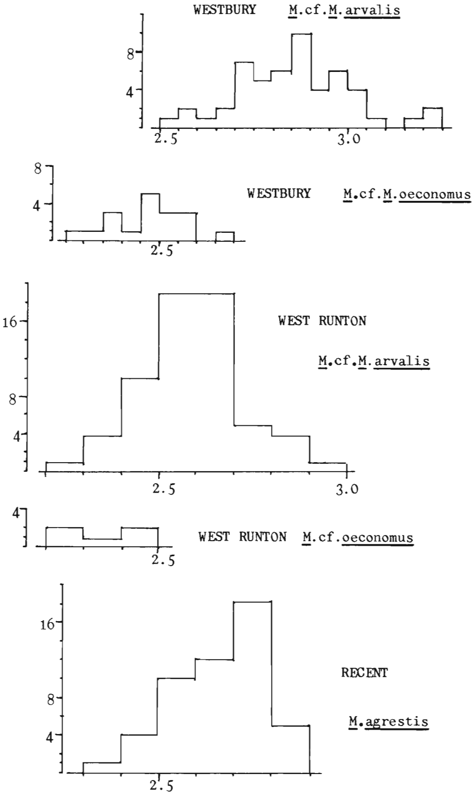
Text-fig. 42*e*

Material. Nineteen lower M1's from Bed 10 (M.34024).

Description. The teeth are rootless, prismatic, flat-crowned, and have cement in the re-entrant folds. The lower M1 comprises a posterior loop, four closed triangles, and simple anterior loop with a single salient angle (text-fig. 42*e*). These teeth are considerably smaller than *M.* cf. *M. arvalis* from Westbury.

Discussion. The morphology of these teeth indicates that they belong to *Microtus*, and the anterior loop and size of the teeth closely compare with *M. oeconomus* (Pallas). The Westbury material is close in size though a little larger than *M.* cf. *M. oeconomus* from West Runton (text-fig. 44) described by Stuart (1975).

M. oeconomus is a common element of the British Upper Pleistocene fauna (Sutcliffe and Kowalski 1976) where it is associated with cold faunas but, like other rodents described here, probably had a broader ecological tolerance in the Middle Pleistocene. Its Middle Pleistocene history is unclear, mainly because of the confused systematics of the microtids, but *M. ratticepoides* and *M. ratticeps* can probably both be regarded as synonyms of *M. oeconomus*.



TEXT-FIG. 44. Histograms of the length (in mm) of lower M1 in *Microtus*. Comparative measurements from Stuart (1975).

Family CASTORIDAE Gray 1821
Castor fiber Linnaeus 1758

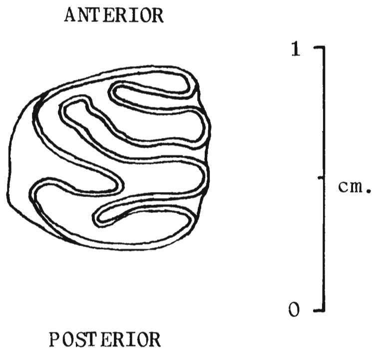
Text-fig. 45

1912 *Castor fiber* L.; Miller, pp. 947–954, text-figs. 197, 198. (Diagnosis and synonomy of living sp.)
1976 *Castor fiber* L.; Sutcliffe and Kowalski, pp. 79–81. (Synonomy.)

Material. Three fragmentary molars (M.34025a–e) and one upper right P4 (M.34026), all from Bed 1.
Description. The upper molar is large, recurved, rootless, and flat-crowned. The crown has a squarish outline in occlusal view, and comprises two large lobes on the outer side and four lobes on the inner side (text-fig. 45), and measures 7·1 mm long by 6·9 mm broad.

Discussion. The very large size of this tooth, its lack of roots, and its enamel pattern are identical to the living beaver *C. fiber* L.

Remains of *C. fiber* have been found from the Lower Pleistocene (Red Crag) up to the Holocene. The presence of beaver is of interest because of its close association with water and woodland.



TEXT-FIG. 45. Upper right P4 of *Castor fiber* L. (M.34026) from Bed 1. Occlusal view.

Order LAGOMORPHA Brandt 1855
Family LEPORIDAE Gray 1821
Lepus cf. *L. timidus* Linnaeus 1758

1974 *Lepus* sp.; Bishop, p. 309.

Material. Six upper molars and one lower molar from Bed 10. B.M.N.H. Colln.

Description. The cheek teeth are hypsodont, have open roots, and are basically cylinders of enamel infilled with cement and dentine, which in all but the first upper premolar are divided into two internally by a re-entrant enamel fold. In the first upper premolar the anterior border is indented by three re-entrant folds.

TABLE 43. Measurements (in mm) of cheek teeth of *Lepus* from Westbury. (B.M.N.H.)

	Length	Breadth
Westbury a. Ur. P1	2·0	3·4
Westbury b. Ur. P3	2·6	4·5
Westbury c. Ur. P3	2·5	4·4
Westbury d. Ur. M1	2·6	4·4
Westbury e. Lr. M1	3·2	3·4

TABLE 44. Faunal list and stratigraphic occurrence of mammal remains from Beds 1, 3–8, and 10 at Westbury, with comparative occurrences at some selected early Middle Pleistocene sites.

Westbury 1 = Fauna of Bed 1
Westbury 2 = Fauna of Beds 3–8
Westbury 3 = Fauna of Bed 10

