PLEISTOCENE RODENTS OF THE BRITISH ISLES

BY

ANTONY JOHN SUTCLIFFE
British Museum (Natural History), London

AND

KAZIMIERZ KOWALSKI
Institute of Systematic and Experimental Zoology,
Polish Academy of Sciences, Kraków, Poland

Pp. 31–147 ; 31 *Text-figures* ; 13 *Tables*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27 No. 2
LONDON: 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 27, *No.* 2, *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Geol.)

ISSN 0007-1471

BRITISH MUSEUM (NATURAL HISTORY)

Issued 29 *July*, 1976 *Price* £7.40

PLEISTOCENE RODENTS OF THE BRITISH ISLES

By A. J. SUTCLIFFE & K. KOWALSKI

CONTENTS

		Page
	Synopsis	35
I.	Introduction	36
	A. History of Studies	37
	B. The Geological Background	40
II.	Localities in the British Isles with fossil rodents	42
	A. Deposits of East Anglia	42
	(i) Red Crag	43
	(ii) Icenian Crag	43
	(iii) Cromer Forest Bed Series	46
	(a) Pastonian of East Runton and Happisburgh	47
	(b) Beestonian	48
	(c) Cromerian, *sensu stricto*	48
	(d) Anglian	48
	B. Terrace and Solifluxion deposits of the Rivers Thames and Lea	48
	(i) Lower Thames	51
	(a) High Terrace of Swanscombe	51
	(b) Clacton	52
	(c) Early Middle Terrace at Aveley, Grays Thurrock and Ilford	53
	(d) Late Middle Terrace at Crayford and Erith	54
	(e) Floodplain Terrace complex	54
	(f) The Middle Terrace/Floodplain Terrace problem	55
	(ii) Upper Thames	58
	(a) Isleworth	58
	(b) Marlow	58
	(iii) River Lea	58
	(a) Water Hall Farm Gravel Pit	58
	(b) Nazeing, Ponders End, Edmonton and Hackney	59
	(iv) Solifluxion and melt-water deposits	59
	(a) Northfleet, Ebbsfleet and Baker's Hole	59
	C. Cave Deposits	60
	(i) Westbury Fissure	60
	(ii) Kent's Cavern	61
	(iii) Tornewton Cave	62
	(iv) Other caves with pre-'Ipswichian' deposits	65
	(v) 'Ipswichian' cave deposits	67
	(vi) Caves with post-Ipswichian deposits	67
	(vii) Caves in Scotland	67
	(viii) Caves in Ireland	68
	D. Other Localities	69
	(i) Cromerian localities	69

		Page
(ii)	Hoxnian localities	69
(iii)	'Ipswichian' localities	69
(iv)	Last Glaciation localities	69
(v)	Holocene localities	72
(vi)	Scottish localities	73

III. CLASSIFICATION AND DISTRIBUTION OF RODENTS IN THE PLEISTOCENE OF THE BRITISH ISLES . . . 73

Family SCIURIDAE Brandt . . . 73
Genus *Sciurus* Linnaeus . . . 73
Sciurus whitei Hinton . . . 73
Sciurus vulgaris Linnaeus . . . 74
Genus *Spermophilus* Cuvier . . . 75
Spermophilus (*Urocitellus*) *primigenius* Kormos . . . 75
Spermophilus (*Colobotis*) *superciliosus* (Kaup) . . . 76
Family GLIRIDAE Thomas . . . 77
Genus *Muscardinus* Kaup . . . 77
Muscardinus avellanarius (Linnaeus) . . . 77
Family CASTORIDAE Gray . . . 78
Genus *Trogontherium* Fischer . . . 78
Trogontherium minus Newton . . . 78
Trogontherium boisvilletti (Laugel) . . . 78
Genus *Castor* Linnaeus . . . 79
Castor fiber Linnaeus . . . 79
Family MURIDAE Gray . . . 81
Genus *Apodemus* Kaup . . . 81
Apodemus sylvaticus (Linnaeus) . . . 81
Apodemus flavicollis (Melchior) . . . 83
Genus *Micromys* Dehm . . . 84
Micromys minutus (Pallas) . . . 84
Genus *Mus* Linnaeus . . . 84
Mus musculus Linnaeus . . . 84
Genus *Rattus* Fischer . . . 84
Rattus rattus (Linnaeus) . . . 84
Rattus norvegicus (Berkenhout) . . . 84
Family CRICETIDAE Rochebrune . . . 85
Genus *Cricetus* Leske . . . 85
Cricetus cricetus (Linnaeus) . . . 85
Genus *Allocricetus* Schaub . . . 86
cf. *Allocricetus bursae* Schaub . . . 86
Genus *Dicrostonyx* Gloger . . . 87
Dicrostonyx torquatus (Pallas) . . . 87
Genus *Lemmus* Link . . . 90
Lemmus lemmus (Linnaeus) . . . 90
Genus *Clethrionomys* Tilesius . . . 92
Clethrionomys glareolus (Schreber) . . . 92
Genus *Pliomys* Méhely . . . 95
Pliomys episcopalis Méhely . . . 95
Genus *Mimomys* Major . . . 95
Mimomys pliocaenicus Major . . . 95
Mimomys reidi Hinton . . . 97
Mimomys newtoni Major . . . 97
Mimomys savini Hinton . . . 98

	Page
Genus *Arvicola* Lacépède	99
Arvicola cantiana (Hinton)	102
Arvicola cantiana-terrestris	103
Arvicola terrestris (Linnaeus)	103
Genus *Pitymys* McMurtrie	105
Pitymys arvaloides Hinton	106
Pitymys gregaloides Hinton	107
Genus *Microtus* Schrank	107
Microtus arvalinus Hinton	108
Microtus agrestis (Linnaeus)	109
Microtus arvalis (Pallas)	112
Microtus nivaloides Major	114
Microtus nivalis (Martins)	114
Microtus ratticepoides Hinton	116
Microtus oeconomus (Pallas)	117
Microtus gregalis (Pallas)	118
Genus *Lagurus* Gloger	120
Lagurus lagurus (Pallas)	120
IV. History of the rodent fauna of the British Isles during the Pleistocene	121
Red Crag	122
Icenian Crag and Pastonian Forest Bed	122
Cromerian *sensu stricto*	122
'Westbury stage'	122
Mundesley Arctic Bed	123
Hoxnian deposits	123
Comparison of the rodent faunas	123
Notes on the Wolstonian-Ipswichian part of the succession	124
Middle Terrace of the Thames interglacial	125
Tornewton Cave Glutton Stratum cold stage	125
Joint Mitnor interglacial	126
Last Glaciation	127
Holocene	128
Ireland	129
V. Acknowledgements	129
VI. References	130
VII. Index	137

SYNOPSIS

For nearly half a century, since its publication in 1926, M. A. C. Hinton's *Monograph of the Voles and Lemmings* has remained the only comprehensive work on British Pleistocene rodents. Subsequent advances in Quaternary studies and the availability of new fossil material have made some updating of this publication necessary. In the present work a brief historical review of the studies of British Pleistocene rodents is followed by a description of the rodent assemblages from the principal fossil localities. Rodent species recorded from the British Pleistocene are then discussed in systematic order and, finally, an attempt is made to relate a generalized sequence of rodent faunas to the climatic sequence usually employed today as the basis for British Pleistocene chronology.

I. INTRODUCTION

Nearly half a century has elapsed since the publication by the British Museum (Natural History) of M. A. C. Hinton's *Monograph of the Voles and Lemmings* in 1926. Today it is still the only comprehensive work on British Pleistocene rodents and remains the standard reference work on this subject. In the meantime there have been great advances in many related fields of study. Hinton did not attempt to relate his sequence of rodent faunas to the glacial–interglacial sequence of climatic events, which was already gaining favour at the time of his studies, and which is known today to be even more complicated than the four glacial and three interglacial stages for so long employed as a basis of Pleistocene chronology.

Excavations in the British Isles since 1926 have produced a wealth of new fossil rodent material which was not available to Hinton. Findings from the Westbury-sub-Mendip Fissure (Somerset), Swanscombe (Kent), Tornewton Cave (Devon) and a series of Late Glacial cave sites in the Peak District (Staffordshire and Derbyshire), excavated and published by various workers, are of special importance. The advent of carbon-14 (^{14}C) dating has permitted the accurate dating of some Upper Pleistocene rodent remains. Studies of pollen and insects are further, relatively new, stratigraphic aids.

On the continent of Europe there have been great advances in rodent studies which provide a basis for the interpretation of rodent migrations into the British Isles and assist in identifying stages of geographical isolation. W. von Koenigswald's recent work (1972, 1973) on the *Mimomys–Arvicola* lineage, based initially on continental European remains and subsequently extended to the British Isles, throws new light on the British Pleistocene rodent sequence.

In the present work the authors have cooperated on a reappraisal of the Pleistocene rodent faunas of the British Isles. One of us (K. Kowalski of Kraków, Poland) is mainly responsible for the systematic part and for comparison with continental evidence ; the other (A. J. Sutcliffe of London) for the stratigraphic sequence of British rodent faunas. Discussions with W. von Koenigswald (Tübingen) about the *Mimomys–Arvicola* lineage have contributed fundamentally to the last-mentioned part of this work.

Although we cover 37 species of rodents from over 100 sites, many problems remain which can only be resolved by further careful collecting. Additional material is needed from critical deposits such as the early and late parts of the Forest Bed Series of Norfolk and from Hinton's Middle Terraces of the Thames, or from deposits of equivalent age. Some of the faunal assemblages which we have listed, such as that from the Otter Stratum of Tornewton Cave, are unique and cannot be compared with deposits of the same age in other parts of the British Isles. We have shown scarcely any evidence of differences between contemporary faunas in different areas, nor of temporal faunal changes within the broad climatic phases used for reference. The systematic relationship between some of the rodent species is still far from clear. All these aspects of rodent studies and many others offer great scope for future research. If this Bulletin provides a stepping stone for such work it will have been worth while.

A. History of Studies

Although publications of the eighteenth century and, in greater number, of the first decades of the nineteenth contain references to the occurrence of remains of beaver in British Quaternary deposits, the first scientific description of fossil rodents from this country did not appear until the middle of the nineteenth century. In 1846 R. Owen published a detailed description, accompanied by excellent drawings, of the remains of *Trogontherium cuvieri* and *Castor fiber* from the Forest Bed deposits of East Anglia. He also mentioned the presence of the remains of *Arvicola* 'which I have been unable satisfactorily to distinguish from *Arvicola amphibia,* or common Water-rat' (1846 : 202) in the sediments of many caves. The bones of the same species were present, according to Owen 'in newer pliocene deposits'. He considered (1846 : 205) the specimens from the 'older pliocene crag near Norwich . . . indicated a species of *Arvicola* intermediate in size between the Water-vole (*Arvicola amphibia*) and the Field-vole (*Arvicola arvalis*)'.

The next important contribution to the study of British Pleistocene rodents was that of W. A. Sanford. His papers on rodents from caves of Somerset (1870a, b) contain not only descriptions of forms still living in Britain (*Arvicola terrestris, Clethrionomys glareolus* and *Microtus agrestis*) but also of species now extinct in this country (*Microtus oeconomus, Lemmus* 'of the type of *L. norvegicus*' and *Dicrostonyx torquatus*). It is interesting to note that Sanford correctly determined the skulls of *D. torquatus* but ascribed jaws of the same species to *Arvicola gulielmi.* He mentioned also the occurrence of a small hamster, '*Cricetus songarus* (Pallas)', and *Spermophilus erythrogenoides*, a species previously discovered and described by H. Falconer (in Murchison 1868).

The first attempt to make a systematic classification of fossil voles, one of the most difficult groups of rodents, was made by H. P. Blackmore & E. R. Alston (1874). They failed to recognize the difference between Recent and fossil species, but were the first to record *Microtus nivalis* in Britain.

A series of works on the 'preglacial' deposits of East Anglia by E. T. Newton (1881, 1882a, b, 1890b, 1891 and 1909) provides an important contribution to the knowledge of the rodents of this area. Newton was the first to state that the vole remains were specifically different from Recent forms and he named a new species, *Arvicola intermedius* Newton 1881. He also published diagnoses of two other new species of rodents, a hamster, '*Cricetus vulgaris Runtonensis* n. subsp.' and a beaver '*Trogontherium minus* n. sp.' His work is of importance in regarding the vertebrate remains, including many rodents, from the 'pre-glacial' deposits of East Anglia as specifically distinct from living forms. He also published the first scientific description (1894, 1899a, b) of the vertebrate remains, including rodents, from the rich late Pleistocene fauna of Ightham Fissures, Kent.

The greatest contribution to the study of British Pleistocene rodents was that of M. A. C. Hinton (1883–1961). His first note on this subject appeared in 1900 and later this group of mammals became the main object of his interest. His work culminated in 1926 with the publication of volume 1 of his *Monograph of the Voles and Lemmings*. Hinton soon became the world authority on Microtinae and his monograph (unfortunately unfinished) is still the standard work in this branch of mammalogy. He was the first to recognize that, since rodent species have short ranges in time, their remains are of special stratigraphic value in the study of the Pleistocene. They thus help the geologist attempting to correlate scattered or isolated cavern deposits with others to which ordinary stratigraphical methods can be applied. The importance of this concept was further expanded by Kowalski (1966).

Hinton (1926a ; 1926b : 126–136) recognized a series of rodent faunas of different ages at British localities. In order of increasing antiquity these were as follows :

Third Terrace of the Thames, in the valley of the River Lea.
Ightham Fissure (Kent) stage.
Late Middle Terrace of the Thames (typical locality Crayford and Erith, Kent).
Early Middle Terrace of the Thames (typical locality Grays Thurrock, Essex).
High Terrace of the Thames (Ingress Vale, Swanscombe, Kent).
Upper Freshwater Bed at West Runton, Norfolk.
Shelly Crag at East Runton, Norfolk.
Norwich Crag and Weybourne Crag of the Norfolk Coast.

Although Hinton did not attempt to relate this division to any sequence of climatic fluctuations, his faunal stages were far ahead of any other palaeontological division of the British Pleistocene at that time.

Hinton also laid the basis for systematic study of the Microtinae (Savage 1963). After 1926 he abandoned nearly completely his study of the British fossil rodents, being involved in problems of pest control and the study of other mammals. He nevertheless published in 1952 a thorough description of rodent remains from the Late Glacial deposits of the Lea Valley.

Hinton's work is not only an important chapter in the history of zoology, but it still forms the standard reference on British Pleistocene rodents. For this reason it seems necessary to mention some of its limitations. He was a monoglacialist, or strictly an antiglacialist, as he postulated only one very late and only moderately cold period in the Pleistocene history of England. This opinion, which he regarded as the established truth, probably also influenced his zoological views. When he came across the fossil remains of species associated today with arctic climate he was inclined to determine them as forms different from Recent ones, since they could not then be used as evidence of particular climatic conditions.

Hinton was a prominent typologist. Although he was not more of a 'splitter' than most of his contemporary zoologists, he nevertheless used subspecific names extensively and was inclined to determine each new variant as a new species. For this reason, even in Hinton's own collection, many intermediate specimens were left undetermined.

Finally, Hinton accepted the multituberculate origin of rodents, a theory now generally rejected. He accepted that microtine evolution has always led from forms with complicated to forms with simple teeth. Strangely enough this did not hinder him in the correct reconstruction of some of the lines of evolution in voles, since among the different tendencies in the late evolution of the teeth of this particular group some lines did indeed progress from more complicated to simpler tooth-patterns.

Relatively few contributions to the study of British Pleistocene rodents have been published since the appearance of Hinton's monograph. These include the work of J. W. Jackson (1932, 1934) ; L. S. Palmer (1934) ; A. Schreuder (1929, 1931, 1950, 1951) ; J. N. Carreck (1957, 1966) ; D. Bramwell (1960, 1964, 1970) ; A. J. Sutcliffe & F. E. Zeuner (1962) ; J. C. Pernetta (1966) ; R. J. G. Savage (1966) ; K. Kowalski (1967) ; W. von Koenigswald (1973) and M. Bishop (1974, 1975). Most of these papers contain site lists of rodents with relatively little general discussion of their stratigraphical or systematic position. The papers by Schreuder (1929, 1931, 1951) are worthy of special mention for containing a thorough redescription and systematic discussion of the beaver remains from Britain. The paper of 1950 contains a list of the voles from the stratigraphically important Middle Pleistocene deposits of Swanscombe, Kent. More recently A. J. Stuart, in a general review of the British Pleistocene fauna (1974), listed the rodent faunas from key sites and discussed their stratigraphical occurrence.

Since the last synthetic work of Hinton (1926b) there has been great progress in other fields of study related to the problem of the history of British rodents. Investigations on the continent of Europe (not without influence from Hinton's work) have brought to light many rich local rodent faunas of Pliocene and Pleistocene age and have made it possible to reconstruct in greater detail the stratigraphical position and evolutionary history of many of these mammals. Recent contributions in the field include the work of J. Chaline (1972), who gives a detailed description of the rodents of the Middle and Upper Pleistocene of France, and of W. von Koenigswald, who studied the phylogenetic lineage of the genus *Arvicola*. In addition, knowledge of the systematic position, ecology and geographical variability of Recent rodents has greatly improved throughout the whole of the Palaearctic region.

In the British Isles there have been extensive geological and palaeobotanical studies (e.g. West 1968), which have provided a more detailed stratigraphic background for rodent studies. In addition the stratigraphic position of many old localities has been clarified and new rodent localities have been discovered. A new aspect of investigation has been provided by zoological studies of insular races of small mammals (Corbet 1961).