	Numbers of identifiable bones/teeth								West Runton	Voigtstedt	Süssenborn	Stránská Skála	Hundsheim	Mosbach
Bed Number	1	3	4	5	6	7	8	10						
Erinaceus sp.	—	—	—	—	—	—	—	2	+	—	—	+	(+)	—
Talpa europaea L.	—	—	—	×	—	—	—	40	+	—	—	+	+	?
T. minor Freudenberg	—	—	—	—	—	—	—	2	—	+	—	—	+	—
Desmana moschata L.	—	—	—	—	—	—	—	15	+	(+)	—	(+)	(+)	+
Neomys cf. *newtoni* Hinton	—	—	—	—	—	—	—	8	+	(+)	—	—	(+)	—
Sorex minutus L.	—	—	—	—	—	—	—	3	—	—	—	+	+	—
S. runtonensis Hinton	—	—	—	×	—	—	—	200	+	(+)	—	+	(+)	—
S. savini Hinton	—	—	—	×	—	—	—	11	+	(+)	—	—	(+)	?
Plecotus auritus L.	—	—	1	?5	—	—	—	1	—	—	—	+	+	—
Myotis cf. *emarginatus* Geoffroy	—	—	—	?1	—	—	—	—	—	—	—	—	+	—
Barbastella barbastellus Schreber	—	1	1	?1	—	—	—	—	—	—	—	—	+	—
Ursus deningeri Reichenau	—	540	160	170	16	2	5	6	+	+	+	+	+	+
Hyaena brevirostris Aymard	1	—	—	—	—	—	—	—	—	—	+	+	(+)	(+)
Crocuta crocuta Erxleben	—	1	—	?1	—	—	—	—	+	—	+	+	?	+
Homotherium latidens Owen	—	1	1	1	—	—	—	—	—	(+)	(+)	(+)	(+)	(+)
Felis (*Lynx*) sp.	1	1	—	—	—	—	—	—	—	—	—	+	—	+
Panthera gombaszoegensis Kretzoi	—	25	5	5	1	—	1	—	—	—	?	+	—	+
P. leo fossilis Reichenau	—	—	3	2	1	—	—	—	—	—	—	?	—	+
Mustela erminea L.	—	1	—	—	—	—	—	20	—	—	—	—	(+)	—
M. nivalis L.	—	—	—	—	—	—	—	20	+	—	—	—	—	+
Gulo gulo L.	—	1	—	—	—	—	—	—	—	—	—	—	—	+
Canis lupus mosbachensis Soergel	—	46	5	8	1	—	—	2	+	+	+	+	+	+
Xenocyon lycaonoides Kretzoi	—	4	1	1	—	—	—	—	—	—	—	+	—	+
Vulpes cf. *vulpes* L.	—	—	—	?1	—	—	—	—	—	—	—	(+)	—	—
Equus caballus mosbachensis Reichenau	—	1	1	3	—	—	—	—	+	—	—	—	—	+
Dicerorhinus etruscus Falconer	7	—	—	3	—	—	—	—	+	+	+	+	+	+
Cervus cf. *elaphus* L.	—	3	2	3	1	1	—	—	+	+	+	+	+	+
Dama sp.	3	—	1	—	—	—	—	1	+	—	—	—	—	—
Bovinae cf. *Bison shoetensacki* Freudenberg	44	—	—	—	—	—	—	—	—	+	+	+	—	+
Bison cf. *priscus* Bojanus	—	10	2	13	1	1	1	1	?	—	—	—	+	+
Caprinae cf. *Soergelia elizabethae* Soergel	—	—	—	?1	—	—	—	—	—	—	+	—	—	—
Ovis or *Capra* sp.	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Hemitragus sp.	—	—	—	?1	—	—	—	—	—	—	—	—	+	—
Apodemus sylvaticus L.	—	—	—	×	—	—	—	1	+	(+)	—	—	+	—
Lemmus lemmus L	—	—	—	1	—	—	—	6	—	—	—	—	—	—
Dicrostonyx torquatus Pallas	—	—	—	—	—	—	—	1	—	—	—	(+)	—	—
Clethrionomys glareolus Schreber	—	—	—	2	—	?1	—	1	+	+	—	(+)	(+)	—
Pliomys episcopalis Méhely	—	—	—	—	—	—	—	1	—	—	—	(+)	+	+
Mimomys savini Hinton	2	—	—	—	—	—	—	—	+	+	+	+	—	—
Arvicola cantiana Hinton	—	—	—	×	—	—	—	100	—	—	—	—	+	+
Microtus (*Allophaiomys*) sp.	2	—	—	—	—	—	—	—	—	—	—	—	—	—
Pitymys gregaloides Hinton	—	—	—	×	—	—	4	1000	+	—	+	+	+	?
P. arvaloides Hinton	—	—	—	—	—	—	8	2	+	—	—	—	—	—
Microtus cf. *arvalis* Pallas	—	—	—	×	—	—	4	100	+	+	+	?	+	+
M. cf. *oeconomus* Pallas	—	—	—	—	—	—	—	19	+	+	—	?	—	—
Castor fiber L.	4	—	—	—	—	—	—	—	+	+	+	+	—	+
Lepus cf. *timidus* L	—	—	1	×	—	—	—	7	+	+	—	—	—	?
Ochotona cf. *pusilla* Pallas	—	—	—	—	—	—	—	1	—	—	—	+	—	?
Bed number	1	3	4	5	6	7	8	10						

Left-hand columns { × = present, numbers not determined (recovered from B.M.N.H. excavations at W.5).
? = uncertain stratigraphic occurrence.

Right-hand columns { (+) = genus present.
? = identification uncertain.

Discussion. The morphology of these remains closely compares with *Lepus*, and D. Mayhew (pers. comm.) has provisionally identified these remains as *L. timidus* L.

There are several records of *Lepus* from the European Middle Pleistocene, but few have been definitely referred to *L. timidus*, and so the exact relationship of these earlier finds to *L. timidus* and *L. europaeus* is not well understood. Stuart (1973) has recorded *L.* of *L. timidus* from the Cromerian *s.s.* of West Runton.

Family OCHOTONIDAE Thomas 1897

Ochotona cf. *Ochotona pusilla* (Pallas 1768)

1974 *Ochotona pusilla* (Pallas); Bishop, p. 309.

Material. One upper right incisor from Bed 10 (M.33560).

Description. The incisor is strongly recurved, has open roots, and in cross-section is of parallelogram shape with a deep groove on its dorsal surface. The enamel covering of the tooth extends to the posterior surface, and the occlusal surface of the tooth is relatively flat and not deeply notched as in *Lepus*.

Discussion. The tooth is indistinguishable from *O. pusilla*, though clearly there is insufficient evidence to confirm its specific identity.Further finds through the excavations of the B.M.N.H. have, however, confirmed the presence of the Pika at Westbury (A. Currant pers. comm.).

O. pusilla is common in the Upper Pleistocene of Europe and records of *Ochotona* are not uncommon in the Middle Pleistocene, but identification with *O. pusilla* is not certain in these cases (Kurtén 1968). This appears to be by far the earliest record of *Ochotona* in the British Pleistocene, for Stuart (1973) records the oldest find as probably late Devensian.

TAPHONOMY AND PALAEOECOLOGY

The mammalian remains fall into three natural groups summarized in Table 45. These three groups reflect three very different environments from which they were derived, and text-fig. 46 shows in more detail the relative abundance of the various mammal species and groups. These diagrams are necessarily approximations to the exact occurrence of the various mammal species, and sample errors without doubt bias some groups, but they provide, nevertheless, a reasonable indication of the three

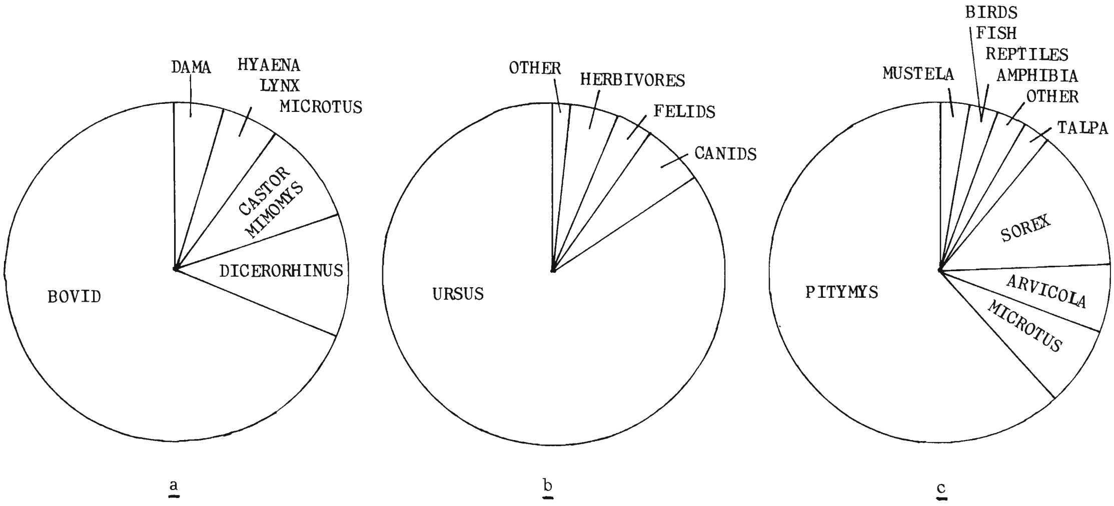
TABLE 45. Biostratigraphic and lithostratigraphic division within the Westbury sequence.