In view of the increasing importance of rodents in stratigraphic studies and of all the additional information which has become available since the publication of Hinton's monograph, it is timely to review the existing data on British Pleistocene rodents. In the description which follows the stratigraphic age of crucial rodent localities of the British Isles will be further examined, the systematic position and synonymy of the rodent species, currently overburdened with too many names connected with insufficiently characterized forms, will be discussed and the history of the rodent population of Britain during the Pleistocene reviewed. Many gaps nevertheless remain in the known sequence of events. This paper does not contain morphological descriptions of the various species of British Pleistocene rodents, a task, important for further stratigraphic and systematic studies, which needs to be carried out in the future. In the meanwhile subspecific designations are not used in the present paper. The nomenclature of living species of rodents here used is based mainly on the work of Ellerman & Morrison-Scott (1966). Information about morphology, biology and distribution of Recent rodents in Britain is available in Miller (1912), Matthews (1952), Southern (1964) and Corbet (1966). Beirne (1947) has discussed the possible arrival dates of some species of rodents into the British Isles.

B. The Geological Background

As previously mentioned, great progress has been made towards a more detailed understanding of the British Pleistocene sequence since Hinton published his monograph in 1926. Some deposits considered to be Pliocene at that time are now regarded as Lower Pleistocene, and there now exists a detailed picture, still being further elaborated from current studies, of alternating glacial and interglacial stages in the British Isles. A recent contribution of special importance is that of West & Wilson (1966), who demonstrated from palaeobotanical studies that the Cromer Forest Bed Series of Norfolk in fact represents two interglacial stages with an intervening cold stage.

At the present time the most generally accepted correlation for the British Pleistocene is that recommended by the Geological Society of London (Mitchell *et al.* 1973), which is shown, with some additional information from other sources indicated, in Table 1.

While in general it seems possible to relate most British rodent faunas to this sequence, there are some parts (notably the Cromerian and Wolstonian–Ipswichian stages) which seem inadequate to account for all the rodent stages currently attributed to them. There can be little doubt that they are more complex than is indicated in the table opposite.

Although, in the 1973 correlation of the Geological Society, the Wolstonian and Ipswichian are recognized as two stages only, an earlier correlation published by the same Society (Evans 1971) proposed a more detailed chronology for this part of Pleistocene time which must be mentioned here, since it has important application to our rodent studies.

From a consideration of information derived from deep-sea cores and other lines of evidence Evans argued that there had been more than one warm phase since the Hoxnian (Holsteinian) Interglacial. Whilst accepting the period from about 100 to 70 thousand years ago (which he regarded as the true Last Interglacial, the Ipswichian or Eemian, equivalent to Zeuner's Late Monastirian shoreline) as the only fully warm period of considerable length since the Holsteinian, he drew attention to other lesser mild phases of post-Holsteinian age about 170 000 and 130 000 years ago, possibly equivalent to the Danish Vejlby I and Vejlby II mild stages, the possible relationship of which is shown in Table 2.

Evans also drew attention to some problems related to the interpretation of this part of the Pleistocene sequence. He pointed out that Zeuner, who regarded the Last Interglacial as double, used the term 'Last Interglacial' for two different ranges of time, that lasting from 180 to 120 thousand years ago (cycles 5w and 4) and also for that lasting from 130 to 70 thousand years ago (cycles 4w and 3). He considered that some confusion had arisen in archaeological circles where 'Last Interglacial' had been used as a reference datum and preferred to restrict this term only to zone 3w.

TABLE 1

Generalized British Pleistocene sequence

	Stages: NW Europe	Stages: S Britain	Climate: Britain	British deposits	Hinton's Rodent Faunas (1926) Probable stratigraphic position
HOLOCENE	Holocene	FLANDRIAN	Temp.		
UPPER PLEISTOCENE	Weichselian	DEVENSIAN	Cold (G+P)		Third Terrace of the Thames in the Lea Valley Ightham Fissure Stage
	Eemian	IPSWICHIAN	Temp.		Late Middle Terrace of the Thames Early Middle Terrace of the Thames
	? Saalian (pars)	WOLSTONIAN (GIPPINGIAN)	Cold (G+P)	CAVE TERRACE & ALLUVIAL DEPOSITS	
MIDDLE PLEISTOCENE	Holsteinian	HOXNIAN	Temp.		High Terrace of the Thames
	? Saalian ? Elsterian	ANGLIAN (LOWESTOFTIAN)	Cold (G+P)		(Hinton's Plio-Pleistocene boundary)
		CROMERIAN	Temp.	CROMER FOREST BED SERIES	Upper Freshwater Bed at West Runton
	'Cromerian'	BEESTONIAN	Cold (P)		
LOWER PLEISTOCENE	Menapian	PASTONIAN	Temp.		Shelly Crag at East Runton
	Waalian	BAVENTIAN	Cold (P)	ICENIAN CRAG (WEYBOURNE & NORWICH CRAGS)	Norwich and Weybourne Crags
	Eburonian	ANTIAN	Temp.		
	Tiglian (U. Villafranchian of Italy)	THURNIAN	Cold		
	– – ? – –	LUDHAMIAN	Temp.	RED CRAG	
	Pre-Tiglian (L. Villafranchian of Italy)	WALTONIAN		(erosion)	
PLIOCENE	Reuverian (Astian of Italy)		Temp.	CORALLINE CRAG	

Based on West 1968, Sparks & West 1972, and Mitchell, Penny, Shotton & West 1973. Hinton's rodent stages (1926) are shown at their most likely position in the last column of the table. (Under Climate: Britain, G = Glacial, P = Periglacial.)

TABLE 2

Possible relationship of continental climatic divisions to British mild phases (after Evans 1971)

Evans' half-cycles (c = cold, w = warm)	Years ago	British stage names	Continental climatic divisions	Mediterranean sea levels
2c	70 000		Early Weichsel, Early Würm	
3w	100 000	IPSWICHIAN	Eemian	Late Monastirian
3c	120 000		Saale 2, Riss 2, Warthe	
4w	130 000		Vejlby 2	Main Monastirian
4c			Minor cold phase	
5w	180 000		Vejlby 1, ? Domnitz	
5c	200 000		Saale 1, Riss 1	
6w		HOXNIAN	Holsteinian	

It follows from Evans' chronology that the terms Saale 2, Riss 2 and Penultimate Glaciation of some authors have been used for periods of time later than Last Interglacial of some other authors, and that great confusion can arise here if stage names such as these are applied incautiously to our studies of British Pleistocene rodents. Likewise the terms Penultimate Glaciation or Wolstonian (when applied away from the type locality) could confusingly be used to mean any period of time from that considered by some writers to be the middle of the Hoxnian/Holsteinian (for example, Mullender's suggestion in Wymer (1974) that the upper part of Lower Loam of Swanscombe is Wolstonian) to that immediately preceding Evans' Interglacial half-cycle 3w. Wymer (1974) has suggested a warm stage during the Wolstonian. Bristow & Cox (in Mitchell *et al.* 1973) have argued, from their study of glacial deposits in East Anglia, that the interglacial deposits at the Hoxnian type locality of Hoxne belong to the last and not penultimate interglacial and they referred the Ipswichian and Hoxnian deposits, which they accepted may have been separated by a cold oscillation, to a single interglacial between the Devensian and Anglian.

In the present paper we will try to overcome such problems, as far as possible, by concentrating on establishing a relative chronology for the rodent faunas of the British Isles which will not be affected by future refinements in the naming of the British Pleistocene sequence, rather than to attempt to refer these faunas too rigidly to a chronology which is clearly incomplete. Let us now make a detailed examination of the rodent faunas from the various British Pleistocene localities.

II. LOCALITIES IN THE BRITISH ISLES WITH FOSSIL RODENTS

Remains of Pleistocene rodents have been found at many localities in the British Isles, notably in the early Pleistocene marine Crag and Forest Bed deposits of East Anglia and in later river terrace and cave deposits. In Ireland they are known only from cave deposits of late Pleistocene age. The location of the principal localities is shown in Fig. 1.

A. Deposits of East Anglia

Extensive areas of Suffolk and Norfolk are covered by Crag and Forest Bed deposits from which rodent remains have sometimes been recovered.

Although recent research (West & Wilson 1966, Norton 1967, West 1968) has greatly increased understanding of the early Pleistocene sequence of East Anglia, all the rodent remains from this region available for the present study are unfortunately from old collections, many of them with imprecise stratigraphic information. A series of rodent faunas can nevertheless be distinguished.

(i) Red Crag. This is a marine shallow-water shore deposit typically laid down in land-locked bays. It is best developed in Suffolk where it consists mainly of shelly sands. There is also a basal nodule bed with rolled and polished fossils, including mastodon teeth, apparently derived by the Crag sea from earlier deposits. The occurrence of these derived fossils, which include mammalian remains of Eocene, Miocene and Pliocene age, makes the study of the Red Crag mammalian fauna extremely difficult. For a long time the deposit was considered to be of Pliocene age and it was not until 1948 that its Lower Pleistocene date was accepted and the occurrence of relatively unmineralized contemporary mammalian remains, associated with the derived fossils, was recognized.

Only a few rodent remains have been found in the Red Crag. *Trogontherium minus* (known from Astian localities on the European continent) and *Hystrix*, represented by teeth (Spencer 1966) and by gnawing on part of a deer antler (Sutcliffe & Collings 1972), are probably derived from pre-Pleistocene deposits and cannot be included in the contemporary Red Crag faunal list.

Castor fiber, recorded from a number of Red Crag localities, including Sutton and Woodbridge (47, Fig. 1) is probably a contemporary species. A rolled microtine tooth from the Red Crag has been provisionally referred by Spencer (1964) to *Mimomys* sp.

(ii) Icenian Crag. A further series of marine deposits, the Icenian Crag (including the Norwich and Weybourne Crags), occupies a basin on the north of the Red Crag outcrop. It was apparently laid down in a more open sea. Its exact relationship to the Red Crag is not fully understood, but its age appears to range from Thurnian, through Antian and Baventian, to Pastonian. According to West (1968), these stages may be equivalent to the Tiglian, Eburonian and Waalian in the stratigraphy of the Netherlands. The relationship between the Norwich and Weybourne Crags is also not clear. The Weybourne Crag, typified by the mollusc *Macoma balthica*, is found at more than one stage. The youngest part of the sequence, including part of the Weybourne Crag, is of Pastonian age and is contemporaneous with the lowest part of the Cromer Forest Bed series. Part of the Norwich Crag of Suffolk may also be Pastonian.

Rodent remains, which have been found in the Norwich and Weybourne Crags of Bramerton (55, Fig. 1), Covehithe (51), Easton Bavents (50), Sizewell (49),Thorpe (48), Trimingham (61) and other localities represent *Mimomys pliocaenicus*, *M. reidi*, *M. newtoni*, *Castor fiber* and *Trogontherium boisvilletti*. Since conditions were unsuitable for the preservation of very small remains, it is not surprising that no teeth of glirids and murids have been found in the deposits. *M. pliocaenicus* and *M. reidi* are typical Tiglian (Upper Villafranchian) elements and confirm a Lower Pleistocene age for at least part of this series.

FIG. 1. Location map of the principal Quaternary rodent localities in the British Isles. Key to numbers opposite.

KEY TO FIG. 1

1 Joint Mitnor Cave, Buckfastleigh, Devon
2 Levaton Cave, Torbryan, Devon
3 Tornewton Cave, Torbryan, Devon
4 Brixham Cave, Brixham, Devon
5 Happaway Cave, Torquay, Devon
6 Kent's Cavern, Torquay, Devon
7 (i) Cow Cave, Chudleigh, Devon
7 (ii) Chudleigh Fissure, Devon
8 Huntspill Cut, Huntspill, Somerset
9 (i) Brean Down, nr Brean, Somerset
9 (ii) Uphill Cave, Uphill, Somerset
10 (i) Hay Wood Rockshelter, Hutton, Somerset
10 (ii) Bleadon Cave, Bleadon, Somerset
10 (iii) Picken's Hole, nr Bleadon, Somerset
10 (iv) Hutton Cave, Hutton, Somerset
10 (v) Banwell Cave, Somerset
11 (i) Rowberrow Cavern, Burrington, Somerset
11 (ii) Aveline's Hole, Burrington, Somerset
12 Gough's Cave, Cheddar, Somerset
13 Westbury-sub-Mendip Fissure, Somerset
14 Clevedon Cave, Clevedon, Somerset
15 Alveston Fissure, Alveston Gloucestershire
16 (i) Minchin Hole, nr Penard, Glamorganshire
16 (ii) Bacon Hole, nr Penard, Glamorganshire
17 (i) King Arthur's Cave, nr Whitchurch, Herefordshire
17 (ii) Great Doward Cave, Whitchurch, Herefordshire
18 Merlin's Cave, Symond's Yat, Herefordshire
19 Beckford, Worcestershire
20 Upton Warren, nr Droitwich, Worcestershire
21 Sugworth, Oxfordshire
22 Fisherton, Salisbury, Wiltshire
23 Thatcham, Berkshire
24 (i) West Wittering, Sussex
24 (ii) Selsey, Sussex
25 Marlow, Buckinghamshire
26 Isleworth, Middlesex
27 Crayford and Erith, Kent
28 Ightham Fissures, Ightham, Kent
29 Northfleet, Kent
30 Swanscombe, Kent
31 Upnor, Kent
32 Murston, Kent
33 Grays Thurrock, Essex
34 Aveley, Essex
35 Ilford, Essex
36 (i) Hackney, London
36 (ii) Angel Road, Middlesex (north London)
36 (iii) Ponders End, Middlesex
37 Nazeing, Lea Valley, Essex
38 Water Hall Farm, Hertfordshire
39 Hitchin, Hertfordshire
40 Barrington, Cambridgeshire
41 Cambridge Fens (including Burwell and Swaffley), Cambridgeshire
42 Copford, nr Colchester, Essex
43 Clacton, Essex
44 (i) Harkstead, Suffolk
44 (ii) Stutton, Suffolk
45 Felixstowe, Suffolk
46 (i) Bobbitshole, nr Ipswich, Suffolk
46 (ii) Stoke Tunnel Beds, Ipswich, Suffolk
47 (i) Sutton, Suffolk
47 (ii) Woodbridge, Suffolk
47 (iii) Kyson, Suffolk
48 Thorpe, Norfolk (see p.96)
49 Sizewell, Suffolk
50 Easton Bavents, Suffolk
51 Covehithe, Suffolk
52 Kessingland, Suffolk
53 Geldeston, nr Beccles, Norfolk
54 Hoxne, nr Diss, Suffolk
55 Bramerton, Norfolk
56 Happisburgh, Norfolk
57 Ostend, Norfolk
58 Bacton, Norfolk
59 Paston, Norfolk
60 Mundesley, Norfolk
61 Trimingham, Norfolk
62 Overstrand, Norfolk
63 Cromer, Norfolk
64 East Runton, Norfolk
65 West Runton, Norfolk
66 Swanton Morley, Norfolk
67 Lynx Cave, Denbighshire (exact location not known)
68 Gwaenysgor Cave, Prestatyn, Flintshire
69 Elder Bush Cave, Wetton, Staffordshire
70 Harborough Cave, Brassington, Derbyshire
71 (i) Fox Hole Cave, High Wheeldon Hill, Earl Sterndale, nr Buxton, Derbyshire
71 (ii) Etches' Cave, Dowel Dale, Earl Sterndale, nr Buxton, Derbyshire
71 (iii) Dowel Cave, Dowel Dale, Earl Sterndale, nr Buxton, Derbyshire
72 Langwith Cave, Upper Langwith, nr Scarcliffe, Derbyshire
73 Pin Hole Cave, Creswell, Derbyshire
74 Hessle, nr Kingston-upon-Hull, Yorkshire
75 Staple Howe, nr Wintringham, Yorkshire
76 Star Carr, nr Scarborough, Yorkshire
77 Kirkdale Cave, Helmsley, Yorkshire
78 Cowside Cave No. 3, Settle, Yorkshire
79 Dog Holes Cave, Warton Crag, nr Carnforth, Lancashire
80 Middlestots Bog, Edrom Parish, Berwickshire, Scotland
81 Corstorphine, nr Edinburgh, Midlothian
82 Loch of Marlee, Kinlock, Perthshire
83 Creag nan Uamh Cave, Inchnadamph, Sutherland
84 Keshcorran Caves, Ballymote, Co. Sligo, Republic of Ireland
85 Edenvale Caves, nr Ennis, Co. Clare
86 Red Cellar Cave, nr Lough Gur, Co. Limerick
87 Castlepook Cave, Doneraile, Co. Cork
88 Castletownroche Cave, Connaberry, Co. Cork
89 Kilgreany Cave, Cappagh, Co. Waterford
90 Ballynamintra Cave, Whitechurch, Co. Waterford
91 Nornour, Isles of Scilly

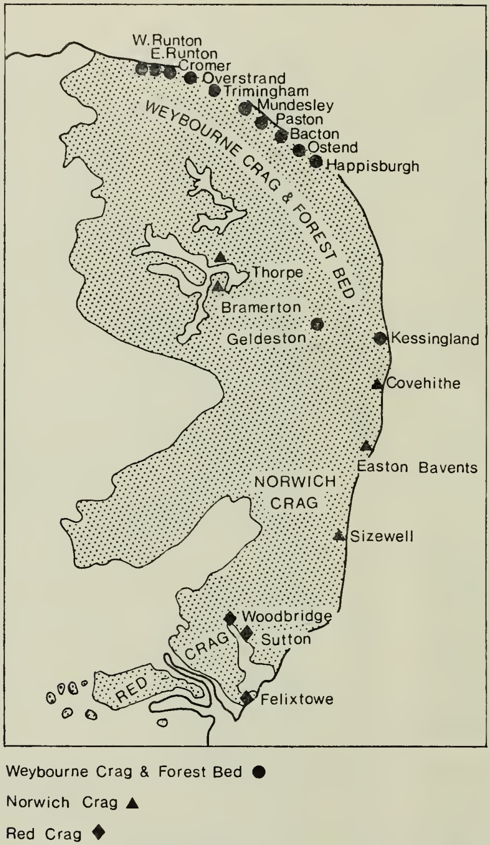


FIG. 2. Location map of Crag and Forest Bed rodent localities in East Anglia.