Local faunal-based stage name	Bed no.	Collective lithostratigraphic names	Dominant faunal element	Derivation of fauna	Climate t = temperate c = cold
Westbury 3	10	Calcareous Member	*Pitymys*	Owl-pellet accumulation	t
Westbury 2	3–9		*Ursus*	Carnivore lair	t
		Siliceous Member			c
Westbury 1	1		Bovid	Derived 'open' fauna	t

faunas. It is important to note that text-fig. 46*b* representing the fauna of Beds 3–9 does not include rodents and insectivores, good samples of which were never available to the author, but which have been forthcoming from the B.M.N.H. excavations.

Bed 1, text-fig. 46a—the high proportion of herbivores and low proportion of carnivores from the gravels of Bed 1, suggests derivation from an 'open' terrestrial fauna. The poor representation of species and the uncertainties of depositional history do, however, cast some doubt upon whether these remains can be regarded as a contemporaneous faunal assemblage or whether a mixed fauna is represented. The teeth and bone fragments of all the remains, excluding the small rodents, tend to be heavily rolled, waterworn, and mineralized to a similar degree. Mineralization which is iron-based, probably occurred *in situ* in the gravel channels which have been extensively encrusted by a lateritic deposit subsequent to their deposition. Nearly all the bones appear to be highly fragmented long bones, which together with the teeth have been exposed to erosion over a long period in a watercourse. The presence of *Castor* and *Mimomys*, both of which rely on permanent surface water, is strong evidence for the existence of permanent surface drainage upon the Mendip Plateau prior to the deposition of Bed 1. The presence of a river course tends to increase the chances of representation of both land and aquatic animals as fossils when an opportunity of burial arises, the land animals being susceptible to drowning, or their remains being washed in by flood or re-excavated by a river, and the aquatic animals may clearly pass directly into river deposits. Behrensmeyer (1975) has demonstrated the large number of factors which affect the dispersal and incorporation of animal bones into the ground from their original habitats, and the remains from Bed 1 have probably had a long and complex history which is impossible to reconstruct. The final stage of burial and deposition within the cavern may have been under fluvio-glacial conditions, so the faunal remains would antedate any such cold episode.

Beds 3–9, text-fig. 46b—this fauna comprises a very large number of carnivores and a relatively small number of herbivores, the inverse proportion of the natural food chain. This situation is common, however, where carnivores use a sheltered environment as a lair, or where a pitfall attracts carnivores



WESTBURY 1 WESTBURY 2 WESTBURY 3

Bed 1 Beds 3–8 Eed 10

TEXT-FIG. 46. Composition of the three main Westbury faunas (small mammals are excluded from Westbury 2).

to accidental deaths (Sutcliffe 1970). In view of the composition of the abundant *Ursus* population discussed earlier, it is most likely that a sheltered cavern was available for bears to hibernate over winter. As may be seen from many examples of other Pleistocene remains in caves, other carnivores also used caves, though apart from *Crocuta* not to the same degree as *Ursus*. Canids and felids are relatively abundant, and all the specimens belong to adults, so it would seem that these carnivores made occasional use of caves, possibly attracted by prey carried back to the lair. The herbivores present among this fauna are probably the prey of the carnivores, though it is difficult to say which herbivores were the prey of which carnivores. Some may, however, have been accidental fatalities if a part of the source area of these remains comprised a ravine which might be expected in the vicinity of a cavern, so remains of very large animals like *Dicerorhinus* may have been chance fatalities, which would of course be exploited by the carnivores. In this respect carnivores may have taken advantage in cornering very large game such as *Bison* which is the largest and most common herbivore. This fauna is so well represented by carnivores that there are few palaeoecological indicators among the rest of the large mammals, and the few there are represent both open grassland and woodland. A full analysis of the small mammals from the B.M.N.H. excavations of the East Basin may provide some useful information, although small mammals from these beds often occur as concentrated pockets which may represent the residue of bird-of-prey pellets, and these small mammals may have been gathered from a wide area.

Bed 10 text-fig. 46c—This fauna mainly comprises small mammals, in particular microtine rodents and insectivores. *Pitymys* accounts for the largest numbers of any one taxon, and *Microtus* and *Sorex* the second largest. Such rich accumulations of small mammals, and this is the richest deposit of its type in the British Isles, are unknown under natural ecological conditions, but can be explained as the residue of bird-of-prey pellets. The relative proportions of the different small mammals present closely compare with proportions observed in Recent Barn Owl pellets (Table 46).

TABLE 46. Relative occurrences of taxa in Recent Barn Owl pellets (from Buckley and Goldsmith 1975) compared with the same taxa in Bed 10 at Westbury.

Comparable genera	Barn Owl	Westbury Bed 10
Talpa	<1%	1%
Sorex	28%	14%
Neomys	1%	1%
Apodemus	6%	<1%
Microtus/Pitymus	51%	62%
Arvicola	<1%	8%
Clethrionomys	3%	<1%
Lagomorph	<1%	<1%
Mustela	<1%	6%
Aves and amphibia	2%	2%
	93%	96%

These typically show that microtine rodents comprised the predominant prey, and second, *Sorex* was the most common element of the diet. Variations in the proportions of prey will depend on the species of owl and the local habitat supporting the small mammals.

Evidence that these remains may represent the residue of owl rather than diurnal raptor pellets is afforded by the preservation of the remains, which comprise uneroded teeth, mandibles, facial portions of skulls, and postcranial bones. The remains have clearly suffered some damage, probably by sedimentary transport, since shrew mandibles no longer bear their incisors and the coronoid process is broken off the majority of microtine mandibles, but the remains do not show the erosion of bone that occurs in the pellets of diurnal raptors (Mayhew 1977).

Since this fauna may represent an owl-pellet accumulation, it cannot be relied upon as an indicator of the immediate local habitat, since these remains may have been brought in from other areas. As Mayhew (1977) has pointed out, the activity rhythms, behaviour, and hunting preferences of birds of prey have to be taken into account to understand the composition of these birds' prey, and so only a generalized picture can be obtained of the local small-mammal fauna and the surrounding habitat.

FAUNAL CORRELATION

The Westbury mammals fall into three natural groups based on their ecology, taphonomy, and stratigraphical occurrence, and between each of these three groups is a hiatus which can be shown to exist on geological grounds, and in the case of the Bed 1 fauna on faunistic grounds. It is proposed that each of the faunas set out in text-fig. 46 be designated a number as shown in Table 46, so that Westbury 1 represents all the faunal elements contained in Bed 1, Westbury 2 all the elements in Beds 3 to 8, and Westbury 3 all the elements in Bed 10. As elaborated elsewhere in this paper, Bed 1 can be regarded as a division from the rest of the infill on sedimentological grounds, Beds 3 to 8 can be regarded more or less as a continuous sedimentological sequence, and Bed 10 can be regarded as a distinct unit unconformable with its surrounding beds. Undesignated bed numbers 2 and 9 may be used and subdivided in future on beds in the East and West Basin Complexes. The full faunal content of these divisions is set out in Table 44. The only reasonable basis for comparison of the Westbury faunas in Britain are the faunas of the Cromer Forest Bed Series, and the faunas of Swanscombe, Kent. Other faunas of the Middle Pleistocene in Britain are either too poor in species, bear unreliable stratigraphic information, or require considerable further research. It is particularly useful to refer to these sites in comparisons since they are currently receiving a considerable amount of attention from research workers.

Table 47 lists those mammals present at Westbury which are also present either at West Runton, or at Swanscombe, or at both. The lowermost and uppermost Swanscombe faunas are considered here, comprising the fauna from the Lower Gravel, since this represents the oldest mammal-rich horizon, and the fauna from the Upper Middle Gravel since this represents the youngest mammal-rich horizon (details mainly from Sutcliffe 1964 and Sutcliffe and Kowalski 1976). The list does not include mammals unique to Westbury, and it does not include mammals ranging through all three sites that show no observable or significant differences. Thus, all the mammals listed are those that appear to be of direct correlative value in considering these three particular sites. The total faunal content of the deposits is given in Table 44 though, as explained earlier, this does not include many beds of the West and East Basin, but this does not affect any of the arguments presented.