(iii) CROMER FOREST BED SERIES. This differs from the earlier Crag deposits in being predominantly estuarine and freshwater, with some beach deposits. Coastal exposures occur at many localities along the Norfolk coast, though these are unfortunately becoming increasingly obscured by sea defence work. Abundant remains of mammals (including rodents) and of plants occur in the Forest Bed. The most important rodent localities are West and East Runton (65, 64), with fewer remains from Ostend (57), Cromer (63), Overstrand (62), Mundesley (60), Paston (59), Bacton (58) and Kessingland (52).

It has long been recognized that all the Forest Bed deposits are not contemporaneous but that they accumulated over a considerable period of time, during which there occurred changes of climate and fauna. West & Wilson (1966), basing their conclusions on a study of plant remains, identified four climatic stages within the Forest Bed Series of deposits. In descending order these are :

Early Anglian	(cold, followed by glacial conditions during the later Anglian)
Cromerian *sensu stricto*	(warm)
Beestonian	(cold)
Pastonian	(warm)

Rodent remains are known from all horizons except the Beestonian. The Ostend Forest Bed presents a problem which is further discussed on pp. 48, 122.

(a) *Pastonian of East Runton and Happisburgh.* Only the earliest part of the Forest Bed sequence is represented at East Runton (64) ; deposits of Cromerian age, *sensu stricto,* apparently being absent. Azzaroli (1953) observed that the large mammals from this locality are Villafranchian species and that mammals present in the later part of the Forest Bed are absent. West (personal communication, 1972) considers, from palaeobotanical studies, that no Cromerian deposits, *sensu stricto,* have yet been proved on the foreshore at East Runton. He found, in descending order, the following sequence :

c. Clay Conglomerate, being reworked estuarine sediment, probably of Pastonian age, redeposited during late Pastonian or Beestonian times.
b. Shelly Crag, of Pastonian age, regarded by Hinton (1926b : 365) as Weybourne Crag.
a. Flint Bed, relating to a pre-Pastonian land surface.

Unfortunately the East Runton section has not been seen really well for many years and all the rodent remains available for the present study are from old collections. Three species of *Mimomys* are recorded ; these are *M. newtoni*, *M. pliocaenicus* and *M. savini.* The occurrence, together in the Shelly Crag, of the last two species, which represent successive stages in the development of the same phyletic line of voles, suggests the natural or accidental mixing of elements from different layers. *M. pliocaenicus* and *M. newtoni* are represented in both the Shelly Crag and among the 'clay pebbles' of East Runton, the holotype of *M. newtoni* being from the former horizon.

The precise stratigraphic range of these three species is far from clear. *M. savini* (represented by a few specimens from the Shelly Crag) is very abundant in the later, Cromerian *sensu stricto,* deposits of West Runton. The occurrence of remains of *M. pliocaenicus* and *M. newtoni* (known also from the earlier Norwich Crag) in the 'clay pebbles' could mean that these rodents persisted into Pastonian times. Such an interpretation would not be out of harmony with the 'Villafranchian' megafauna of this locality. The rolled condition of some of the remains could alternatively indicate their derivation from an earlier deposit.

Trogontherium boisvilletti and *Castor fiber* have also been found at East Runton.

A second Forest Bed locality, where the deposits are apparently of Pastonian age only, is Happisburgh (56). Remains of *Castor fiber* and also fir cones bearing marks which appear to indicate gnawing by squirrels (Newton 1882a) have been found there.

(b) *Beestonian.* No rodent remains are known from Beestonian deposits.

(c) *Cromerian* sensu stricto. The Upper Freshwater Bed of West Runton (65), defined by West (1961) as the type deposit of the Cromerian interglacial, contains abundant rodent remains. The following species are represented: *Apodemus sylvaticus, Trogontherium boisvilletti, Castor fiber, Cricetus cricetus, Mimomys savini, Clethrionomys glareolus, Pitymys arvaloides, P. gregaloides, Microtus arvalinus, M. nivaloides* and *M. ratticepoides. Muscardinus* recorded by Hinton (in Barrett-Hamilton & Hinton 1910–21, **2** : 351) from the 'Forest Bed' can possibly be added to the above list.

The rodent fauna with at least 11 species is unusually rich. It is predominantly of forest and meadow type, testifying to a mild climate; no arctic elements are present. The presence of *Cricetus* in this fauna is difficult to explain.

Sciurus whitei is represented from the marine 'Monkey Gravel' at West Runton, which overlies the Upper Freshwater Bed.

(d) *Anglian.* Newton (1882b) described some isolated worn teeth of *Spermophilus*, found in association with remains of arctic plants, in the Arctic Freshwater Bed near Mundesley (60). This deposit, which is immediately overlain by glacial till, has been interpreted as an indication of oncoming cold conditions in early Anglian times.

The rodent fauna of the Forest Bed deposits at Ostend (57) near Bacton presents a stratigraphic problem, since it cannot be accurately related to the above sequence. The remains include *Arvicola bactonensis* and *A. greeni* (Hinton 1926b : 386, 389), now both regarded as synonyms of *A. cantiana*, which led Hinton to conclude (p. 391) that the Ostend deposit is later than the Upper Freshwater Bed of West Runton. The specimens were collected over a century ago by the Rev. C. Green and unfortunately lack reliable stratigraphic information.

B. Terrace and Solifluxion deposits of the Rivers Thames and Lea

The richest series of rodent-bearing deposits related to a British river system is that of the River Thames and River Lea. The deposits of these rivers have been extensively worked commercially for gravel and brickearth and there have been many deep excavations for building foundations in the London area, leading to frequent discoveries of rodent remains (Fig. 3).

Three main series of deposits occur in association with these rivers, the exact relationship between which is often difficult to determine. Firstly, there are the terrace deposits of their upper courses, including Marlow and Isleworth in the Upper Thames, and Water Hall Farm Pit, Nazeing, Ponders End, Edmonton and Hackney on the River Lea. Deposits of both interglacial and glacial age occur here, those representing glacial stages merging with buried channels in the Lower Thames Valley province, where they are inaccessible for study in consequence of later rise of sea level.

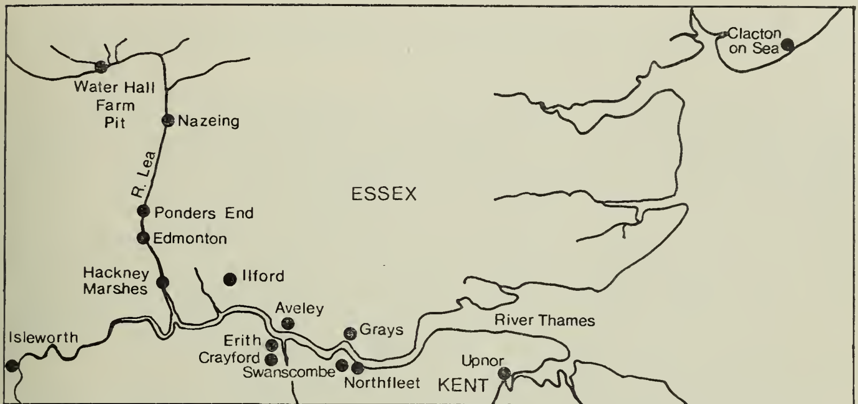


FIG. 3. Location map of rodent localities in the Thames estuary and the Lea valley.

Secondly, there are terraces of the Lower Thames, including Swanscombe, Clacton, Ilford, Aveley and Grays, Crayford and Erith. Hinton (1926b : 126–131) classified these as the High Terrace of the Thames (Swanscombe), the Early Middle Terrace (Grays Thurrock), and the Late Middle Terrace (Crayford and Erith). Whereas each terrace of the upper part of the river is of approximately constant height above the present-day bed of the river and thus becomes progressively lower as it is followed downstream, these terraces of the Lower Thames (which are related to former high sea levels) have approximately horizontal aggradation surfaces and they do not extend further upstream than the head of the contemporary tidal limit of the river. All are of interglacial or interstadial age and they can be correlated with raised beaches of similar heights along the open coastline. The cold stages which occurred between the accumulation of these terraces of the Lower Thames are represented by deposits submerged in the buried channels of the present-day river, previously mentioned.

Thirdly there are solifluxion and hillwash deposits, the heights of which are unrelated to the terrace system, with the deposits of which they are often interbedded. Northfleet is the only rodent locality, probably of this category, known to the writers.

It follows that, in an area as complicated as the valleys of the Rivers Thames and Lea, the exact relationship between the various rodent-bearing deposits is difficult to interpret. The literature on this subject, which goes back for nearly a century and a half, is voluminous. The general sequence was discussed by King & Oakley (1936) and in a number of important papers by Zeuner (e.g. 1954), who produced a schematic section from the Ebbsfleet Valley to Swanscombe, Kent, showing his interpretation of the relationship between the various deposits there. He interpreted the solifluxion and loess deposits with Levallois industries of Baker's Hole and Ebbsfleet as earlier than deposits of both Main Monastirian and Late Monastirian age, which he regarded as Last Interglacial, although only the Late Monastirian is accepted as Last Interglacial by Evans (p. 40).

During recent years J. N. Carreck has made a detailed further study of many of the mammalian localities in the Thames estuary, especially those in Kent, together with related museum collections and previous literature. On a basis of all lines of evidence he relates (*in litt.*) the deposits of some of the more important localities, here given in ascending stratigraphic order, as follows :

1. Interglacial deposits of Swanscombe, with Clactonian and Acheulean industries.
2. Interglacial deposits of Grays Thurrock and Little Thurrock (including the Orsett Road brickearths, but not those of West Thurrock, which are slightly later), Ilford and Aveley. The Ilford mammoth is a transitional form between *Mammuthus trogontherii* and *M. primigenius*. The Ilford fauna does not include any cold elements.
3. Deposits of the Baker's Hole cold stage at Ebbsfleet/Northfleet. The first true mammoth, *M. primigenius*, intermediate in form between the mammoths of Ilford and Crayford, appears at this locality in non-estuarine deposits overlying coombe rock (solifluxion) deposits. There are several associated Levallois industries.
4. Interglacial deposits of Crayford and Erith. Carreck found that the mammoth from the Lower Crayford Brickearth is more advanced than that from stage 3, though not so advanced as Last Glaciation mammoths from such localities as Ponders End, in the Lea valley, north London. He suggested that a layer of shattered chalk at the base of the Crayford sequence may be equivalent to the Baker's Hole cold stage and that the Crayford Gravel and Lower Brickearth, which are interglacial, follow immediately in time. The Crayford fauna suggests more open grassland conditions than indicated at Ilford or Grays, and there is a Levallois industry more advanced than that at Baker's Hole.
5. Other interglacial deposits, with hippopotamus, suggest that there may have been a further amelioration of climate. Carreck considers that the hippopotamus may have survived to a very late stage during the Last Interglacial. The Last Glaciation was characterized by a more advanced mammoth than that from Crayford.

Carreck pointed out that most of the Grays mammals were collected over a century ago, possibly from more than one terrace, which makes the study of this locality difficult ; he drew attention to the hazards of confusing the Baker's Hole cold stage, which he regarded as occurring within the Ipswichian Interglacial, with the Wolstonian/Saale Glaciation.

Carreck's chronological conclusions are of very far-reaching importance, with two points of special interest. Hinton's supposition that the Crayford deposits are later than those at Grays receives further support, but unlike the Geological Society (Mitchell *et al.* 1973), which regards the Northfleet coombe rock as Wolstonian and earlier than Ilford (which is regarded as Ipswichian), Carreck regards the Ilford deposits as being earlier than those of Northfleet.

Let us now consider in more detail the various deposits in the valley of the Thames and its tributaries where remains of fossil rodents have been found.

(i) Lower Thames.

(a) *High Terrace of Swanscombe.* One of the most important British rodent localities is the world-famous Swanscombe skull site (see Ovey (1964) for a fuller account). A series of estuarine deposits is aggraded to a height of approximately 31·5 m (103 ft) O.D. and is believed to have accumulated when the sea level rose to this height. Solifluxion deposits bring this figure to a total of 35·5 m (113 ft). Rodent remains have been found in two gravel pits, separated by a distance of about a third of a kilometre and now both disused. These are Barnfield Pit, where skull fragments of Acheulean Man were found, and Dierden's Pit, Ingress Vale. The following sequence of deposits has been described from Barnfield Pit :

6. The Upper Gravel. This is regarded as a solifluxion deposit, later than the terrace proper. No mammalian remains have been found in it.
5. The Upper Loam, with an Acheulean industry but no mammalian remains.
4. The Upper Middle Gravel, occupying a channel in the underlying deposits and containing an Acheulean industry. The top of this stratum, which is at about 31·5 m (103 ft) O.D., is regarded as the true surface of the terrace deposits proper. This deposit contains the '*Homo* layer' in which the human remains were found.
3. The Lower Middle Gravel, with an Acheulean industry.
2. The Lower Loam, with an *in situ* Clactonian activity horizon at its base and a knapping floor higher up. A zone of subaerial weathering, with many well-preserved animal footprints, is present on the surface of this deposit.
1. The Lower Gravel, with an early Clactonian industry, resting on a bench of underlying rock at 21–27 m (70–90 ft).

The deposits contain a rich molluscan fauna which has recently been re-examined by Kerney (1971). He concluded that the Lower Gravel, Lower Loam and the very base of the Lower Middle Gravel accumulated under temperate conditions, after which the climate became cooler.

Rodent remains have been found in the Lower Gravel (Carreck 1959), in the Lower Loam (remains recently excavated by Waechter), and in a silt bed in the Upper Middle Gravel at a level slightly higher than the '*Homo* layer' (Schreuder 1950). A few rodent remains have also been found at Ingress Vale. The distribution of rodent species at these two localities is shown in Table 3.

The exact relationship between the deposits of Barnfield Pit and Ingress Vale is uncertain. *Arvicola cantiana* occurs at both the latter site and in the Lower Loam of Barnfield Pit, suggesting a possible correlation of the two. Kerney (1971 and personal communication) found at Ingress Vale a temperate molluscan fauna associated with an industry which is culturally more advanced than that in the Lower Gravel and Lower Loam, suggesting to him a possible equivalence to the base of the Lower Middle Gravel.

The Swanscombe rodent remains are insufficiently abundant to permit reconstruction of any environmental and climatic changes, but the species of voles found in the

Table 3

Distribution of rodent species at Barnfield Pit and Ingress Vale, Swanscombe, Kent

	Barnfield Pit				
	Lower Gravel	Lower Loam	Lower Middle Gravel	Upper Middle Gravel	Ingress Vale
Trogontherium boisvilletti					×
Castor fiber		×			
*Apodemus sylvaticus**					×
Clethrionomys glareolus				×	
Arvicola cantiana		×			×
Lemmus sp.				×	
Microtus arvalinus		×		×	
M. ratticepoides		×		×	
Microtus sp. (*arvalis-agrestis* group)				×	
Pitymys arvaloides	×	×			

* Cited in earlier papers as *A. whitei.*

Lower Loam suggest that during the deposition of this layer a meadow environment may have prevailed. There are no arctic and no forest species, but such negative evidence is not decisive.

Although the Swanscombe deposits are generally regarded as being of Hoxnian Interglacial age, there is increasing evidence that a substantial interval may have elapsed between the deposition of the Lower Gravels/Lower Loam complex and of the overlying Middle Gravels. In general the rodent fauna of the lower unit quite closely resembles that of the Upper Freshwater Bed of West Runton. *Pitymys arvaloides, Microtus arvalinus* and *M. ratticepoides* occur in both the Upper Freshwater Bed at West Runton and in the Lower Loam at Barnfield Pit. The two abovementioned species of *Microtus* persist into the Upper Middle Gravel. *Mimomys savini,* characteristic of Cromerian assemblages *sensu stricto,* is nevertheless absent from Swanscombe, where it is replaced by *Arvicola,* absent from the Upper Freshwater Bed. It is of interest that by Upper Middle Gravel times *Lemmus* had appeared and *A. cantiana* may have disappeared. At the present day *Lemmus* is a rodent of northern latitudes. Whereas we have no means of demonstrating that its habit is not a recent adaptation, the occurrence of this genus could be interpreted as further evidence of the cool conditions indicated by the mollusca.

Recently Mullender (in Wymer 1974) has examined pollen from the Lower Loam of Barnfield Pit and found a marked break in the profile with a great increase in pine and near disappearance of alder. He equated the lower part of the Lower Loam with the Hoxnian Late-temperate Zone II and the upper part with the Wolstonian. If this interpretation were to be accepted then the later deposits of Barnfield Pit could no longer be referred to the Hoxnian, which would lead us to fresh problems of nomenclature for this part of the sequence.

(b) *Clacton.* The exact age relationship between the deposits of Clacton and Swanscombe is not clear, though Clacton is generally regarded as a further Hoxnian locality intermediate in age between the Lower Loam and Middle Gravel of Barnfield Pit. The Clacton deposits, which lie at about sea level, are at a lower altitude than those at Swanscombe. West (1972) suggests that slight downwarping has occurred in the Clacton area, which may explain this difference. There is a Clactonian industry. Plant remains from Clacton, studied by Pike & Godwin (1952), suggest about one-third of an interglacial sequence, during which mixed deciduous forest of the warmth maximum was replaced by coniferous forest.

Only a few rodent remains have been found in the Clacton deposits. These are *Trogontherium* cf. *cuvieri* (= *T. boisvilletti*) and *Clethrionomys* sp. (Singer *et al.* 1973), *Castor* sp. and *Microtus* of the *agrestis* group (Hinton 1923b), and *Arvicola* cf. *praeceptor* (= *A. cantiana*) (Warren 1955, quoting Hinton).

(c) *Early Middle Terrace at Aveley, Grays Thurrock and Ilford.* Hinton (1926b : 129) defined Grays Thurrock (33) as the type locality of this terrace of the Thames, with which the present writers also include Ilford (35) and Aveley (34). Table 4 lists those rodent species whose remains have been found at these localities.

The age of the deposits at these localities has been the subject of much discussion which is yet to be concluded. Hinton (1926b : 129–131) considered that the species of *Arvicola* from Grays (*A. praeceptor*, = *A. cantiana*) was not closely related to modern species of that genus. He considered that the latest Forest Bed deposits (presumably Ostend), the High Terrace of the Thames and the Early Middle Terrace were close in time. Zeuner (1945) considered Grays to be Hoxnian.

Hoxnian terrace deposits do indeed occur in the Grays area, though remains of fossil mammals do not seem to have been found in them. Wymer (1957) records terrace deposits of Hoxnian age with Clactonian implements resting on a bench at 15 m (49 ft) O.D., but points out that the Grays brickearth is later than this deposit. Most of the Grays rodent remains were found in the brickearth in a small pit near Orsett Road (Hinton 1901), about 650 m (700 yds) west of Wymer's site.

West (1969) studied plant remains from the three sites mentioned above and concluded that Aveley and Ilford are of Ipswichian age, and that Grays is interglacial, probably also Ipswichian. He pointed out that there was at this time apparently an important aggradation phase which resulted in the spreading of alluvium up to levels of between 12 and 15 m (40–50 ft) O.D.

The age of the Grays–Ilford–Aveley deposits will be further discussed below. From the evidence of the *Arvicola* remains, Grays Thurrock would appear to be relatively early.

TABLE 4

Distribution of rodent species at Grays Thurrock, Aveley and Ilford, Essex

	Grays Thurrock	Aveley	Ilford
Castor fiber	×		×
Apodemus sylvaticus	×		
Clethrionomys glareolus	×	×	
Arvicola cantiana	×	×	×
Microtus agrestis	×	*Microtus* sp.	×

(d) *Late Middle Terrace at Crayford and Erith.* A rich rodent fauna has been collected from the Thames terrace deposits of Crayford and nearby Erith ; it has been described by Kennard (1944). Owing to the lenticular character of the deposits at these localities there is little constancy in the details of the succession. Three broad divisions can, however, be identified. In descending order there are :

3. The Upper Brickearth, apparently not fluviatile but the result of sludging.
2. The Lower Brickearth and *Corbicula* Bed, up to 9 m (30 ft) O.D., laid down in a sluggish stream and in more strongly running water respectively. Levallois artefacts have been found in this deposit. Most of the rodent remains are from the *Corbicula* Bed.
1. The Lower Gravel, deposited by a fast-flowing river. The top was a land surface occupied by Levallois man, who left many artefacts.

Most of the rodent remains have been found in the *Corbicula* Bed, which is a sandy development of the Lower Brickearth. The following species are represented : *Spermophilus primigenius, Microtus oeconomus, M. nivalis, M. agrestis, Arvicola* sp., *Lemmus lemmus* and *Dicrostonyx torquatus.*

The age of the Crayford deposits is a topic requiring extensive further study. Hinton (1926b : 131) considered Crayford to be later than Grays, with a major intervening change of fauna. This view is also supported by Carreck (*in litt.*). At the present time Crayford is widely considered to be of Ipswichian age and both the freshwater and land mollusca found in the *Corbicula* Bed suggest conditions warmer than at the present time. The associated rodent fauna, however, is a typical assemblage of the 'penultimate' Glaciation. *Spermophilus primigenius* is unknown from the sediments of the Last Glaciation in Europe and, although *Microtus nivalis* was present during the Last Glaciation in many parts of Europe, and still survives in the mountains of central and south Europe, there is no evidence that it survived into the Last Glaciation in Britain.

It has been suggested that the lemmings burrowed into the *Corbicula* Bed from a later land surface, or alternatively that the remains were derived from an earlier deposit. Field evidence, however, suggests that the rodent remains are contemporary with the *Corbicula* Bed.

A total absence of forest species of land mollusca indicates that the country was open grassland. Living species of *Spermophilus* are also predominantly grassland animals. This could be interpreted as the beginning or end of an interglacial stage, though it is pointed out by Turner (in prep.) that riverside trampling by large herbivores can also give rise to clearances in otherwise wooded areas.

The Crayford deposits apparently date from some time during Wolstonian–Ipswichian times. Their precise stratigraphic position will be further discussed below and in Section IV (pp. 125–126).

(e) *Floodplain Terrace complex.* A series of lower terraces of Last Interglacial and Last Glaciation age in the Thames estuary have produced an abundance of remains of large mammals but, with one exception (*Castor* from the Upper Floodplain Terrace of the River Medway, a river flowing into the Thames estuary, at Upnor, Kent), no rodent remains are known from them.

(f) *The Middle Terrace/Floodplain Terrace problem.* Although no stratigraphically significant rodent remains have been found in the Floodplain Terrace complex of the Thames estuary, and although Hinton did not mention this terrace in his monograph (his 'Third Terrace of the Thames' is actually a terrace of the upper part of the River Lea), abundant rodent remains which are probably of Upper Floodplain Terrace age have nevertheless been found in many British cave deposits. The present section would be incomplete without some discussion of the status of this terrace.

It has already been pointed out that various workers have presented evidence that the period of time regarded by the Geological Society (Mitchell *et al.* 1973) as Hoxnian–Wolstonian–Ipswichian was, in fact, more complicated than this sequence suggests. Zeuner (1945) described evidence for a minor cool phase dividing what he regarded as the Last (Ipswichian) Interglacial into an earlier and a later part. He considered that there were two stages of high sea level during the Last Interglacial, the Main Monastirian or 18 m and subsequent Late Monastirian or 8 m shorelines, interrupted by an intra-Monastirian fall of sea level. These stages were accepted by Evans (1971 ; see pp. 40–42), though he argued that the earlier of these two stages should not be called Last Interglacial and observed that some confusion seemed to have arisen in archaeological circles where 'Last Interglacial' had been used for both.

Zeuner correlated the so-called Taplow Terrace of the Thames estuary (our Middle Terrace complex belongs here ; the term 'Taplow' is best abandoned in the estuary since Taplow is in the upper part of the Thames and the terrace there is not estuarine) with the Main Monastirian sea level and the Upper Floodplain Terrace with that of the Late Monastirian. Both these supposed terraces are highly fossiliferous, with apparently different mammalian megafaunas.

When Zeuner described his interpretation of the Last Interglacial terrace sequence of the Thames estuary very little palaeobotanical evidence was available to him. During recent years, however, fossil plant remains have been found at a number of Last Interglacial localities there, the most important being Trafalgar Square (Franks 1960), Seven Kings Station, Ilford (West *et al.* 1964) and Aveley (West 1969), and here problems have arisen. The plant remains from these localities were assigned to the pollen zones shown in Table 5.

To those who had been studying the terraces and mammalian faunas of the Thames estuary, these results were surprising. Whereas Ilford and Aveley had appeared to be part of the Middle Terrace of the Thames and Trafalgar Square part of a lower terrace, the Upper Floodplain Terrace (i.e. Zeuner's two terraces of the Last Interglacial, representing two distinct periods of time), only one climatic fluctuation, with the climatic optimum of Zone IIb represented at all three sites, could be recognized from the pollen evidence. Was Zeuner wrong in separating the two stages of his supposed Last Interglacial, the Middle and 'Upper Floodplain' Terraces of the Thames estuary really being only one terrace, or are the floral remains from two separate climatic events so similar that these terraces cannot be distinguished on palaeobotanical evidence? Mammalian and morphological evidence suggests that, in agreement with the views of Zeuner and Evans, the latter

Table 5

Pollen zonation of some 'Ipswichian' interglacial sites in the Thames estuary

Pollen Zones			Flora	Ilford	Aveley	Trafalgar Square
Last Glaciation						
Last Interglacial	h–i	IV	Pine, birch			
	g	III	Oak, hornbeam, silver fir		Mammoth	
	f	IIb	Mixed oak forest		Straight-tusked elephant	
	e	IIa				
	d	Ib	Birch, pine			
	c	Ia				
'Penultimate' glaciation						

N.B. The Trafalgar Square deposits are of Zone IIb age, and should be shown somewhat higher than indicated.

alternative is the more likely even though palaeobotanical evidence supports only a single terrace (Fig. 4).

Even the chronological interpretation of the Ilford sequence is not without problems. West *et al.* (1964) referred the gravel under the Ipswichian brickearth and plant deposit at Seven Kings Station to the Gipping cold stage, but Carreck (*in litt.*) has pointed out that there is considerable lateral variation of the Ilford deposits with interglacial species of mollusca and mammals frequently present in the gravels and sands.

Let us now consider the large mammals of these Thames sites in some detail. At Trafalgar Square (supposedly Upper Floodplain Terrace) Zone IIb contains remains of hippopotamus, straight-tusked elephant, a rhinoceros which is probably *Dicerorhinus hemitoechus,* fallow deer, red deer, giant ox, bison, lion and other animals. No mammoth or horse remains were found. This is a faunal assemblage which occurs commonly in British cave deposits with localities as widely spread as Joint Mitnor Cave, Devon, and Kirkdale Cave, Yorkshire (Sutcliffe 1960).

The Ilford–Aveley fauna appears to be entirely different. At Ilford most of the elephant remains are of an early form of mammoth with affinities to the Middle Pleistocene *Mammuthus trogontherii,* though straight-tusked elephant is also represented. Two species of rhinoceros are present, *D. hemitoechus* and *D. kirchbergensis.* This last species is also common in the preceding Hoxnian Interglacial. There is an abundance of horse ; both hippopotamus and fallow deer are absent.

At Aveley straight-tusked elephant in Zone IIb is replaced by mammoth in Zone III. Comparison of rodent species unfortunately cannot be made, since no diagnostic remains have been found in the Upper Floodplain Terrace. *Arvicola cantiana* is present in the Middle Terrace at Aveley, Ilford and Grays Thurrock.

The megafaunas of Aveley and Ilford on the one hand, and of Trafalgar Square on the other, are so different that it is difficult to believe that they are contemporary, though consideration must be given to the possibility of their representing different stages within a single climatic fluctuation.

The evidence does not seem to support the latter alternative. The hippopotamus level at Trafalgar Square is Zone IIb. A vast amount of Zone IIb clay was excavated for cement-making at Aveley but no hippopotamus remains were found. The Ilford plant remains cover Zones IA–IIb but there were no hippopotamus remains there ; two specimens formerly attributed to this animal have since been shown to have been incorrectly identified.

It has been pointed out, in support of there having been only one temperate stage, that most of the Ilford mammal remains were recovered over a century ago, during excavations for brickearth which were relatively shallow and did not extend into

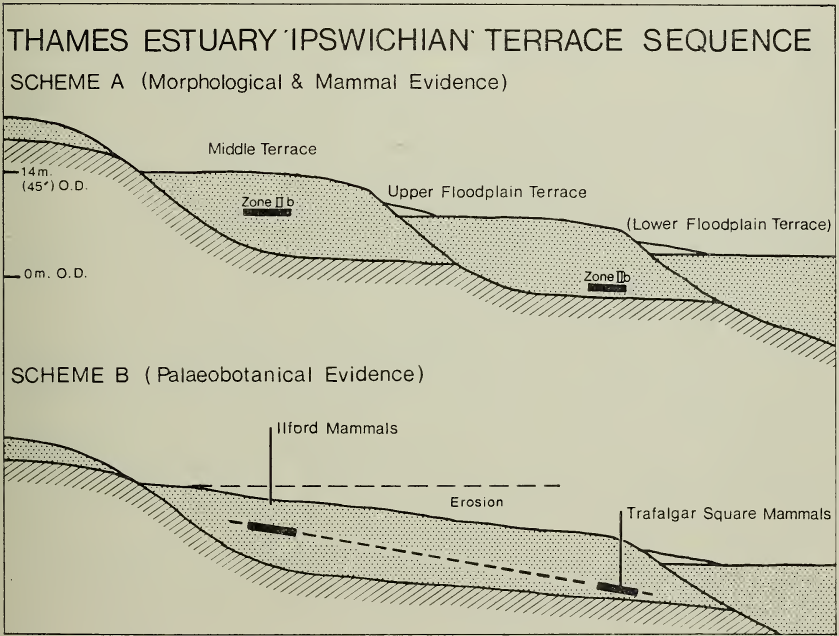


FIG. 4. Schematic section of Thames estuary Ipswichian terraces, showing alternative interpretations of the stratigraphic succession. Reproduced from Sutcliffe & Bowen (1973 : 18).

underlying gravel deposits, which were of no commercial value. The organic deposit described by West *et al.* (1964) at Seven Kings Station underlay the brick-earth, so it is possible that the Ilford mammalian fauna is later than Zone IIb (perhaps Zone III), that is the Trafalgar Square fauna might have been found in the basal part of the Ilford terrace had excavations been carried deeper. According to this theory Trafalgar Square represents an earlier stage than Ilford ; according to the twin terrace theory it is later. The former interpretation presents several difficulties. In spite of extensive commercial excavation of sand and clay in the London area, no such relationship has ever been observed ; the Upper Floodplain Terrace does appear to be a good morphological feature ; the Ilford mammoth is relatively primitive ; the Ilford fauna has never been recognized in any British cave, with the possible exception of Hutton Cave, whereas the Trafalgar Square fauna with hippopotamus occurs frequently, suggesting that such deposits have been subject to less denudation and are more recent.

In the absence of diagnostic rodent species in the Upper Floodplain Terrace of the Thames the above problem cannot at present be resolved from studies in the Thames area. It will be further critically examined below, in the section on hippopotamus faunas in caves and in Section IV.

(ii) Upper Thames.

(a) *Isleworth.* Remains of *Microtus oeconomus* and *M. gregalis* were found at Willment's Gravel Pit, Isleworth, in a deposit where they were associated with remains of temperate mollusca and insects (Coope, 1975) and with plant remains dated by ^{14}C to 43 140 + 1520 or − 1280 years B.P. (Birmingham 319). This deposit was overlain by sands and gravels containing remains of reindeer and cut by many fossil ice wedges. A description of the site, by J. Simons, is in preparation. The sequence is interpreted as indicating deteriorating climatic conditions after an inter-stadial during the Last Glaciation. It is probably the earliest occurrence of *M. gregalis* in Britain ; this species appears to be restricted there to the Last Glaciation and to have disappeared before the end of that stage.

(b) *Marlow.* A small sample of brickearth, found in the Treacher collection at the British Museum (Natural History) and labelled as coming from a brickearth pit 1 mile north-east of Marlow, was found to be rich in rodent remains, predominantly dissociated teeth. They were examined by Dr G. B. Corbet who found that most of them were apparently of *Microtus arvalis.* There was also one first lower molar of *M. oeconomus.* The lack of any second upper molars of *M. agrestis* and the occurrence of only one first lower molar of *M. oeconomus* among the many first lower molars (which teeth distinguish these last two closely related species from *M. arvalis*) suggest *M. arvalis* was the principal species present.

The age of the Marlow rodents is uncertain, but it is likely to be Last Glaciation. Neither *M. arvalis* nor *M. oeconomus* survives on the mainland of Britain at the present day.

(iii) River Lea.

(a) *Water Hall Farm Gravel Pit.* An important sequence of Pleistocene deposits occurs at Water Hall Farm, Hertfordshire. Here the valley of the River Lea has cut through earlier glacial deposits which still cap the hills on either side. In the valley bottom the River Lea is flanked on one bank by its present-day floodplain, on the other by a slightly higher terrace in which have been found abundant remains of interglacial mammals, including *Hippopotamus* and *Palaeoloxodon antiquus*. Remains of *Mammuthus* have also been found. At the base of the sequence of deposits in this terrace there was formerly exposed a white marl with remains of amphibia and of the rodents *Microtus agrestis*, *M. oeconomus* and *M. nivalis*. Since most of the commercial excavation of the interglacial terrace, since concluded, was carried out by mechanical excavators, the exact stratigraphic relationship between the hippopotamus layer and the rodent layer remains unproved, but nearly the whole of the ossiferous gravel deposit for which the pit was worked overlay the rodent-bearing marl and there seems no doubt that the rodent remains antedate those of the hippopotamus. Unfortunately no rodent remains have been found in the upper deposits.

The sequence of events at this locality is provisionally determined as follows :

1. Boulder clay and glacial deposits. Not later than 'penultimate' glaciation.
2. Retreat of ice and valley deepening by River Lea.
3. Deposition of marl with remains of amphibia and rodents.
4. Deposition of interglacial deposits with *Hippopotamus* and *P. antiquus* overlying the rodent marl. Last Interglacial.
5. Further deepening of Lea Valley and formation of present floodplain. Last Glaciation to present day.