Comparisons with European faunas offer a more valuable basis for correlation of the Westbury faunas, since European sites of Middle Pleistocene age are so much more abundant, and many of the Westbury mammals are otherwise unknown in the British Pleistocene. Tables 44 and 48 indicate the possible correlations of the Westbury faunas with some of the better-documented European sites.

Westbury 1—Great Britain. While this fauna is very impoverished in numbers and species, and may be a mixed assemblage, *Mimomys* is present, whereas the faunas in the overlying beds contain *Arvicola*. As has already been discussed, the presence of *Mimomys* is taken by most authors to indicate an upper age limit of Cromerian *s.s.* Stuart and West (1976) have suggested that the replacement of *Mimomys* by *Arvicola* occurred around about the Cromerian Zone III–Zone IV boundary, and this is discussed below in considering the presence of *Arvicola* at Westbury. As far as the fauna of Bed 1 is concerned, the presence of *Mimomys* indicates that this fauna is no later than the Cromerian *s.s.* as defined at West Runton. The presence of *Microtus* (*Allophaiomys*) suggests that this fauna, or a part of it, pre-dates the Cromerian, and this contention is supported by the presence of *Hyaena brevirostris*, which is also recorded from Bacton, Mundesley, and Sidestrand, where

Pastonian sediments are present at all three sites (Stuart 1974), and by the presence of a small *Dama* species possibly comparable to *Dama* from East Runton (Table 47). Bovid remains from the Cromer Forest Bed series are too poorly known to allow a comparison with the small bovid from Bed 1, which itself cannot be accurately described on isolated teeth, but a small *Bison* species does appear to be present as well as a larger species at several sites. The presence of *Dicerorhinus etruscus* merely confirms that this fauna belongs to the early Pleistocene.

Westbury 1—Europe. Table 48 shows a few European sites where some of the more important elements such as *Hyaena brevirostris* and *Mimomys savini* are recorded, while *Microtus* (*Allophaiomys*) is recorded from earlier sites such as Betfia 2 (Romania), and Monte Peglia (Italy). These sites appear to represent stages from the base of the Middle Pleistocene (Betfia 2) probably up to Cromerian *s.s.* (Süssenborn). Unfortunately the Westbury 1 fauna is so poor that comparison abroad in this instance is of little further help, though once again the presence of *M.* (*Allophaiomys*) suggests an earlier rather than later date.

TABLE 47. Species from Westbury that are also common to either West Runton or Swanscombe, comprising elements of use in determining the relative ages of respective faunas.

	West Runton	Westbury					Swanscombe		Late Pleistocene
		W1		W2	W3		LG	UMG	
Desmana moschata	●				○				
Sorex runtonensis	●			●	●	▮			
Sorex savini	●			●	●	▮			
Neomys newtoni	●				○	▮			
Talpa europaea	●			○	○				○
Mimomys savini	●	●	▮						
Arvicola cantiana			▤	●	●				○
Pitymys gregaloides	●			○	○	▮			
Microtus cf. *arvalis*	●			○	○			●	●
Lemmus lemmus			▤	●	●			●	●
Hyaena brevirostris		●	▮						
Canis lupus	●			●	●		○	○	○
Ursus deningeri	●			○	○	▮			
Equus caballus	●			●	●		○	○	○
Dicerorhinus etruscus	●			●		▮			
Dama	●	●		●	●		○	○	●

○ — species significantly differs biometrically from related form marked ●.

▮ — represents the disappearance or extinction of the species.

▤ — represents first appearance of species.

LG = Lower Gravel, Swanscombe.
UMG = Upper Middle Gravel, Swanscombe.

TABLE 48. Occurrences of key mammal species at various European Pleistocene sites, grouped within the three *Mimomys* and *Arvicola* faunal groupings of Koenigswald (1973)

⋱ = species replaced —— = species not extant + = present − = absent at site ? = cf.	Lower Pleistocene	Stránská Skála Czechoslovakia	Koneprusy C718 Czechoslovakia	Voigtstedt East Germany	Sussenborn East Germany	West Runton Great Britain	Westbury 2 and 3	Mauer West Germany	Hundsheim Austria	Erpfingen 1 and 3 West Germany	Sudmer-Berg 2 West Germany	Mosbach II West Germany	Tarko (Ur. fauna) Hungary	Uppony I (Ur. fauna) Hungary	Heppenloch West Germany	Swanscombe (composite) G.B.	Upper Pleistocene
Talpa europaea small sp.	+	−	+	+	−	+ ⋱											
T. europaea large sp.		+	−	−	−	−	+	+	+	+	−	?	+	+	+	−	+
Sorex savini		−	+	?	−	+	+	−	+	+	+	?	+				
S. runtonensis	+	+	+	?	−	+	+	−	−	?	−	−	−				
S. kennardi-subaraneus gp.		−	−	−	−	−	−	−	+	+	+	−	+	+	+	?	
Lemmus sp.	+	−	+	−	−	−	+	−	−	+	−	−	+	−	−	+	+
Dicrostonyx sp.	+	+	+	−	−	−	+	−	−	−	+	−	+	+	−	−	+
Pliomys episcopalis		−	+	−	−	−	+	+	+	+	+	+	+				
Mimomys savini	+	+	+	+	+	+ ⋱											
Arvicola cantiana							+	+	+	+	+	+	+	+	+	+	
Ursus deningeri		+	+	+	+	+	+	+	+	?	−	+	+ ⋱	?—			
U. spelaeus														?	+	+	+
Canis lupus mosbachensis		+	+	+	+	+	+	+	+	+	+	+	+ ⋱				
C. lupus large sp.														+	+	+	+
Xenocyon lycaonoides	+	+	+	−	−	−	+	−	−	−	−	+	−				
Panthera gombaszoegensis	+	+	+	−	?	−	+	−	−	−	−	+	−	?—			
P. leo fossilis		−	−	−	−	−	+	+	−	−	?	+	− ⋱				
P. leo spelaea														−	+	+	+
Dicerorhinus etruscus	+	+	+	+	+	+	+	+	+	−	−	+	+				
D. kirchbergensis							−	−	−	−	−	+	−	−	−	+	
Equus caballus mosbachensis		−	+	−	−	+	+	+	−	+	−	+	−				
E. sussenbornensis		+	−	−	+	−											
Bison priscus		−	−	−	−	?	?	+	+	+	−	+	+	+	+	−	+
B. schoetensacki	+	+	+	+	+	−	−	−	−	−	−	−	+	−	−	−	
		Mimomys savini fauna						*Arvicola* fauna, group 1						*Arvicola* fauna, group 2			

The Westbury 1 fauna appears to represent remains derived from the land surface, and comprises elements which in the British context suggests affinities with the Pastonian, and in Europe can be compared with a number of sites of Cromerian *s.l.* date.

Westbury 2 and Westbury 3. These two faunas are considered together since the important fossils *Arvicola cantiana*, *Lemmus lemmus*, *Pitymys*, large *Microtus* cf. *M. arvalis*, *Ursus deningeri*, *Canis lupus mosbachensis*, *Sorex savini*, and *S. runtonensis* are common to both sequences yielding mammal faunas (Tables 44 and 47). There are no grounds to suggest that these two faunal groups did not exist within the same temperate stage. The common elements of the fauna represent species identical in size and morphology, and the only differences in the faunas is their mode of accumulation, one under the conditions of a carnivore lair and the other as a bird-of-prey pellet deposit. The fauna of Bed 10 also contains some important records so far unrecorded in the rest of the sequence, which provide an upper limit of correlation, and this in turn reflects the fact that Westbury 3 belongs to the same temperate stage as Westbury 2.

Great Britain. Table 44 shows the complete list of mammals comprising the Westbury 2 and Westbury 3 faunas and this is compared with other British and foreign sites, while Table 47, as discussed in the introduction to this section, shows a shortened list with some of the more critical occurrences in the three British sites of West Runton, Westbury, and Swanscombe. Both of these tables indicate that correlation of Westbury 2 and 3 can be excluded with Swanscombe, and can also be excluded with any other site in Great Britain apart from the Cromer Forest Bed Series, Sugworth, and possibly the basal deposit at Kent's Cavern. Of the forty-three species listed, only twenty-five are recorded from any British Pleistocene site apart from those excluded above. Many taxa, including *D. etruscus*, *Soergelia*, *Xenocyon*, *Felis gombaszoegensis*, and *Pliomys*, become extinct in the Middle Pleistocene, while other species are replaced by more evolved species such as *Ursus deningeri* by *U. spelaeus*, *C. lupus mosbachensis* by a large *C. lupus*, *Equus caballus mosbachensis* by a smaller *E. caballus*, and *S. runtonensis* by *S. araneus*. With so many distinguishing features, the Westbury 2 and 3 faunas can be shown to antedate all British faunas attributed to the Hoxnian interglacial, and with so many fundamental differences in the Westbury faunas, a relatively long period of time must separate Westbury 2 and 3 and the oldest Hoxnian faunas such as that from the Lower Gravel of Swanscombe.

Having set an upper limit for Westbury 2 and 3, their correlation with older faunas must be considered. Of the 43 species listed in Table 44, 27 are recorded from the combined total of all the Cromer Forest Bed localities, and 23 from West Runton alone. This might at first suggest that the Westbury 2 and 3 faunas are as distinct from the Forest Bed Series as from the Hoxnian faunas. However, an examination of Table 44 shows that the species common to both Westbury and West Runton are important key species *Sorex runtonensis*, *S. savini*, *Neomys newtoni*, *U. deningeri*, *C. lupus mosbachensis*, *D. etruscus*, *E. caballus mosbachensis*, and *Pitymys*. The species present at Westbury but absent from the Forest Bed localities can largely be explained ecologically, since the bat species would be expected to occur in the cave environment of Westbury, the over-representation of carnivores at Westbury is explained by a carnivore lair, and selection of the small mammals may occur where the remains are derived from bird-of-prey pellets. If one therefore excludes the bats, the rare carnivores, and the rare small mammals, twenty-one of twenty-seven Westbury species are represented at West Runton. Of these some of the more important records are set out in Table 47, showing that although many elements are common to West Runton and Westbury 2 and 3, several of the Westbury representatives show significant size increases over their West Runton counterparts. These increases are all in species where there are documented records of evolutionary size trends in the Middle Pleistocene, which implies that the faunas of Westbury 2 and 3 are later than the fauna of West Runton. This is shown to be the case by the presence of *Arvicola* and absence of *Mimomys* in Westbury 2 and 3, which has already been discussed under the sections devoted to these taxa. *Arvicola* is also recorded from Ostend, Norfolk, and this fauna includes *S. runtonensis*, *S. savini*, *D. moschata*, *Talpa europaea*, *C. glareolus*, and *Microtus* cf. *M. arvalis* (Stuart and West 1976). The common elements of the Westbury 2 and 3 faunas compare with the Ostend fauna very closely, not only in the fundamental common presence of *Arvicola*, but also in that *T. europaea* is represented at both sites by a large animal, the size of the living species. The present writer agrees with Stuart and West (1976) that the Ostend fauna probably belongs to the same stage as the Westbury fauna, but as discussed in the final section of this paper, believes that Ostend may not belong to the Cromerian but possibly to a hitherto unrecognized temperate stage. Stuart and West (1976) were able to analyse pollen containing sediment adhering to Ostend fossils, which they ascribed to Zone IV of the Cromerian, and so believed that the replacement of *Mimomys* by *Arvicola* could be placed at around about the Zone III–Zone IV boundary. On this basis they assigned Westbury and its European equivalents to Zone IV of the Cromerian also. The problem is that Westbury 2 and 3 faunas show some important differences from the West Runton fauna apart from *Arvicola* being present, many of which have been outlined above and further arguments are presented below in the context of European correlation, and it is difficult to see how so many differences can be accounted for within an interval of time representing a single vegetational zone.

Only two other British sites yielding early Middle Pleistocene mammals can be usefully referred to. The first is Sugworth, near Oxford, which has been attributed to Zone III of the Cromerian, and has a mammal fauna which includes *Mimomys savini*, *Pliomys episcopalis*, *Talpa minor*, and *Dicerorhinus etruscus* (Stuart 1980). Of all the microtine rodents common to Sugworth and Westbury (*Pliomys*, *Clethrionomys*, and *Microtus* cf. *arvalis*) all the Sugworth species are significantly smaller, and *Mimomys* is present as opposed to *Arvicola*. The second site is Kent's Cavern, in which the basal breccia has yielded *Pitymys gregaloides*, *Arvicola cantiana*, and probably *Homotherium latidens* (Campbell and Samson 1971). This basal horizon may be the same age as the Westbury 2 and 3 faunas, but until it can be re-excavated, little reliability can be put on the stratigraphic information available from the early collections.

In the British context the Westbury 2 and 3 faunas are pre-Hoxnian, but appear to postdate the Cromerian in containing *A. cantiana*, a very large form of *Microtus arvalis* and *Pitymys gregaloides*, an advanced form of *Ursus deningeri*, and advanced forms of *Desmana moschata*, *Neomys newtoni*, and *Talpa europaea*. Smaller differences are seen in other taxa, and of several new records to the British Middle Pleistocene, the occurrence of *Lemmus*, *Dicrostonyx*, *Pliomys*, *Sorex minutus*, and *T. minor* may be of particular significance in correlating these faunas.

Europe. Table 44 listing the faunal elements of Westbury, also shows where these mammals are recorded at European localities such that as far as possible at least one record is given for each taxa present at Westbury, and Table 48 lists some stratigraphically important taxa present at these and other British and European sites. The form of Table 48 follows the divisions of faunas proposed by Koenigswald (1973), that is, distinguishing sites where *Mimomys* is represented (*M. savini* fauna), sites where *Arvicola* is represented in association with *Pliomys* and *S. savini* (*Arvicola* fauna, group 1), and sites where *Arvicola* is represented but where many of the early Middle Pleistocene elements are missing (*Arvicola* fauna, group 2). The replacement of *Mimomys* by *Arvicola* was a profound evolutionary jump, and it is hard to conceive that it occurred across a Zone III–Zone IV period within one interglacial as suggested by Stuart and West (1976). One would expect, if this were the case, contemporaneous representation of both forms at sites such as Westbury, especially perhaps in owl-pellet accumulations gathered over a wide area. It seems much more reasonable to equate Westbury with the European sites placed within the Elster (Mindel) complex postdating sites such as Voigtstedt, and predating Holsteinian sites such as Heppenloch. Koenigswald's *Arvicola* fauna group 1 comprises sites placed within this complex (Table 48) on the association of *Arvicola*, *Pliomys*, and *S. savini*. Many European authors refer to a Mindel interstadial in correlating faunas of a post-Cromerian *s.s.* and pre-Holsteinian character, but since the evidence from deep-sea cores indicates that there may be between five and seven early Middle Pleistocene temperate stages, these faunas may well belong to a fully interglacial stage or stages. The composition of *Arvicola* 1 faunas certainly suggests a considerable time period separates some of these faunas, and that fully interglacial conditions probably existed, since, for example, the Sudmer-Berg 2 fauna indicates warm forest conditions (Koenigswald 1973) yet is in the immediate vicinity of the maximum of the Elster glaciation, and it is certainly difficult to explain so many approximately contemporary faunas so rich in species occupying an interstadial period. It seems most likely therefore that many of the *Arvicola* 1 faunas are separated from sites such as West Runton and Voigtstedt by at least one glaciation. Süssenborn is of some interest in this respect since it has yielded a fauna of Cromerian *s.s.* aspect very like Voigtstedt, but has been attributed to the onset of the Elster glaciation on the presence of cold elements such as *Ovibos* and *Rangifer* (Kahlke 1969*a*, 1969*c*). The apparent sudden appearance of *Arvicola* is easier to understand if Arvicola 1 faunas represent a stage, or stages, separated from *Mimomys savini* faunas by a glaciation, and there are several other indications that these faunas belong to different stages.