(b) *Nazeing, Ponders End, Edmonton and Hackney*. A complex series of deposits, mainly of late Last Glaciation and Holocene age, occupies the valley of the lower part of the River Lea. Rodent remains have been found at a number of localities there. The most important of these is at Nazeing, where a series of channel, lake and marsh deposits have been palaeobotanically dated as ranging from Late Glacial to post-Glacial vegetation Zone VII, providing the latest known survival dates in Britain for a number of rodent species (Hinton 1952). The late Pleistocene part of the sequence produced remains of *Microtus oeconomus*, *M. gregalis*, *Arvicola terrestris*, *Lemmus lemmus* and *Dicrostonyx torquatus*. Of these the last-mentioned species and *M. gregalis* were still present in Late Glacial pollen Zone III and *M. oeconomus* appears to have survived possibly until post-Glacial Zone V. *Arvicola terrestris* also persisted into the Flandrian and *Apodemus sylvaticus*, *Clethrionomys glareolus* and *M. agrestis* appear in Zones V–VI, by which time post-Glacial re-afforestation had reached an advanced stage.

Remains of *Dicrostonyx torquatus* have been found at three other late Pleistocene localities in the Lea Valley : Ponders End (Warren 1916), Angel Road, Edmonton (Hinton 1912) and at Hackney.

(iv) Solifluxion and melt-water deposits.

(a) *Northfleet, Ebbsfleet and Baker's Hole*. Burchell (1935) recorded finding rodent remains associated with those of mammoth and rhinoceros in non-estuarine deposits filling a channel cut through a coombe rock (solifluxion) deposit at Baker's Hole, between Northfleet and Swanscombe, Kent. As previously mentioned (p. 50) Carreck (*in litt.*), from the study of the mammoth remains from this site, considered that the deposits, which indicate an ameliorating climate following the deposition of the coombe rock, are later than those of Ilford but earlier than Crayford. Stuart (*in litt.*), who has recently re-examined the Burchell specimens in the British Museum (Natural History) together with a few specimens collected more recently by Kerney and Sieveking, gives the following list of species : *Clethrionomys glareolus*, *Microtus arvalis/agrestis* and *Arvicola cantiana*. He found that in teeth of the last-mentioned species the enamel is clearly differentiated, as in *Mimomys*, with no *A. cantiana-terrestris* intermediate forms (see notes on *Arvicola*, pp. 99–102). This suggests a relatively early date for the Northfleet rodent remains, a conclusion in agreement with Carreck's observations on the mammoth remains. Burchell (1935) listed *Microtus arvalis* (here interpreted as *M. arvalis/agrestis* group), *M. nivalis* and *M. anglicus* (= *M. gregalis*) from his excavations, but the last two have not been confirmed by Stuart's re-examination of the available specimens.

C. Cave Deposits

Remains of Pleistocene rodents have been found in many caves in the British Isles. Most such deposits accumulated in consequence of animals accidentally falling down shafts or of their remains being carried into caves by birds of prey. Since, however, the entrance parts of caves are vulnerable to destruction by processes of denudation, many formerly-existing rodent deposits have since disappeared ; it is unusual to find any rodent remains in caves of earlier than Upper Pleistocene age. Kent's Cavern and a recently discovered fissure at Westbury-sub-Mendip, Somerset, are probably the only exceptions. A Lower Pleistocene cave deposit with megafauna has also been found at Dove Holes, Derbyshire (Crag age), but unfortunately no contemporary rodent remains have been recorded. In contrast, cave deposits with Last Glaciation and Holocene rodent remains are very numerous.

Few of these sites have produced stratified sequences of rodent faunas, either because the deposits accumulated during only a short period of time, because they had been disturbed before excavation, or because they were excavated before the importance of stratigraphy had become adequately appreciated.

The following are the most important rodent caves in the British Isles.

(i) Westbury Fissure (13). The recently discovered fissure infilling at Westbury-sub-Mendip, described by Bishop (1974, 1975), is of special importance, since its rich mammalian fauna indicates a stage slightly later than the type Cromerian of West Runton, not otherwise well represented in the British Pleistocene. Bishop described, in descending order, the following sequence of deposits :

III. 'Rodent Earth' (layer 10, the upper part of the 'Calcareous Group', layers 2–9 below). A deposit with an abundance of remains of rodents and other small mammals, possibly an accumulation of pellets of birds of prey.

II. 'Calcareous Group' (layers 2–9, excluding the 'Rodent Earth'). Predominantly limestone breccias with abundant remains of bears. The cave was probably a bear den at this stage.

I. 'Siliceous Group' (layer 1). Water-laid deposits with some rolled bones and teeth.

Table 6

Stratigraphic distribution of rodent species in the Westbury Fissure (after Bishop 1974, with personally communicated additions)

	Bed number	*Castor fiber* Linn.	*Apodemus sylvaticus* Linn.	*Dicrostonyx* sp.	*Lemmus* sp.	*Clethrionomys glareolus* Schreber	*Pliomys episcopalis* Méhely	*Arvicola cantiana* Hinton	*Pitymys gregaloides* Hinton	*Microtus arvalinus* Hinton
III. 'Rodent Earth'	10		×	×	×	×	×	×	(common) ×	×
II. 'Calcareous Group' (excluding 'Rodent Earth')	2–9		×		×			×	×	×
I. 'Siliceous Group'	1	×								

The distribution of rodent species in the Westbury fissure is shown in Table 6.

The age of the deposit has been discussed in detail by Bishop (1974). From the 'Calcareous Group', excluding the 'Rodent Earth', he recorded a fauna including *Homotherium latidens, Felis gombaszoegensis, Ursus deningeri, Xenocyon lycaonoides, Canis lupus mosbachensis, Dicerorhinus etruscus* and *Equus mosbachensis*. Rodents from this level are *Apodemus sylvaticus, Lemmus* sp. (the earliest record of this genus in the British Pleistocene), *Arvicola cantiana, Pitymys gregaloides* and *Microtus arvalinus*. The same species are represented in greater abundance in the 'Rodent Earth', which Bishop regarded as the last stage of the 'Calcareous Group'. Remains of *Pliomys episcopalis* (the first record in the British Pleistocene), *Dicrostonyx* sp. (the earliest record in the British Pleistocene) and *Clethrionomys* were also found in the 'Rodent Earth'.

Bishop regarded the Westbury fauna as later than the type Cromerian of West Runton but not later than Elsterian. He drew attention to its similarity to that of the classic 'late Cromerian' sites of Europe (in particular Mauer, Hundsheim, Tarkö and Mosbach) and equated the Westbury 'Rodent Earth' with the *Arvicola* fauna group 1 of Koenigswald (1973) (see pp. 100–101). This stage was previously unrecognized in the British Pleistocene sequence.

(ii) Kent's Cavern. Unfortunately most of the rodent remains found in Kent's Cavern were excavated during the nineteenth century and only sparse stratigraphic information is associated with them. The following species have been found there (Hinton 1915, Kennard 1945–6, British Museum (Natural History) collection) :

Castor fiber, *Apodemus flavicollis*, *Clethrionomys glareolus*, *Arvicola terrestris*, *Dicrostonyx torquatus*, *Lemmus lemmus*, *Pitymys gregaloides*, *Microtus agrestis*, *M. oeconomus* and *M. gregalis*. In addition, Campbell & Sampson (1971) recorded a specimen of *Arvicola greeni* (regarded here as a synonym of *A. cantiana*) among specimens collected from the cave by J. MacEnery between 1825 and 1829. This is a typically Last Glaciation–Holocene fauna, with the exception of *P. gregaloides*, not recorded elsewhere in Britain in deposits later than those of the Westbury Fissure, and *A. cantiana*. The occurrence of *P. gregaloides* and also sabre-toothed cat, *Homotherium*, in Kent's Cavern has been interpreted by both Hinton (1926b) and Campbell & Sampson (1971) as evidence of a Cromerian stratum somewhere in Kent's Cavern.

The sequence of deposits in the cave varies from one chamber to another (for details see Campbell & Sampson). The principal deposits, in descending order, are as follows:

5. Black Mould, with Mesolithic and later artefacts and fauna.
4. Granular Stalagmite, with Mesolithic and Neolithic artefacts and fauna.
3. Cave Earth, including a local area of hearths known as the Black Band. Middle to Upper Palaeolithic industries. Mammalian fauna including woolly mammoth, woolly rhinoceros and hyaena.
2. Crystalline Stalagmite.
1. Breccia, with many bear remains and with a Lower Palaeolithic industry.

The upper part of the above sequence is typically Last Glaciation (the Cave Earth) to Holocene. Most of the rodent remains probably come from the upper levels. *Pitymys gregaloides*, on the other hand, is a Middle Pleistocene species probably derived from the Breccia, the age of which is at present uncertain. *Homotherium*, *P. gregaloides* and *A. cantiana* are all recorded from the Westbury Fissure. At the present time it seems most likely that the earliest remains from Kent's Cavern are of Westbury Fissure age. There is no conclusive evidence of fauna as early as Cromerian *sensu stricto*. It may be inferred that the Crystalline Stalagmite represents a major break in sedimentation, possibly because the cave entrance had become sealed.

(iii) Tornewton Cave (3). The most important sequence of stratified cave deposits with rodent remains known from the British Isles is that of Tornewton Cave, south Devon (Sutcliffe & Zeuner 1962, Kowalski 1967). Deposits in the shaft-like Main Chamber of this cave and of the talus deposits outside span a cold–interglacial–cold sequence which is unique in showing differences between the rodent faunas of the two cold stages concerned. The relationship between this sequence and that of the terraces of the River Thames will be considered in Section IV, pp. 124–127.

The principal deposits in the Main Chamber of Tornewton Cave (excluding some superficial deposits excavated during the nineteenth century and a series of stalagmite floors), in descending order, were found to be as follows:

5. 'Diluvium'. Most of this deposit was excavated during the nineteenth century. The remaining part contained a few remains of wolf, hyaena, bear, bovid and

reindeer. A Holocene molluscan fauna has been identified by M. P. Kerney from this horizon and it is probable that the mammalian remains are a mixture of derived Pleistocene and contemporary Holocene species.

4. The Reindeer Stratum. Most of this deposit was excavated from the Main Chamber of the cave during the nineteenth century. Abundant rodent remains, associated with remains of wolf, hyaena, horse, rhinoceros, reindeer, a bovid and a sparse Upper Palaeolithic industry were nevertheless recovered more recently from an extension of this stratum in the talus outside the cave. The stratum is of Last Glaciation age.
3. The Hyaena Stratum. A deposit with abundant remains of spotted hyaenas, which animals apparently occupied the cave as a lair, associated with occasional remains of hippopotamus, narrow-nosed rhinoceros, red and fallow deer, lion, wolf and bear. This is an interglacial assemblage, tentatively referred to the 'Ipswichian'.
2. The Bear Stratum. A deposit with abundant remains of brown bears, which animals used the cave as a lair at this stage.
1. The Glutton Stratum. The earliest fossiliferous deposit in the cave, with numerous remains of brown bears associated with occasional remains of glutton (wolverine) and reindeer. This deposit represents an earlier cold phase.

Table 7 shows the stratigraphic distribution of rodent remains in the Main Chamber and (Reindeer Stratum only) in the talus of Tornewton Cave. It will be seen from the table that, in the Glutton Stratum, *Microtus oeconomus* and *M. nivalis* make up the bulk of the rodent fauna. *Lagurus lagurus* (from the only British locality with this genus), *Allocricetus bursae* and *Cricetus cricetus* are typical species of the 'penultimate' glaciation. *Dicrostonyx torquatus* and *Lemmus lemmus*

TABLE 7

Number of rodent specimens from the main deposits of Tornewton Cave

	Glutton Stratum	Bear Stratum	Hyaena Stratum	Reindeer Stratum	'Diluvium'	Total
Apodemus sylvaticus	1	–	1	–	8	10
Cricetus cricetus	4	–	–	–	–	4
cf. *Allocricetus bursae*	4	–	–	–	–	4
Dicrostonyx torquatus	7	2	–	7	1	17
Lemmus lemmus	1	1	–	–	–	2
Clethrionomys glareolus	11	3	–	12	4	30
Arvicola sp.	36	1	2	14	2	55
Microtus agrestis	170	4	6	123	77	380
Microtus nivalis	298	4	–	–	–	302
Microtus oeconomus	1066	15	–	19	9	1109
Microtus gregalis	–	–	–	43	12	55
Lagurus lagurus	62	1	–	–	–	63
Total	1660	31	9	218	113	2031

The count is based on the number of determinable specimens, not individuals. The apparent greater abundance of remains in the Glutton Stratum is the result of more extensive sampling of this deposit. Remains from minor deposits not included above bring the total number of specimens determined to 2383.

are present but not abundant. *Microtus gregalis* is absent. Sylvan species are very rare, though a few remains of *Clethrionomys glareolus* occur with this predominantly meadow and steppe assemblage. A single tooth of *Apodemus sylvaticus* probably represents contamination of the deposit. The rodent fauna of the Glutton Stratum has affinities to that of Crayford, Kent, from which it was probably not greatly separated in time.

Only a few rodent remains were collected from the Bear Stratum. The fauna does not differ in composition from that of the underlying Glutton Stratum though, with the exception of one tooth of *Lagurus lagurus* and four of *Microtus nivalis*, the typical 'penultimate glaciation' elements are lacking. Their absence could be accidental, however, since they are also rare in the Glutton Stratum. The absence of lemmings could indicate a slight amelioration of climate.

Rodents are poorly represented in the Hyaena Stratum. *Apodemus sylvaticus*, represented by only one specimen, is a forest species. *Microtus agrestis* and *Arvicola* sp. are ecologically neutral.

The Reindeer Stratum has a predominantly cold fauna with the typically Last Glaciation *Microtus gregalis* and with *Dicrostonyx torquatus*.

The apparent mixture of arctic and sylvan species in the 'Diluvium' is in agreement with this deposit being of Holocene age, with derived Pleistocene remains. *Apodemus sylvaticus* reappears here. The climate was milder than before.

The sequence of rodent faunas described above is of great importance as it makes possible, for the first time, distinction between mammalian assemblages, indistinguishable on the basis of the larger mammals, of the two cold stages concerned. Arctic elements (for example, lemmings) appear twice in the sequence, but are lacking from the interglacial Hyaena Stratum. The lower cold stage is characterized by, among other rodents, *Cricetus cricetus*, cf. *Allocricetus bursae*, *Lagurus lagurus* and *Microtus nivalis*, all absent from the Reindeer Stratum, where they are replaced by large quantities of *M. gregalis* which, on the other hand, is absent from the Glutton Stratum.

Distinction is also possible between the teeth of *Arvicola* from the Glutton Stratum and those from the Reindeer Stratum. W. von Koenigswald (1973 and personal communication) has found that although the form from the latter deposit is *A. terrestris*, that from the Glutton Stratum is an intermediate form tending towards *Arvicola cantiana*, known from the Middle Pleistocene deposits of Swanscombe (see pp. 100–102).

In addition to the deposits of the Main Chamber of Tornewton Cave two important rodent deposits were found in positions where they could not be directly related to the main sequence. These are the Otter Stratum, in a small chamber adjoining the Main Chamber, and the Upper Rodent Stratum, on the rock platform outside the cave mouth.

The Otter Stratum was found to contain an abundance of remains of brown bears associated with some mammalian species unrecorded elsewhere in the Pleistocene of the British Isles, notably *Cyrnaonyx*, the clawless otter, and *Crocidura*, the white-toothed shrew (Rzebik 1968). It was composed of a mixture of broken stalagmite blocks, some containing faunal remains, in an earthy matrix, suggesting some disturbance of the deposit. The following rodent specimens were collected from it.

Cricetus cricetus	2 specimens
Lagurus lagurus	1 specimen
Dicrostonyx torquatus	1 specimen
Lemmus lemmus	1 specimen
Microtus nivalis	4 specimens
Microtus oeconomus	82 specimens
Apodemus sylvaticus	2 specimens
Clethrionomys glareolus	19 specimens
Microtus agrestis	5 specimens
Arvicola sp.	8 specimens

This fauna appears to be a mixture from two originally separate layers. Remains from a warm period, including *Microtus oeconomus*, predominate. They point to a last interglacial age. No Hoxnian elements are present. *Lagurus lagurus, Cricetus cricetus* and *Microtus nivalis*, on the other hand, are species of the 'penultimate' glaciation. In an attempt to separate the two faunal assemblages some of the stalagmite blocks were dissolved in acid. Only temperate species (*Microtus agrestis*, 1 determinable specimen ; *M. oeconomus*, 6 ; *Arvicola* sp., 1 ; *Clethrionomys glareolus*, 4 ; *Apodemus sylvaticus*, 1) were found in the stalagmite. The exact stratigraphic relationship between the Otter Stratum and the deposits of the Main Chamber of Tornewton Cave is unfortunately uncertain, since the overlying deposits were excavated during the nineteenth century and are no longer available for examination. The cave was apparently still inhabited as a lair by bears, making it probable that the deposit antedates the Hyaena Stratum. On the other hand, it seems to be later than the Glutton Stratum since Koenigswald has found that, whilst the *Arvicola* from both the Glutton Stratum and the Otter Stratum is an intermediate form between *A. cantiana* and *A. terrestris*, that from the Otter Stratum is slightly more advanced, though not so advanced as the form from the Reindeer Stratum, which is *A. terrestris*. The Otter Stratum fauna appears to be a unique assemblage, unknown from any other locality in the British Isles.

The deposit known as the Upper Rodent Stratum occupied a rift on the rock platform outside the main entrance to Tornewton Cave. It was only a short distance below the surface and is probably of modern date. The following species are represented : *Apodemus sylvaticus*, 58 specimens ; *Clethrionomys glareolus*, 14 ; *Microtus agrestis*, 86 ; *Arvicola terrestris*, 2 ; *Micromys minutus*, 1. All these species live near the cave at the present day, no extinct species are represented ; and *M. minutus* is a late arrival probably associated with neighbouring plough-land.

In conclusion the relative proportions of the various ecologic groups of rodents represented in Tornewton Cave are shown in Table 8.

(iv) Other caves with pre-'Ipswichian' deposits. In light of the faunal sequence demonstrated at Tornewton Cave, it would be surprising if other rodent faunas dating from the time interval between the Hoxnian and the warm stage represented by the Hyaena Stratum of Tornewton Cave were not to be found in caves from time to time. At present this period is one of some obscurity.

TABLE 8

The relative proportions of the various ecologic groups of rodents found in Tornewton Cave

Layer	Tundra and steppe	Boreal	Forest	Neutral
Upper Rodent Stratum	0	0	44·7	55·3
'Diluvium'	11·5	8·0	10·6	69·9
Reindeer Stratum	22·9	8·7	5·5	62·8
Hyaena Stratum	0	0	2·3	97·7
Bear Stratum	25·8	48·4	9·6	16·1
Glutton Stratum	22·7	64·2	0·7	12·4

Tundra and steppe elements include *Dicrostonyx torquatus*, *Lemmus lemmus*, *Microtus gregalis*, *M. nivalis*, *Lagurus lagurus*, *Cricetus cricetus* and *Allocricetus*. Boreal elements include *M. oeconomus*. At the present day this species lives mainly in the taiga belt but it also occurs, under milder climatic conditions, in marshland. The forest element is represented by *Apodemus sylvaticus* and *Clethrionomys glareolus*. *Arvicola* sp. and *M. agrestis* are 'neutral' in their ecologic requirements. *Micromys* has been omitted from the table since it was probably introduced by man.

Some isolated pre-'Ipswichian' rodent-bearing cave deposits have nevertheless apparently been found. Hinton (1926b) regarded the rodents of Clevedon Cave (14) and Banwell Cave (10), Somerset, as probably contemporary with those of Crayford which, we have observed, are similar to those of the Glutton Stratum of Tornewton Cave. The rich material from Clevedon Cave is of special interest, as it contains only two species of rodents, *Microtus nivalis* and *M. oeconomus*. Hinton (1907a) wrote: 'Dr H. C. Male very generously presented me with a small series of the numerous jaws of *Microtus* which he found in the Clevedon deposit.' In the material described by Hinton, which is still preserved in the British Museum (Natural History), there are exclusively remains of the species mentioned above. It is possible that Dr Male did not present Hinton with the material of the other rodents, but it does not seem possible that he retained jaws of *Microtus agrestis*, as they are difficult to distinguish from those of *M. nivalis* except by a specialist. It seems probable that the Clevedon Cave remains accumulated at a time when the rodent fauna was composed exclusively of *M. oeconomus* and *M. nivalis*.

Hinton's specimens from Banwell Cave have not been seen by the present writers. The only available specimens, representing *Arvicola* sp. and *Microtus* sp., are stratigraphically inconclusive.

The Gough's Cave (12) rodent fauna is composed of *Arvicola* sp., *Microtus agrestis*, *M. oeconomus* and *M. nivalis*. The last-mentioned species suggests an age equivalent to the Glutton Stratum at Tornewton Cave, though the occurrence of a late Upper Palaeolithic industry in the cave indicates a more recent date for most of the deposits.

The occurrence of *M. nivalis* among various rodent remains excavated by J. Simons from Cow Cave, Chudleigh, Devon (7), suggests that there may be a pre-'Ipswichian' deposit there.

Hutton Cave, Somerset (10), may provide a further example of a pre-'Ipswichian' rodent locality. One of the rodents found there, cf. *Allocricetus bursae*, is known elsewhere in the British Isles only from the Glutton Stratum of Tornewton Cave.

A primitive form of mammoth further supports a relatively early date for the fauna of this cave.

(v) 'Ipswichian' cave deposits. Sites, in addition to Tornewton Cave, include the hippopotamus-bearing deposits of Joint Mitnor Cave, Devon (1), with *Arvicola cantiana-terrestris* transition form (determined by W. von Koenigswald) and *Microtus agrestis*; Minchin Hole, Glamorganshire (16), with the same species; the nearby Bacon Hole (16) recently excavated by C. Stringer (1975) with *Arvicola* sp., *M. agrestis*, *Clethrionomys glareolus* and *M. oeconomus*; and Alveston Fissure, Gloucestershire (15), with *M. agrestis* and *Clethrionomys* sp. Rodent remains from the interglacial site of Kirkdale Cave, Yorkshire (77), include *Arvicola* sp., *M. agrestis*, *Clethrionomys* sp., *Apodemus sylvaticus* and *Dicrostonyx torquatus*. This cave was excavated over a century ago. *Dicrostonyx* is out of place and suggests some mixing of material.

The rodent fauna of this stage is typically sparse, with *Arvicola cantiana-terrestris* transition form and *Microtus agrestis* the most common species.

(vi) Caves with post-Ipswichian deposits. Cave deposits dating from the Last Glaciation and Holocene are far more numerous than earlier deposits, since there has been less time for them to be destroyed by denudation. Many examples are known. The distribution of rodent species at some of the more important cave sites believed to date from this period is shown in Table 10 (pp. 70–71; for references, see Section III).

The interpretation of these rodent faunas must unfortunately be undertaken with caution since many of the deposits in which they were found had been disturbed by burrowing animals; some important rodent caves were excavated during the nineteenth century, so that adequate stratigraphic information is lacking. A fairly consistent Pleistocene faunal assemblage is nevertheless apparent, with *Sciurus vulgaris*, *Muscardinus avellanarius*, *Apodemus flavicollis* and *Rattus rattus* probably not arriving until Holocene times. A series of excavations recently conducted by the Peakland Archaeological Society in Derbyshire and Staffordshire (Bramwell 1960, 1964, 1970; Pernetta 1966) is of special interest for the light thrown on the rodent faunas of the end of the Pleistocene and early Holocene. The two lemmings, *Lemmus* and *Dicrostonyx*, appear to have been common until the end of the Pleistocene after some of the large Pleistocene mammals, such as woolly rhinoceros and hyaena, had disappeared; *Microtus oeconomus* seems to have survived into post-Pleistocene times. The apparent absence of lemmings at Levaton Cave (2, a Pleistocene site with mammoth, woolly rhinoceros, red deer, reindeer and hyaena) suggests that, during part of the Last Glaciation (probably an interstadial), *Lemmus* and *Dicrostonyx* may have been absent from the fauna, at least in the south of England. The Ightham fissures, Kent (Abbot 1917; Newton 1894, 1899a, b), are further important cave sites with rodent remains of Last Glaciation age. All the fissures do not appear to be contemporary, however, and there may have been some mixing of Holocene material.

(vii) Caves in Scotland. A series of small caves near Inchnadamph in Scotland (83) are of special interest as including the most northerly British fossil rodent locality. From one of them, Creag nan Uamh Cave, Newton (in Peach & Horne 1917) recorded *Dicrostonyx torquatus*, *Microtus agrestis* and *M. ratticeps* (= *M. oeconomus*). Remains of brown bear, reindeer and lynx were also found at the same site. The age of these remains is uncertain, but the caves are situated in wild mountainous country and the possibility that they are of relatively late age needs to be taken into consideration. Some bones of brown bear found in a nearby cave have recently been dated by ^{14}C as only about 2700 years old (Burleigh 1972).

(viii) CAVES IN IRELAND. Most rodent species living in Ireland today are probably post-Pleistocene arrivals. Only four possibly Pleistocene species need to be considered here. Their distribution at cave sites is shown in Table 9.

The exact stratigraphic position of these various remains is uncertain, although it seems unlikely that any of the Irish mammalian faunas are earlier than Last Glaciation. Mitchell (1969) considered that the mammals could not all be attributed to one phase, suggesting that, although the remains of giant deer and reindeer found beneath the peat bogs were known to be of Late Glacial age, the Castlepook Cave fauna dated from an (earlier) interstadial of the Last Glaciation. A recently obtained ^{14}C date for part of a mammoth bone from Castlepook Cave (33 500 ± 1200 years B.P., University of Dublin 122) confirms Mitchell's supposition.

Both *Lemmus* and *Dicrostonyx* are northern species which might be expected to have reached Ireland in advance of other rodent species. Associated species in

TABLE 9

Distribution of rodent species at Irish cave sites

						Edenvale caves, Co. Clare (85)				Keshcorran Caves, Co. Sligo (84)	
	Ballynamintra Cave, Co. Waterford (90)	Kilgreany Cave, Co. Waterford (89)	Castlepook Cave, Co. Cork (87)	Castletownroche Cave, Co. Cork (88)	Red Cellar Cave, Co. Limerick (86)	Alice and Gwendoline Caves	Catacombs	Newhall Caves	Barntick Cave	Coffey Cave	Plunkett Cave
Apodemus sylvaticus	×	×	×			×	×	×	×	×	×
Dicrostonyx torquatus	×	×	×	×	×	×	×	×		×	×
Lemmus lemmus			×	×							
Microtus agrestis		?									

Castletownroche Cave include mammoth, both mammoth and spotted hyaena being present in Castlepook Cave.

Although *Apodemus sylvaticus* has been recorded from several cave sites, Barrett-Hamilton & Hinton (1910–21) observed that in some instances it was most abundant in the upper layers, implying a possible late arrival in Ireland. Scharff *et al.* (1918), on the other hand, considered that at Castlepook Cave *Apodemus* was part of the Pleistocene fauna.

An imperfect skull of *Microtus agrestis* from Kilgreany Cave presents a problem, since this is the only possible fossil record of *Microtus* from Ireland, where this genus does not occur even at the present day. Savage (1966) observed that the skull is notably fresh and unaltered and drew attention to the occasional occurrence of vole skulls in north-east Ireland in owl pellets dropped by passing Scottish owls. There are no other records of *Microtus* in Ireland and the chance introduction of this specimen by owls or human activity needs to be taken into consideration.

D. Other Localities

(i) Cromerian localities. Stuart (1974) recorded *Mimomys* cf. *savini* associated with *Dicerorhinus* cf. *etruscus* from a site at Sugworth, near Oxford (21). He considered that the site is unlikely to be later than Cromerian.

(ii) Hoxnian localities. Carreck (1959) recorded *Pitymys* sp. from an interglacial tufa near Hitchin, Hertfordshire (39). This locality is unlikely to be later than Hoxnian in age. Other Hoxnian localities are Copford, Essex (42, Brown 1852 ; Turner 1970), with *Trogontherium boisvilletti*, and the Hoxnian type site of Hoxne with *Trogontherium boisvilletti* (Spencer 1956), *Apodemus* sp., *Lemmus* sp., *Arvicola* sp. and *Microtus* sp. (personal communication from Dr R. G. Wolff).

(iii) 'Ipswichian' localities. Six important East Anglian mammalian localities, usually regarded as of Ipswichian age (including the type Ipswichian locality, Bobbitshole) have produced rodent remains as shown in Table 11.

It has been claimed by Koenigswald (pers. comm.) that although the *Arvicola* from Barrington and from the Stuart collection from Swanton Morley (two hippopotamus localities) is *A. cantiana-terrestris* transition form, that from the Stuart collection from Stutton (a locality without hippopotamus) is *A. cantiana*, suggesting affinities with the Grays–Ilford–Aveley fauna of the Thames estuary. Stuart (1974), on the other hand, considers that the Barrington remains include both '*cantiana*' and '*terrestris*' and not merely intermediate forms, suggesting that the above interpretation is oversimplified. Stuart (*in litt.*) records *A. cantiana* from Harkstead, a locality near to and probably of the same age as Stutton.

Other 'Ipswichian' localities with rodent remains are Hessle (74) with *Arvicola* and Selsey (24) with *Castor*.

(iv) Last Glaciation localities. The Last Glaciation brings us within the range of radiocarbon dating. Four sites, two of them thus dated, will be mentioned here.

At Upton Warren, Worcestershire (20), remains of *Dicrostonyx* (determined by Carreck) were found in association with mammoth, woolly rhinoceros and reindeer

Distribution of rodent species at Bri

	Ightham Fissures, Kent	Brixham Cave	Happaway Cave, Torquay	Levaton Cave, Torbryan	Chudleigh Fissure	Bleadon Cave	Uphill Cave	Hay Wood Rockshelter	Picken's Hole	Rowberrow Cavern	Aveline's Hole
		Devon				Somerset					
*Sciurus vulgaris**								×			
Spermophilus superciliosus	×					×			×		
*Muscardinus avellanarius**											
*Castor fiber**								×			
Apodemus sylvaticus	×		×	×				×		×	×
*A. flavicollis**	×		×								×
*Rattus rattus**											×
Clethrionomys glareolus	×	×	×		×			×		×	×
Arvicola terrestris	×	×	×	×	×			×			×
Dicrostonyx torquatus	×				×					×	×
Lemmus lemmus	×				×		×				×
Microtus agrestis/arvalis group	×	×	×	×	×	×		×			×
M. oeconomus	×			×	×	×		×	×		×
M. gregalis	×	×	×		×	×	×		×		×
* Probably post-Pleistocene.	Pleistocene megafauna and rodents with admixture of post-glacial sylvan elements	Associated Pleistocene megafauna	Probably mostly post-Pleistocene	Associated Pleistocene megafauna	Pleistocene microfauna	Pleistocene microfauna	Pleistocene microfauna	Holocene, confused strata	Upper Pleistocene megafauna	Pleistocene microfauna	Pleistocene megafauna and rodents with admixture of post-glacial rodents

…st Glaciation and Holocene cave sites

…ordshire		Derbyshire													
King Arthur's Cave	Merlin's Cave = ? Wye Cave	Harborough Cave	Langwith Cave	Dowel Cave		Etches' Cave		Fox Hole Cave		Pin Hole Cave	Elder Bush Cave, Staffordshire	Dog Holes Cave, Lancashire	Cowside Cave No. 3, Yorkshire	Gwaenysgor Cave, Flintshire	Lynx Cave, Denbighshire
			×		×										
			×							×					
										×		×			
			×	×	×				×	×		×			×
					×		×			×					
			×												
	×		×	×	×		×		×	×	×	×		×	
	×		×	×	×	×	×		×	×	×	×	×		
×	×	×	×	×		×		×		×	×	×		×	×
	×		×	×		×				×	×	×			
×	×		×				×		×	×	×	×	×		×
×	×		×	×	×	×	×				×	×	×		×
×	×		×	×						×					
Roman remains	Microfauna only	Post-Pleistocene	Associated Pleistocene megafauna	Late Pleistocene levels	Holocene levels	Late Pleistocene levels	Holocene levels	Late Pleistocene levels	Holocene (Beaker age) level	Pleistocene megafauna and rodents with admixture of post-glacial rodents	Upper Pleistocene megafauna	Pleistocene microfauna	Pleistocene microfauna	Associated Pleistocene megafauna	Associated probable late Palaeolithic and Romano-British remains

TABLE II

Rodent species from East Anglian 'Ipswichian' sites

	Suffolk					
	Stutton (47)	Harkstead (44)	Stoke Tunnel Beds (46)	Bobbitshole, Ipswich (46)	Barrington (40), Cambridgeshire	Swanton Morley (66), Norfolk
Apodemus sylvaticus	×			×		×
Clethrionomys cf. *glareolus*						×
Arvicola cantiana	×	×				
Arvicola cantiana-terrestris transition form			×		×	×
Arvicola sp.				×		
Microtus agrestis	×	×		×	×	
M. oeconomus		×				

List based on specimens in the Ipswich Museum (Stutton, Stoke Tunnel Beds, Harkstead and Bobbitshole), British Museum (Natural History) (Barrington), and Stuart Collection from Swanton Morley (Stuart 1974).

in terrace deposits of the River Salwarpe (Coope *et al.* 1961). Associated insect remains indicate cold continental conditions. There are ^{14}C dates of 41 500 ± 1200 years (GRO 595) and 41 900 ± 800 years (GRO 1245).

At Beckford, Worcestershire (19), remains which are probably *Microtus arvalis* have been determined by Dr G. B. Corbet from specimens separated by Coope from material collected by D. J. Briggs from deposits of the Carrant Brook, in a terrace equivalent to number 2 terrace of the Warwickshire Avon or the main terrace of the River Severn. Associated mammals include mammoth, woolly rhinoceros and horse. There is a cold insect fauna and ^{14}C dates of 27 650 ± 250 years (Birmingham 293) and 27 300 ± 500 (Birmingham 595).

At Fisherton, Wiltshire (22), *Dicrostonyx torquatus*, *Microtus oeconomus* and *Spermophilus superciliosus* were associated with remains of large Pleistocene mammals. In spite of earlier suggestions *Microtus nivalis* is absent. This is a typical Last Glaciation faunal assemblage.

At Brean Down, Somerset (9), remains of *Dicrostonyx* were found in association with arctic fox and reindeer in talus deposits regarded by Apsimon *et al.* (1961) as being of Late Glacial age (early Zone II).