As has already been discussed in relation to West Runton, a large form of *Talpa europaea* is present in Westbury 2 and 3, and this form appears to be characteristic of *Arvicola* 1 faunas and all later faunas while a small form is characteristic of earlier sites, and is often referred to as *T. fossilis* (Table 48). An exception appears to be Stránská Skála from which *T. europaea* of the same size as the living species has been described (Rzebik 1972), though it is unfortunately not clear from which horizon these specimens came, and several horizons of differing ages are present at this site. As Kukla (1975) has shown, a part of the mammalian-bearing sequence of Stránská Skála appears to cover the Brunhes–Matuyama boundary, widely accepted as dating to 700,000 years B.P. This part of the sequence includes *Dicrostonyx*, *Pitymys gregaloides*, *Pliomys lenki*, *Mimomys*, and *Talpa*, though unfortunately it is not specified which species of *Talpa* is present. Whatever the case, the greater and older part of the Stránská Skála fauna appears to belong to the base of the Middle Pleistocene, so as far as considering *Talpa* is concerned, the typical Cromerian *s.l.* form is represented by the small *T. europaea* (= *T. fossilis*).

Several taxa either appear for the first time, or become well represented in *Arvicola* 1 faunas. These include the large bison, *Bison priscus*, and a large lion *Panthera leo fossilis*, and *Dicerorhinus kirchbergensis* makes its first appearance (Mosbach). Other species such as *Hyaena brevirostris*, *Equus robustus*, and *E. sussenbornensis* make their last appearance amongst *Mimomys savini* faunas. Of the species ranging through both the *Mimomys* and *Arvicola* many, such as *Microtus arvalis/agrestis*, *Pitymys gregaloides*, *Neomys*, *Desmana*, and medium-sized *Sorex* species, show small but discernible morphological differences and size differences to their equivalents in *Mimomys* faunas. Where *Ursus deningeri* is associated with *Arvicola* faunas, it has become highly evolved in the *U. spelaeus* direction.

The *Arvicola* 1 faunas are easily distinguished from the *Arvicola* 2 faunas, which include Hoxnian and Holsteinian sites, by the disappearance and extinction of many taxa at these later sites as indicated in Table 48. A surprising feature in the Westbury 2 and 3 faunas is the large-sized *Lemmus* which is typical of the later Pleistocene and not of the *Arvicola* 1 faunas. Conversely a large form is recorded from Sackdilling, Germany, but the fauna here, though largely a *Mimomys* type fauna, appears to be intermixed with later deposits causing some confusion in correlation (Koenigswald 1973). In the *Microtus* and *Pitymys* populations, *Microtus* becomes the dominant vole at sites equated with the *Arvicola* 2 faunas (Jánossy 1969*a*, *b*, 1975), or both are present in about equal numbers as for example at Petersbuch (Koenigswald 1973), but in the *Arvicola* 1 faunas *Pitymys* is by far the most common vole, as is the case at Westbury.

FAUNA—CONCLUSIONS

Westbury 1. The remains of this assemblage have been derived from the land surface, and may be of mixed origin, though all exhibit a similar state of preservation and all suggest an early Pleistocene date (pre-Cromerian), so it is convenient to include all the remains from Bed 1 under the faunal grouping of 'Westbury 1' at present. The content and preservation of the fauna indicate that permanent surface drainage existed on Mendip prior to Bed 1 times.

Westbury 2 and 3. These faunas are temperate, though contain elements that suggest climatic deterioration, in particular *Dicrostonyx*, *Lemmus*, and *Gulo*. Both faunas contain typical 'Cromerian' elements allowing distinction from sites equated with the Hoxnian and Holsteinian interglacials, but both faunas contain elements which allow distinction from *Mimomys* faunas of the early Middle Pleistocene. Westbury 2 and 3 correlate very closely with European faunas placed within the Mindel Complex (N.B. Mosbach), and as such probably represent a temperate period between the Cromerian and Hoxnian in Britain. The faunas also correlate with the fauna from Ostend, Norfolk, which lies between sediments of Cromerian and Anglian age, and tentative correlation is made with the fauna from the basal stratum of Kent's Cavern.

The Westbury 2 fauna represents remains largely derived from a carnivore lair, while the Westbury 3 fauna represents remains derived from owl pellets, and as such neither faunas reflect the ecological conditions of the immediate vicinity of the cave. On a wider scale the faunas indicate that relatively open vegetational conditions predominated, probably on the higher ground, while the surrounding lowlands probably supported woodland and bore rivers from which the woodland and aquatic elements of the small mammal fauna are derived.

The Westbury 3 fauna contains a number of elements that suggest the onset of a colder climate, notably *Lemmus* and *Dicrostonyx*, but it should be noted that there are also in the Westbury 2 fauna indications to suggest that adaptions to a less warm climate were already made. These include the adaption to the cave habitat of certain carnivores, the presence of elements such as *Gulo* and *Lemmus*, and possibly some of the size changes of certain taxa such as *Mustela* and *Ursus* which are sensitive to climatic change.

EVIDENCE OF MAN

A full description and discussion of the flints recovered from this site is beyond the scope of the present paper, and these will doubtless be treated by others elsewhere. The main intention is to outline discoveries made up to 1975, and to place them within the context of discoveries elsewhere in Britain and Europe.

As has been mentioned earlier, the presence of small pieces of flint in the Calcareous Member beds suggested that a human agency had introduced them to the site since it was difficult to explain their presence on geological grounds. This theory was strengthened when larger pieces of flint were found showing possible signs of human workmanship. Three of these flints, a struck flake, a crude bifacial pebble, and a large bifacial ovate flint, have been figured in the literature (Bishop 1975), of which the two bifacial implements were described as showing earliest Acheulian workmanship in the British context.

By 1975 a large number of small flints had been recovered from Bed 5, as well as sporadic finds in Bed 7 and 8. The flint is easily distinguished from intrusive surface finds (the surface yields Neolithic material) since it is deeply patinated to a chalk-white colour, and is often rotted to the extent that it crumbles to a powder. This phenomenon has been described by Schmalz (1960), Curry (1963), and Fairbairn and Robertson (1972), the cause of which Schmalz showed to be the attack by alkaline solution on the dense, fine-grained aggregate of ahedral quartz crystals of flint, which reduced grain size and increased porosity. A useful result of this breakdown described by Curry (1963), is that microfossils which are present in flint, can be separated and identified. Since this is a destructive process, here involving possible artefacts, only a few small samples were thus treated, one of which yielded a microfauna which could be dated as Coniacian (Upper Chalk). This is of interest in bearing upon conjecture made earlier on the possible proximity of Cretaceous rocks to the Mendips early in the Pleistocene.