(v) HOLOCENE LOCALITIES. Two rodent species, now extinct in the British Isles, survived into post-Pleistocene times. These are *Castor fiber* and *Microtus oeconomus*. Localities for *Castor fiber* include the Cambridge Fens (41), Staple Howe, Yorkshire

(75), Star Carr, Yorkshire (76), and Thatcham, Berkshire (23). *Microtus oeconomus* has been found in the Huntspill Cut (8) in the Somerset levels and on Nornour, Isles of Scilly (91).

(vi) Scottish localities. Other Scottish rodent finds include *Dicrostonyx* from Corstorphine, Edinburgh (81), and *Castor fiber* from the Loch of Marlee, Perthshire (82), and Middlestots Bog, Berwickshire (80). The various ages of these remains have not been determined.

III. CLASSIFICATION AND DISTRIBUTION OF RODENTS IN THE PLEISTOCENE OF THE BRITISH ISLES

In this section rodents represented in the British Pleistocene are discussed in systematic order. For completeness of taxonomic reference authors and dates of both families and genera are given, though these are generally omitted from the references. In the few cases where the currently used name of an extinct species is based on non-British material the original reference, marked **, is given in the synonymy. With these exceptions, only names used for fossil specimens from the British Isles are cited in the synonymy and each name is given only once, with reference to the first paper where it appeared. The type localities of extinct species of rodents are indicated * in the locality lists or, if non-British, in the sections on general distribution.

Locality lists for each species are divided into (a) English and Welsh, (b) Scottish and (c) Irish sites; they are given in ascending stratigraphic order, as precisely as possible on the basis of current information. Where several records are believed to be of similar age they are grouped together, in alphabetical order, at the appropriate position. Numbers refer to site locations in Fig. 1. Published records at generic level only are generally not included in the locality lists. Though coverage is basically restricted to the Pleistocene, Holocene records of *Castor fiber* and *Microtus oeconomus* are also included since both these species are now extinct in the British Isles. Post-Pleistocene arrivals in the British Isles are briefly mentioned for the sake of completeness.

Family **SCIURIDAE** Brandt 1855

Genus ***SCIURUS*** Linnaeus 1758

Sciurus whitei Hinton 1914

Squirrel, extinct

1914 *Sciurus whitei* Hinton : 193–195, fig. 10.

Locality : *West Runton, Norfolk (65) : Hinton 1914.

Hinton described a new species of squirrel, *S. whitei*, from a unique fourth upper premolar (BM(NH), M 10720) from the marine 'Monkey Gravel' overlying the Cromerian Upper Freshwater Bed at West Runton, Norfolk.

Fig. 5. Distribution of remains of *Sciurus whitei* Hinton in the British Isles.

No other fossil remains of this species have been found in the British Isles, though a number of fir cones from Cromerian deposits of the Forest Bed of Norfolk bear marks suggesting that they had been gnawed by squirrels (Newton 1882a). Newton (1881, 1882a, 1891) described and figured a humerus from Ostend, Norfolk (57), which agreed closely in form with that of the living red squirrel, *S. vulgaris* Linn., but he was not certain whether it came from the Forest Bed or from a Recent alluvial deposit.

On the continent of Europe, remains of *Sciurus* are known from a number of Early and Middle Pleistocene localities in France and Hungary, though they have usually been left without specific determination. Janossy (1962) discovered remains of a squirrel approaching *S. whitei* at the Middle Pleistocene locality of Tarkö in Hungary, and described them as belonging to a new subspecies, *S. whitei hungaricus* Janossy 1962. In his opinion *S. whitei* may represent an ancestral form of *S. vulgaris*.

Sciurus vulgaris Linnaeus 1758

Red squirrel

The red squirrel is a widespread Palaearctic species, still common in parts of the British Isles. It occurs principally in woodland, but also in scrub beyond the Arctic circle. Its remains have been found in Late Pleistocene sediments of Europe from France to the Ukraine, but are nowhere common.

There are no indisputable records of *S. vulgaris* in the Pleistocene of the British Isles. Its remains are known from Dowel and Langwith Caves, Derbyshire (71, 72 : Bramwell 1960, Mullins 1913). The Dowel Cave record is from a Holocene stratum. The stratigraphic position of the remains from Langwith Cave was not determined, but the occurrence of *Rattus rattus* Linn., the black rat, suggests that some Holocene mammalian remains were present in addition to the rich Pleistocene fauna of the cave.

Genus ***SPERMOPHILUS*** Cuvier 1825 [= *Citellus* Oken 1816][1]

It was long suspected that the ground squirrels of the British Pleistocene represent two species. Hinton (in Barrett-Hamilton & Hinton 1910–21 : 724) wrote :

> Dr Forsyth Major studied the material [of ground-squirrels] with great care many years ago and we believe that he concluded that at least two species occur in the British Pleistocene ; unfortunately his results were never published. The writer in turn has made some progress with a similar investigation, but has not been able to complete his work yet. In his view also there are two species at least, both extinct, one being allied to the living *Citellus* [= *Spermophilus*] *erythrogenys*, the other more nearly related to *C.* [= *Spermophilus*] *eversmanni*.

Following studies of specimens from the British Museum (Natural History) the two forms have recently been distinguished by I. M. Gromov of Leningrad (*in litt.*) as *Citellus* [= *Spermophilus*] *superciliosus*, from the Upper Pleistocene, and *C.* [= *S.*] *primigenius* from deposits of earlier age.

Spermophilus (Urocitellus) primigenius Kormos 1934

Ground squirrel, extinct

1876	*Spermophilus* ; Cheadle : 70–71.
1882b	*Spermophilus Altaicus* ? ; Newton : 51–54, pl. 2.
1885	*Spermophilus erythrogenoides* Falconer ; Lydekker : 212–213.
1934	** *Spermophilus primigenius* Kormos : 314–315, fig. 45.
1947	*Citellus erythrogenoides* Falc. ; Jackson : 168.

Localities : Mundesley, Norfolk (60) : Newton 1882b.

Crayford and Erith, Kent (27) : Cheadle 1876, Lydekker 1885–87, Whitaker 1889, Newton 1890a, 1894, Barrett-Hamilton & Hinton 1910–21, Kennard 1944, Jackson 1947.

Distribution in the British Isles. Remains of this species of ground squirrel have been found abundantly in the Middle Terrace deposits of the Thames at Crayford and Erith, Kent. Cheadle (1876) attributed remains which he had found at Erith to *Spermophilus* sp. Subsequent writers (Lydekker, Whitaker, Newton, Barrett-Hamilton & Hinton, Kennard, Jackson) regarded the form represented at these localities as *S. erythrogenoides*. A skull from Erith was subsequently determined as *Citellus* [= *Spermophilus*] *primigenius* by Gromov, who wrote as follows (*in litt.*, translation) :

> Specimen M 9605, a deformed skull with a fragment of mandible, belongs to a large form of *Citellus* (*Urocitellus*) *primigenius* Korm., approaching in its dimensions the Polish *C.* (*U.*) *polonicus* Gromov, though it preserves the basic characters of the former. The skull also has some characters typical for *C. nogaici* Top. : a well-marked basin which divides the hypo- and entoconid parts on the grinding surface of M_3, a weakly developed posterior crest on M^3, a weakly developed narrowing on the hypoconid of P_4, and a *foramen mentale* shifted upwards. The second of these characters, as well as the presence of tiny cusps on the bottom of the

[1] Although the name *Citellus* Oken 1816 has been extensively used hitherto for these ground squirrels, Oken (1815–16) is not consistently binominal (Ellerman & Morrison-Scott 1966 : 3) and was rejected as unavailable by fiat of the International Commission on Zoological Nomenclature (Opinion 417, 1956).

external valleys of M_1–M_3, occurs also in *C. polonicus*. Finally, peculiar to the British remains is the forward shifting of the crests of the masseteric plate on the mandible. It is probably a distinct subspecies.

Some isolated worn teeth of *Spermophilus* described by Newton (1882b : 54) as close to *S. altaicus* (= *S. eversmanni*) were found in deposits now regarded as of early Anglian age at Mundesley, Norfolk. They provide the earliest record of *Spermophilus* in the British Isles and are provisionally referred to *S.* (*Urocitellus*) *primigenius*.

General distribution. *S. primigenius* (type locality Kalkberg, Nagyharsanyberg) is known from Villafranchian as well as from later (Günz, Günz–Mindel) deposits of Hungary. It is also present in the Middle Pleistocene of the Ukraine and Germany (Gromov 1965). According to Chaline (1972), ground squirrels, which he was unable to determine specifically, were present during the Mindel and Riss glaciations in France.

The living representatives of the subgenus *Urocitellus* – the long-tailed ground squirrels *S. undulatus* (Pallas 1779) and *S. parryi* Richardson 1827 – inhabit steppes as well as meadows in the tundra-zone of central and eastern Asia and North America.

Spermophilus (Colobotis) superciliosus (Kaup 1839)

Ground squirrel, extinct

1839 ** *Spermophilus superciliosus* Kaup : 112.
1866 *Spermophilus erythrogenoides* (Falc.) ; Dawkins & Sanford : xxxix (nomen nudum).
1866 *Spermophilus citillus* Pallas ; Dawkins & Sanford : xxxix.
1868 *Spermophilus erythrogenoides* ; Falconer, in Murchison : 452–454, pl. 35.
1974 *Citellus* sp. ; Stuart : 246.

Localities : Langwith Cave, Derbyshire (72) : Mullins 1913, Barrett-Hamilton & Hinton 1910–21.

Mendip Hills Caves (Bleadon Cave and others) : Dawkins & Sanford 1866, Falconer 1868, Stevens 1869, Sanford 1870a, b, Newton 1882a, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Fisherton, Wiltshire (22) : Falconer 1868, Stevens 1869, Barrett-Hamilton & Hinton 1910–21.

Ightham Fissures, Kent (28) : Newton 1894, 1899b, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Picken's Hole (layer 3), Somerset (10) : Stuart (1974).

Pin Hole Cave, Derbyshire (73) : Jackson 1947.

Distribution in the British Isles. *S. superciliosus* is a characteristic element of the fauna of the Last Glaciation.

General distribution and systematic remarks. *S. superciliosus* was described by Kaup from Eppelsheim in Germany. It is an element of the Late Pleistocene (Würm) fauna, present in almost the whole of Europe, including France, Germany, Poland, the European and Asiatic part of the Soviet Union, Czechoslovakia and Hungary. Its living relatives inhabit the steppe zone of eastern Europe and Asia.

FIG. 6. Distribution of remains of *Spermophilus* (*Urocitellus*) *primigenius* Kormos (▽) and *S.* (*Colobotis*) *superciliosus* (Kaup) (●) in the British Isles.

In Britain it has usually been recorded as *S. erythrogenoides*, a name first used by Falconer (in Murchison 1868) for remains from caves of the Mendip Hills. Hinton (in Barrett-Hamilton & Hinton 1910–21 : 723) stated that recent study tended to show that this name must be treated as a synonym of *S. superciliosus*.

I. M. Gromov of Leningrad studied the specimens from Ightham Fissures, Kent, and made the following remarks (*in litt.*, translation) :

> Two mandibular rami, no. M 11867, are typical remains of *Citellus* (*Colobotis*) *superciliosus* Kaup, broadly distributed in the northern part of continental Europe in Late Pleistocene ; during some part of this time it evidently also inhabited the British Isles. From the characteristic features of this species, as shown by the above-mentioned material, the following can be stated : width of P_4 no more than 11 per cent greater than its length, *processus articularis* short and broad below the head, posterior incision of the mandible relatively small, *foramen mentale* situated far from the anterior border of the masseteric plates, etc.

Family **GLIRIDAE** Thomas 1897

Genus ***MUSCARDINUS*** Kaup 1829

Hinton (in Barrett-Hamilton & Hinton 1910–21 : 351) recorded a single tooth of *Muscardinus* from the Forest Bed of Norfolk. This specimen has not been seen by the present writers. *Muscardinus* is nevertheless known from some Cromerian localities on the European continent so that its presence in Britain in Cromerian times is not improbable.

Muscardinus avellanarius (Linnaeus 1758)

Common or hazel dormouse

Although remains of this species have been found at a number of cave sites – Dog Holes and Pin Hole Caves (79, 73) : Jackson (1934, 1947) ; Great Doward Cave (17) : British Museum (Natural History) – all these remains are probably of Holocene age.

The hazel dormouse is now distributed in southern, western and central Europe, including southern Sweden and Britain, and in Asia Minor. On the continent of Europe it has been found in interglacial deposits as early as Tiglian. It was also present in France during the last interglacial (Chaline 1972).

Family **CASTORIDAE** Gray 1821

Genus ***TROGONTHERIUM*** Fischer 1809

Trogontherium minus Newton 1890

Giant beaver, extinct

1890b *Trogontherium minus* Newton : 447–448.

Localities : Red Crag of Felixstowe and *Woodbridge, Suffolk (45, 47) : Newton 1890b, 1891, 1902, Barrett-Hamilton & Hinton 1910–21, Schreuder 1929, 1951.

According to Schreuder (1951), who made a very thorough study of the genus *Trogontherium*, this species is more primitive than the other representatives of the genus, *T. cuvieri* Fischer and *T. boisvilleti* (Laugel).

T. minus is also known from Astian (Pliocene) sediments of Perpignan, France. The Red Crag specimens (like many other Crag fossils) are probably derived from earlier deposits and cannot be regarded as part of the contemporary Lower Pleistocene fauna.

Trogontherium boisvilletti (Laugel 1862)

Giant beaver, extinct

1846 *Trogontherium Cuvieri* ; Owen : 184–189, figs 71–73.
1848 *Diabroticus Schmerlingi* ; Pomel : 167.
1862 ** *Conodontes Boisvilletti* Laugel : 715–718.
1866 *Castor trogontherium* Cuvier ; Dawkins & Sanford : xxxvi.
1902 *Dipoides Lydekkeri* Schlosser : 117.
1951 *Trogontherium boisvilletti* Laugel ; Schreuder : 403.
1956 *Trogontherium* sp. ; Spencer : 354.

Localities : Sizewell, Suffolk, and Thorpe, Norfolk[1] (49, 48, Norwich Crag) : Lydekker 1885, Schreuder 1951.

East Runton (64, Pastonian Forest Bed) : Newton 1882a, 1892, Barrett-Hamilton & Hinton 1910–21, Schreuder 1951.

Bacton, Cromer, Kessingland, Mundesley, Overstrand, Paston and West Runton (58, 63, 52, 60, 62, 59, 65, 'Cromerian') : Lyell 1840, Owen 1846, Dawkins & Sanford 1866, Owen 1869, Newton 1881, 1882a, Lydekker 1885, Reid 1890, Hinton 1914, Schreuder 1929, 1931.

Clacton, Copford, Hoxne and Swanscombe (43, 42, 54, 30, Hoxnian) : Brown 1852, Newton 1902, Schlosser 1902, Stopes 1904, Newton 1916, Schreuder 1929, 1951, Spencer 1956, Sutcliffe 1964, Singer *et al.* 1973.

Range : *T. boisvilletti* was apparently present in Britain during the Tiglian, Cromerian and Hoxnian. Its remains have been found frequently in deposits of

[1] See also footnote on p. 96.

Fig. 7. Distribution of remains of *Trogontherium boisvilletti* (Laugel) in the British Isles.

the Norfolk Forest Bed ; only a few Hoxnian specimens are known. These are a solitary incisor from Ingress Vale, Swanscombe (Newton 1902, Stopes 1904, Schreuder 1929, 1951, Sutcliffe 1964), a cheek tooth from Copford (Brown 1852, site dated as Hoxnian by Turner 1970, BM(NH) 27985), a femur and eight cheek teeth from Hoxne (Spencer 1956) ; and part of a skull from Clacton (Singer *et al.* 1973).

General distribution. *T. boisvilletti* is known from the early Pleistocene in Britain, Holland, France (type locality Saint-Prest, near Chartres) and western parts of Germany. Further to the east it is, according to Schreuder (1951), replaced by a slightly different species, *T. cuvieri* Fischer, first described from the border of the Azov Sea. *T. cuvieri* was present in Germany during the Holsteinian Interglacial. According to Lehmann (1953), *T. cuvieri* is a more advanced species than *T. boisvilletti* and may be its descendant. If this is true, the British Hoxnian remains may represent *T. cuvieri*, but there are too few suitable specimens to allow a detailed determination.

Genus *CASTOR* Linnaeus 1758

Castor fiber Linnaeus 1758

Beaver

1846 *Castor europaeus* ; Owen : 190–200, figs 74–75.
1864 *Castor veterior* Lankester : 355–356.
1889 *Castor fiber* Linn. (= *europaeus* Owen) ; Whitaker : 336.
1908b *Castor plicidens* Maj. ; Major : 630–635, figs 132–136.
1964 *Castor* sp. ; Spencer : 338.

Localities : Sutton and Woodbridge, Suffolk (47, Red Crag) : Lankester 1864, Newton 1891, Barrett-Hamilton & Hinton 1910–21, Schreuder 1929.

East Runton (64, Pastonian Forest Bed) : Major 1908b.

Bacton, Kessingland, Mundesley, West Runton (58, 52, 60, 65, Forest Bed) : Dawkins & Sanford 1866, Owen 1869, Newton 1881, 1882a, 1891, Major 1908b, Barrett-Hamilton & Hinton 1910–21, Hinton 1914, Schreuder 1929, 1931, Friant 1962.

Westbury-sub-Mendip Fissure (13, lower middle Pleistocene) : Bishop 1974.

Clacton (43, Hoxnian) : Barrett-Hamilton & Hinton 1910–21, Hinton 1923b, Sutcliffe 1964.