The most impressive feature of all the larger pieces of flint found is that over 75% show possible signs of human workmanship, either as struck flakes or bifacial implements. The latter tend to show a well-developed biface on one particular edge of the flint, while flakes appear to simply be waste flakes, showing no clear signs of retouching, so if an artefact industry is truly present at Westbury, it is one that appears to be based upon the manufacture of core-tools.

The most widely accepted earliest evidence of men in Britain comes from the Hoxnian interglacial. The Upper Middle Gravels of Swanscombe have yielded a human skull associated with an Acheulian industry (Ovey 1964), and this stratum has generally been accepted as being of Hoxnian age, though on this point recent investigators (Conway 1972; Hubbard 1981) have raised new questions regarding the interpretation of this site. Artefacts unquestionably provide the earliest evidence of man in Britain, the best-documented finds being of the Clactonian and Acheulian industries from the early temperate basal horizons at Clacton, Hoxne, and Swanscombe (Wymer 1974; Gladfelter 1975). In Britain the Clactonian industry (based on flake-tools) has been held to have predated the Acheulian (Wymer 1974; Ohel 1977), and so an analysis of the Westbury finds is of great importance if a flint industry is truly represented.

The possible presence of an Early Acheulian industry at Westbury may explain a number of problematic finds in Britain of similar typology. The first of these is from Kent's Cavern, where the Basal Breccia has yielded artefacts of Early Acheulian type associated with a mammalian fauna which the author has compared elsewhere in this paper with that of Westbury, and which Campbell and Samson (1971) also regarded as pre-Hoxnian. Another group of finds, some of which may belong to the Early Acheulian, are from Caversham which Treacher, Arkell, and Oakley (1948) equated with the Early Acheulian of the Somme (Abbevillian). There is, however, no associated fauna with this group of artefacts, and the stratigraphic position of the Caversham Channel is somewhat doubtful. Roe (1968) recognized two typological groups of ovate hand-axes from these deposits, but in view of the long ranges which such groups appear to have, believed only the broadest of correlations could be made.

Many prehistorians have claimed that the 'eoliths' from the Crags of East Anglia were human artefacts (summary in Coles 1968), but most authorities now believe these flints were fashioned by natural agencies. If man was present in East Anglia in pre-Hoxnian times, then flint artefacts will be very difficult to differentiate amongst the wealth of naturally occurring flint flakes and fragments, and then only relatively advanced artefacts, typologically speaking, may be recognized. A good example of this is perhaps that described by Moir (1923) from the Anglian Till at Sidestrand, Norfolk, which very convincingly has the appearance of an artefact.

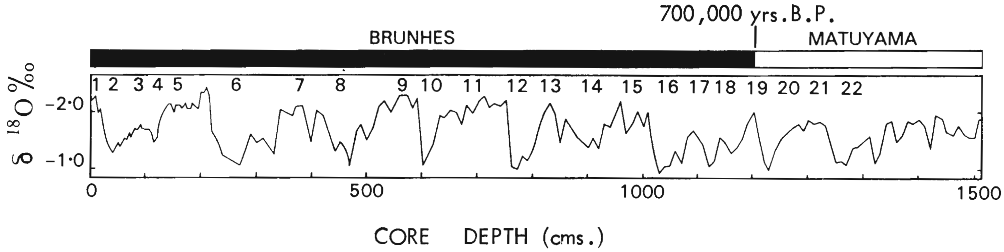
In the European context, the closest parallel with Westbury on typological and faunal grounds, are the artefacts from the 45-m terrace of the Somme, termed the Abbevillian. This industry, based on crude bifaces and flakes, has been recovered in association with a fauna allied to the British Cromerian, and was mainly excavated in the last century when artefacts were enthusiastically collected at the expense of properly recording the stratigraphy and contained fauna. A better parallel on faunal grounds is Mauer near Heidelberg, where a human mandible was found, which has been attributed by a number of authors to *Homo erectus*, but no associated artefact industry was recovered. The Hungarian site of Vértesszöllös, on the other hand, has yielded a fauna closely similar to Westbury, remains of *Homo erectus*, and a crude pebble tool industry, but here the artefact industry seems to have been separate but contemporary with the development of hand-axe traditions further west (Coles and Higgs 1969).

Further study of the flints from Westbury will hopefully confirm whether or not a human industry is really represented, the most striking argument in favour of a human agency at present being upon geological grounds, while a typological analysis, not attempted here, needs to be undertaken on a larger sample.

CORRELATION—DISCUSSION

Pleistocene correlations pose tremendous difficulties because of the incompleteness of the continental record, particularly in the Middle and Lower Pleistocene where for most sites there is no radiometric dating technique that can be applied. The development of research in the field of oxygen isotope stratigraphy has revolutionized Quaternary research (for review see Bowen 1978), and classical models of the Quaternary based on the continental record are being entirely revalued in the light of studies of continuous sequences of sediments from the oceans.

The relative completeness of the oceanic record provides a sound basis for a stratigraphic framework, and correlations of Last Glaciation events have already been established on this basis. Kukla (1975, 1977) has extended these principles to show how continental sequences throughout the



TEXT-FIG. 47. Oxygen isotope composition in core V-28-238 from Shackleton and Opdyke (1973), showing isotope stages 1 to 22.

Brunhes epoch may be correlated with the oceanic record. Radiometric and geomagnetic methods provide the most directly applicable means of correlation between the oceans and continents, and where these are not available, as is most often the case, correlation must for the time being be on a 'floating' basis until enough data is available to tie in correlations.

The deep-sea core V28–238 has been proposed as a standard for the later Pleistocene (Shackleton and Opdyke 1973) and is used here as a basic stratigraphic framework for correlations (text-fig. 47, Table 49).

Of all European pre-Elsterian stratigraphy, the best understood is the sequence in the Netherlands in which four interglacials (Interglacials I, II, III, and IV) and three intervening glacials (Glacial A, B, and C) precede the Elsterian (Zagwijn and Doppert 1971; Zagwijn and Doppert 1978). Of prime importance in the Dutch sequence is the fact that the Brunhes–Matuyama reversal is situated

TABLE 49. Age estimates of stage boundaries in core V-28-238 (from Shackleton and Opdyke 1973).

Boundary	Depth (cm)	Age (yrs.)
1–2	22	13,000
2–3	55	32,000
3–4	110	64,000
4–5	128	75,000
5–6	220	128,000
6–7	335	195,000
7–8	430	251,000
8–9	510	297,000
9–10	595	347,000
10–11	630	367,000
11–12	755	440,000
12–13	810	472,000
13–14	860	502,000
14–15	930	542,000
15–16	1015	592,000
16–17	1075	627,000
17–18	1110	637,000
18–19	1180	688,000
19–20	1210	706,000
20–21	1250	729,000
21–22	1340	782,000

between Interglacials I and II, indicating that these interglacials may be correlated with palaeotemperature stages 21 and 19 respectively (Table 50). Glacial B is of special interest since Zagwijn and Doppert (1971) describe an interstadial within this cold stage. As such it is quite possible that Glacial B correlates with palaeotemperature stages 16 to 18, where stage 17 represents the interstadial, for as Shackleton and Opdyke (1973) have noted, stages 16 to 18 appear to represent one long glaciation, one of the longest of the Pleistocene in fact. Palaeotemperature stage 12 is here equated with the Elsterian tills of Europe and Anglian tills in East Anglia as it represents a fully glacial stage sufficient

TABLE 50. Tentative correlation of early Pleistocene stages in Britain (including Westbury 2 and 3) with those of the Netherlands, with V-28-238 stages (text-fig. 46) and polarity determinations. British correlations are divided into two possibilities: Scheme A and Scheme B. Stages in upper case represent interglacials, those in lower case glacials. From Shackleton and Opdyke (1973), Zagwijn (1975), Zagwijn and Doppert (1978), and West (1980).

		Polarity	Palaeotemperature stages	Netherlands	Great Britain	
					Scheme A	Scheme B
	Middle Pleistocene	Brunhes	11	HOLSTEINIAN	HOXNIAN	HOXNIAN
			12	Elsterian	Anglian	Anglian
			13	INTERGLACIAL IV	CROMERIAN	[WESTBURY]
			14	Glacial C	Beestonian	
			15	INTERGLACIAL III	PASTONIAN	CROMERIAN
			16 17 18	Glacial B	d c Pre Pa b a	Beestonian
700,000 yrs. B.P.			19	INTERGLACIAL II	—	PASTONIAN
	Lower Pleistocene	Matuyama	20	Glacial A	—	Pre Pa ?
			21	INTERGLACIAL I	—	—
			22	Menapian Glacial	—	Pre Pa ?
			23	LEERDAM	—	—
		Jaramillo	24	Glacial	—	Pre Pa a
				BAVEL	—	—
				Glacial	—	—
				WAALIAN	? CHILLESFORD	
				Eburonian	? Baventian	
		Olduvai		TIGLIAN	ANTIAN THURNIAN LUDHAMIAN	

to give rise to the widespread ice sheets which characterize this glaciation, unlike stage 14. Shackleton (1977) has suggested that more ice accumulated during stage 12 than has done so in any subsequent glaciation. If these correlations are correct, then Interglacials III and IV may correlate with stages 15 and 13. Interglacial IV is associated with marine sediments of the Urk Formation, at the base of which K/Ar datings of augite derived from the Rhine sediments give a date of about 400,000 years B.P. (Frechen and Lippolt 1965). This date based on volcanic detrital material has been taken by most authors to be too young, so a correlation of Interglacial IV with stage 13 seems feasible given that the date of the boundary of stages 13 and 14 is estimated at just over 500,000 years (Table 49).

Correlating therefore with the Dutch sequence, which is currently the best continental sequence that can be equated with the deep-sea record, two possible schemes or 'floating stratigraphies' become the most likely correlatives in the British Middle Pleistocene (Table 50). In scheme A the Cromerian of Britain is correlated with Interglacial IV after West (1980) on the strength that the vegetational history is unlike that of Interglacials I, II, and III. With normal polarity found in the Pastonian, 'Pre Pastonian a' (West 1980), and Baventian, these may then fit into scheme A as shown in Table 50, or may be older as shown in the lower half of scheme B. Scheme B takes into account the view central to this paper, that a temperate period may exist between the Cromerian and the Hoxnian, and is represented in Britain by Westbury and the channel fill at Ostend, Norfolk.

The view that the Ostend deposits (Bed d of West 1980) and those of Westbury do not belong to the Cromerian on the grounds of their mammal faunas has been put forward under the previous section. Looking at the stratigraphical and palynological evidence as presented by West (1980), there is no reason why the deposit at Ostend should not be later than Cromerian. Bed d at Ostend which has yielded the mammal fauna of Westbury type, is a channel fill cutting through weathered clays (Bed c) with a rootlet bed at the top. The latter on palynological grounds is ascribed to Zone IVa of the Cromerian, and termination of deposition of Bed c was followed by the establishment on its surface of a land surface evidenced by the rootlet bed, and deep weathering. At a later stage still, this land surface was cut through by a river and Bed d was deposited. Bed d is ascribed by West to the same stage as Bed c, Cr IVa, but a different pollen assemblage biozone, yet the geological evidence clearly leaves room for a considerable hiatus between Beds c and d.

Correlation following scheme B (Table 50) would then imply that the Cromerian may be the equivalent of Interglacial III in the Netherlands and palaeotemperature stage 15. Interglacial III is represented by a pollen assemblage from Rosmalen (Ridder and Zagwijn 1962; Zagwijn 1974), but West (1980) excludes correlation with the Cromerian on the low frequencies of *Abies* and *Tilia.* With all the attendant uncertainties of correlating pollen assemblages on relative abundances of different taxa given differences in local habitats, regional distribution, and environment, it seems no more unreasonable to correlate the Cromerian with Interglacial III, than with Interglacial IV whose palynological characteristics remain unknown.

Some weight to the above correlations is added in considering the pre-Cromerian succession in scheme B. The section at Beeston is particularly interesting, since between sediments representing a cold climate are deposits yielding thermophilous plant taxa, and deposits representing a marine transgression (West 1980). This appears to represent an interstadial, and this may very well correlate with the interstadial of Glacial B in the Netherlands, so the Beestonian may in turn correlate with stages 18 to 16. The Pastonian would therefore correlate with stage 19 and Interglacial II as all show normal polarity. This palaeotemperature stage appears to have been of relatively short duration, and this may be reflected by the fact that Zone III does not appear to be fully represented in the Pastonian, suggesting the temperate climate was short lived. An earlier rather than later date for the Pastonian is also favoured because of the presence of small numbers of Tertiary relic taxa. Below the Pastonian the record is harder to interpret, but West (1980) described four substages all representing cool or cold climatic conditions. Non-sequences exist between them all and the Pastonian, so more than one cold stage may be represented. The most widespread of these horizons in East Anglia is the Pre-Pastonian a, correlated by West (1980) with Lu4c of the Ludham borehole. Normal polarity has been recorded in Pre-Pa a sediments at Sidestrand (Montfrans 1971), which may therefore equate with the Jaramillo event and a cold stage within the Menapian complex.

Returning to Westbury and Ostend, and their possible correlation within scheme B, palaeotemperature stage 14, which would separate them from the Cromerian, does not appear to be a fully glacial stage, a consistent observation in deep-sea records (Shackleton and Opdyke 1973). Looking at the deep-sea record it therefore seems justified to regard stages 13 to 15 as a long temperate period interrupted by a deterioration in climate (stage 14), just as stages 16 to 18 have been regarded as a protracted glacial period. In terms of vegetational history this would entail the full cycle of pollen zones I to IV within stage 15, but the character of pollen zones following the Cromerian Zone IV would doubtless depart from the conventional zonal sequence. In terms of the mammalian faunas, the correlation of Westbury 2 and 3 in scheme B would account for the presence of boreal mammals and for the palaeoecological adaptions seen. Thus the deteriorating climate from Cromerian Zone IV times might explain the adaption of *Ursus deningeri* and other carnivores to a cave habitat, the evolution of *Arvicola*, the immigration of *Dicrostonyx*, *Lemmus*, *Gulo*, and *Soergelia*, and the various size changes seen in the voles, mustelids, and insectivores associated with adaption to colder climates.

The deep-sea record has demonstrated that many changes in climate occurred during the Pleistocene, and has shown how pigeon-hole classifications based on incomplete continental successions have proved misleading in understanding Quaternary stratigraphy. The correlation of continental deposits must primarily rely on geomagnetic studies and radiometric dates, while between these few fixed points, the bulk of our knowledge of Pleistocene sites must be arranged within floating stratigraphies based on conventional studies such as palaeontology and lithostratigraphy.

The Westbury site has shown that the study of mammalian fossils from Pleistocene sites is still an invaluable stratigraphic tool, often more so than palynological based stratigraphy, since evolutionary traits and changes can be observed as well as climatic-based changes in the content of assemblages.

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