Swanscombe (Barnfield Pit), Kent (30, Hoxnian) : BM(NH).

Grays Thurrock and Ilford, Essex (33, 35) : Lankester 1864, Dawkins & Sanford 1866, Whitaker 1889, Hinton 1900b, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Selsey, Sussex and Upnor, Kent (24, 31, Last Interglacial) : BM(NH).

Kent's Cavern, Devon (6) : BM(NH).

Cambridge Fens, Cambridgeshire ; Hay Wood Rockshelter, Somerset ; Staple Howe, Yorkshire ; Star Carr, Yorkshire ; Thatcham, Berks (41, 10, 75, 76, 23, Holocene) : Montagu 1924, Brewster 1963, Fraser & King 1954, Wymer 1962.

Loch of Marlee, Perthshire, and Middlestots Bog, Edrom Parish, Berwickshire (82, 80) : Barrett-Hamilton & Hinton 1910–21.

Fig. 8. Distribution of fossil remains of *Castor fiber* Linn. in the British Isles.

Range. Remains of *C. fiber* have been found in deposits in the British Isles ranging in age from lowest Pleistocene (Red Crag) to Holocene. The species spread to Scotland but apparently never reached Ireland. Barrett-Hamilton & Hinton (1910–21) considered that the beaver did not become extinct in Britain before the thirteenth century A.D.

General distribution. Although limited to a small number of relict localities as a result of extermination by man, *C. fiber* is still widely distributed in Europe and Asia. Its fossil remains are known from the Pliocene and Pleistocene of Europe and Asia.

Systematic remarks. The beaver remains from the Red Crag were described by Lankester (1864) under the new name *C. veterior*. Newton (1891) considered that this species was conspecific with *C. fiber* and Schreuder (1929) proved it by a detailed comparison. C. I. F. Major (1908a) described some remains from the Forest Bed at East Runton as belonging to *C. plicidens*, a species described by him from Val d'Arno in Italy. Schreuder (1929) showed that the folding of tooth-enamel is a character depending upon the individual age of the animal and *C. plicidens* is therefore a synonym of *C. fiber*. Later it was found that individuals of '*C. plicidens*' sometimes appear among postglacial beavers. Viret (1954), however, studying the skull of a Villafranchian beaver from St Vallier in France, found some morphological differences from the Recent beaver and was inclined to retain the name *C. plicidens* for all the beavers from that period, not only for specimens with folded enamel. According to Lehmann (1957) these differences are rather of a subspecific character and he designated the Villafranchian beavers as '*Castor fiber plicidens* Major 1875'. Until statistical analysis of the variability of the living beaver has been made, it seems preferable to use only the specific name *Castor fiber* Linn. for the Astian (Upper Pliocene) as well as for the Pleistocene beavers.

Family **MURIDAE** Gray 1821

Genus ***APODEMUS*** Kaup 1829

Apodemus sylvaticus (Linnaeus 1758)

Wood mouse

1846 *Mus musculus* (?) ; Owen : 209, fig. 79.
1881 *Mus sylvaticus* ; Newton : 258–259.
1910 *Micromys* (= *Mus*) *sylvaticus* (Linné) ; Jackson : 328.
1910b *Mus* sp., allied to *M. sylvaticus* ; Hinton : 489–507.
1915 *Apodemus* sp. ; Hinton : 580.
1915 *Apodemus whitei* Hinton : 580–581.
1915 *Apodemus sylvaticus* L. ; Hinton : 581–582.

LOCALITIES : West Runton (Upper Freshwater Bed), Norfolk (65) : Newton 1881, 1882a, 1891, Barrett-Hamilton & Hinton 1910–21, Hinton 1915, BM(NH).

Westbury-sub-Mendip Fissure, Somerset (13) : Bishop 1974.

Hitchin, Hertfordshire (39) : Carreck 1959.

Swanscombe (Ingress Vale), Kent (30) : Stopes 1904, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1915, Sutcliffe 1964, BM(NH).

Hoxne, Suffolk (54) : Wolff (*in litt.*, *Apodemus* sp.).

Grays Thurrock, Essex (33) : Hinton, Kennard & Newton 1900, Hinton 1915.

Stutton, Suffolk (44) : Stuart 1974 (*A. sylvaticus* group).

Bacon Hole, Glamorganshire (16) : det. A. J. Stuart (*in litt.*).

Kirkdale Cave, Yorkshire (77) : Owen 1846, Dawkins & Sanford 1866.

Swanton Morley, Norfolk (66) : Stuart 1974 (*A. sylvaticus* group).

Tornewton Cave, Devon (3) : Kowalski 1967, BM(NH).

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, BM(NH).

Dog Holes Cave, Lancashire (79) : Jackson 1910, BM(NH).

Great Doward Cave, Herefordshire (17) : Bristol University Spelaeological Society, det. K. K.

Gwaenysgor Cave, Flintshire (68) : Jackson 1947.

Ightham Fissures, Kent (28) : Newton 1894, Barrett-Hamilton & Hinton 1910–21, Hinton 1915, Carreck 1957, BM(NH).

Langwith Cave, Derbyshire (72) : Mullins 1913.
Levaton Cave, Devon (2) : Carreck 1957.
Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.
Rowberrow Cavern, Somerset (11) : BM(NH).
Dowel Cave, Derbyshire (71) : Bramwell 1960.
Happaway Cave, Devon (5) : BM(NH).
Lynx Cave, Denbighshire (67) : Blore 1966.
Nazeing, Essex (37) : Hinton 1952, BM(NH).
Joint Mitnor Cave, Devon (1, Layer 10, Holocene) : BM(NH).
Ballynamintra Cave, Co. Waterford (90) : Barrett-Hamilton & Hinton 1910–21, Jackson 1929b.
Castlepook Cave, Co. Cork (87) : Scharff, Seymour & Newton 1918, BM(NH).
Edenvale Caves (Alice and Gwendoline, Catacombs, Newhall, Barntick), Co. Clare (85) : Barrett-Hamilton & Hinton 1910–21, Scharff 1906.
Keshcorran Caves (Coffey, Plunkett), Co. Sligo (84) : Barrett-Hamilton & Hinton 1910–21, Jackson 1929b, Scharff *et al.* 1903.
Kilgreany Cave, Co. Waterford (89) : Jackson 1929b.

Fig. 9. Distribution of fossil remains of *Apodemus sylvaticus* (Linn.) in the British Isles.

Distribution in the British Isles. *A. sylvaticus* was present in the British Isles during the Cromerian, Hoxnian and Ipswichian interglacials. It probably disappeared from the country at the time of the cold stage represented by the Tornewton Cave Glutton Stratum. A solitary specimen from this deposit may have been introduced from a higher, interglacial, level. This species was present during the Last Glaciation and during the Holocene. Most of the localities, especially caves, cannot be accurately dated, and it is difficult to decide if *A. sylvaticus* was present throughout the Holocene without interruption. It may have reached Ireland during Upper Pleistocene times.

General distribution. *A. sylvaticus* is now widely distributed in Europe, north Africa and western Asia. The fossil remains of this or nearly related species are known from the Pleistocene of Europe and China. The oldest of them are dated as Tiglian, with further records from deposits of Cromerian, Holsteinian and later date.

SYSTEMATIC REMARKS. Hinton (1915 : 580) referred the teeth from the Cromerian Upper Freshwater deposits of West Runton to *Apodemus* sp. Although he found that their pattern was indistinguishable from that of *A. sylvaticus* he considered that the material was insufficient for fine determination. From Swanscombe (Ingress Vale) (*loc. cit.*) he described a new species, which he named *A. whitei*, from part of a maxilla differing slightly from recent specimens of *A. sylvaticus*. However, the characters concerned lie within the range of individual variability and there does not seem to be any good reason for regarding the West Runton form as a distinct species.

Apodemus flavicollis (Melchior 1834)

Yellow-necked mouse

1894 *Mus Abbotti* Newton : 195, pl. xi, fig. 8 (not *M. abbotti* Waterhouse).
1899a *Mus Lewisi* Newton : 381.
1915 *Apodemus lewisi* Newton ; Hinton : 582–584.
1921 *Apodemus Flavicollis* Melchior ; Hinton : 78.

LOCALITIES : Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924.
Dowel Cave, Derbyshire (71) : Bramwell 1960.
Etches' Cave, Derbyshire (71) : Pernetta 1966.
Happaway Cave, Devon (5) : Hinton 1915, BM(NH).
Ightham Fissures, Kent (28) : Newton 1894, 1899a, b, Hinton 1915, BM(NH).
Kent's Cavern, Devon (6) : Hinton 1915.
Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

DISTRIBUTION IN THE BRITISH ISLES. Remains of *A. flavicollis* have been found almost exclusively in very late sediments. Many of the records must nevertheless be considered doubtful in view of the great difficulty in distinguishing remains of this species from those of *A. sylvaticus*. The remains recorded from Dowel Cave were found in a Neolithic layer (Bramwell 1960 : [10]–pages unnumbered) and those from Etches' Cave were in early postglacial layers (Pernetta 1966 : 12, 15). Hinton (1921) considered that the Aveline's Hole remains were probably a late introduction. The same may be true for the Ightham Fissures. The Kent's Cavern and Happaway specimens were excavated a century ago. From Pin Hole Cave, Derbyshire (Jackson 1934), remains of *A. flavicollis* have been recorded from both the superficial levels and at a depth of more than 3 m (10 ft), where they were apparently associated with Upper Pleistocene faunal remains.

GENERAL DISTRIBUTION. At the present time *A. flavicollis* is widespread in Europe and east as far as the Urals and Caucasus. It is absent from a large part of western Europe (France, Belgium, Holland), but is present in England and southern Sweden. Nothing is known about the fossil remains. It is absent from the Pleistocene of France (Chaline 1972). It is difficult to decide whether this species represents a natural migration at the end of Pleistocene or during the Holocene or whether it was brought by man.

SYSTEMATIC REMARKS. According to Hinton (1915), *A. lewisi*, described from the Ightham Fissures by Newton (1899a, b), is closely related to, if not identical with, *A. flavicollis* Melchior. Jackson (1934) determined his material as '*A. flavicollis* (= *A. lewisi*)'. The lack of an anterior accessory cusp on M_1 is, according to Hinton (1915), of no significance in specific determination, because the cusp is apparently absent in slightly worn teeth of *A. flavicollis*. It seems probable that the holotype of *A. lewisi* is nothing but a Recent specimen of *A. flavicollis*.

Genus ***MICROMYS*** Dehm 1841

Micromys minutus (Pallas 1771)

Harvest mouse

This species was probably introduced into Britain by man in postglacial times. According to Barrett-Hamilton & Hinton (1910–21) it is unknown there in a fossil state. Remains found at Tornewton Cave (Kowalski 1967) are from a surface fissure unconnected with the main sequence of deposits and are unlikely to be of any antiquity.

M. minutus, now widely distributed in Europe and Asia, is present in England and perhaps in the southern parts of Scotland. The genus *Micromys*, and probably the Recent species, is known in continental Europe from the late Pleistocene.

Genus ***MUS*** Linnaeus 1758

Mus musculus Linnaeus 1758

House mouse

The house mouse was introduced into Britain by man. Barrett-Hamilton & Hinton (1910–21) discussed some early data about its fossil occurrence in Britain and considered that all are erroneous or refer to Recent remains. There is no evidence for the occurrence of the house mouse in Britain before the Iron Age.

Genus ***RATTUS*** Fischer 1803

Rattus rattus (Linnaeus 1758)

Black rat

Although remains of the black rat have been recorded from Aveline's Hole (Hinton 1921) and Langwith Cave (Mullins 1913) these are probably Recent. The black rat was introduced into the British Isles by man during the historical period.

Rattus norvegicus (Berkenhout 1769)

Brown rat

The brown rat is a recent addition to the British mammalian fauna. Jackson (1929b) records its remains from Kilgreany Cave, Ireland, in an upper layer with remains of domestic animals and prehistoric material, but these are probably of very recent date.

Family **CRICETIDAE** Rochebrune 1883
Genus ***CRICETUS*** Leske 1779
Cricetus cricetus (Linnaeus 1758)
Common hamster

1909 *Cricetus vulgaris Runtonensis* Newton : 110–113, fig. (unnumbered).
1967 *Cricetus cricetus* (Linnaeus 1758) ; Kowalski : 119–120.

LOCALITIES : West Runton (Upper Freshwater Bed), Norfolk (65) : Newton 1909, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Osborn 1922, BM(NH).
Tornewton Cave (Glutton Stratum), Devon (3) : Kowalski 1967, BM(NH).

FIG. 10. Distribution of fossil remains of *Cricetus cricetus* (Linn.) in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. Representatives of the genus *Cricetus* appeared twice in Britain : in the Cromerian interglacial and during the cold stage represented by the Tornewton Cave Glutton Stratum. The Tornewton Cave remains represent at least two individuals.

GENERAL DISTRIBUTION. *C. cricetus*, the only living member of its genus, occurs at the present time in eastern Europe and in the western part of Asia. It is also present in western and central Europe where its range is insular and seems to be characterized by gradually increasing expansion. It occurs in steppes, parklands and meadows. In Europe its occurrence is now associated with arable fields. Fossil remains of *Cricetus* are known from the early, middle and late Pleistocene of western, central and eastern Europe, especially in deposits indicating a cold and arid environment.

SYSTEMATIC REMARKS. All the fossil remains of the genus *Cricetus* are very uniform in their dental morphology and do not differ from the Recent ones. They do, however, vary greatly in size. On this basis many new forms have been described, some under specific, others under subspecific names. The specimen from the Cromer Forest Bed, BM(NH) M18352, an upper jaw with a tooth-row 9·3 mm long, is the holotype of a form known as *Cricetus runtonensis* or *C. cricetus runtonensis*. According to Schaub (1930), it is a synonym of *C. c. major* Woldřich described from the late Pleistocene deposits of Czechoslovakia. Other palaeontologists use the name *C. runtonensis* to designate larger representatives of *Cricetus* from the early Pleistocene, usually without giving sufficient morphological reasons for its distinctness from later populations. According to Fahlbusch (1969), there are some peculiarities in the pattern of M_2 in *C. runtonensis*, but a similar morphology can also be found in some Recent specimens. In the opinion of one of us (K. K.) the large early Pleistocene hamsters are at most subspecifically distinct from those of the late Pleistocene and present day. The great variability of this species in the Pleistocene was connected with changing climatic conditions.

Genus ***ALLOCRICETUS*** Schaub 1930

cf. ***Allocricetus bursae*** Schaub 1930

Hamster, extinct

1870a *Cricetus songarus*; Sanford: 51, 56, fig. 6.
1870b *Cricetus* (*Mus*) *songarus* (Pallas); Sanford: 128–129; pl. viii, fig. 6.
1913 *Phodopus sanfordi* Hinton, in Barrett-Hamilton & Hinton 1910–21: 383, fig. 53.
1967 *Phodopus songorus* (Pallas); Kowalski: 113–114.

Localities: Hutton Cave, Somerset (10): Sanford 1870a, b, Newton 1909, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Tornewton Cave (Glutton Stratum), Devon (3): Kowalski 1967, BM(NH).

Fig. 11. Distribution of remains of cf. *Allocricetus bursae* Schaub in the British Isles.

Distribution in the British Isles. The occurrence of this species in the Glutton Stratum of Tornewton Cave shows that it was present during the pre-hippopotamus cold stage represented by this deposit. Although the age of the Hutton Cave fauna is unknown, the occurrence of remains of a relatively primitive form of mammoth suggests that this record is at least as early as that from Tornewton Cave.

General distribution and systematic remarks. Small representatives of Cricetidae are common in the early, middle and late Pleistocene of Europe. The uniform structure of the teeth in Cricetidae makes the systematic determination of their remains very difficult. According to Schaub (1930), the small hamsters of the late Pleistocene of Europe should be referred to *Phodopus songorus*. Janossy (1961) later stated that Schaub based his determination on incorrectly determined Recent specimens and claimed that the small hamster described by him is conspecific with Recent *Cricetulus migratorius*. The same name was used for English specimens by Kurtén (1969). Chaline (1972) did not find this species in France, but determined all late Pleistocene small French hamsters as *Allocricetus bursae* Schaub 1930. A more detailed study of English specimens will be necessary before it is possible to decide whether they belong to one or two species and what species there are.

In the earliest description of British hamster remains (those from Hutton), Sanford (1870) applied the name *Cricetus songarus*. Hinton (in Barrett-Hamilton & Hinton 1910–21 : 383) considered that the remains should be placed in the genus *Phodopus* and that they could not be synonymized with *P. songorus* but needed a new name, for which he proposed *P. sanfordi*. No reasons for this decision are given. If the British specimens are conspecific with *A. bursae* Schaub then this name is a junior synonym of *P. sanfordi* Hinton and must be replaced by it.

Small hamsters are now an element of the steppe fauna, and their species are broadly distributed in south-eastern Europe as well as in western and central Asia. *C. migratorius* ranges from south-eastern Europe to China. This species, partly cited under the name of *A. bursae* Schaub, is known as a fossil from the late Pleistocene of Germany, Switzerland, Spain, France, Czechoslovakia, Hungary, Poland and the Soviet Union.

Genus ***DICROSTONYX*** Gloger 1841

Dicrostonyx torquatus (Pallas 1779)

Collared lemming

1869	*Lemmus torquatus* ; Stevens : 110, 113.
1870a	*Arvicola Gulielmi* Sanford : 51, 55, fig. 2.
1870b	*Arvicola Gulielmi* Sanford : 125, pl. viii, fig. 2.
1874	*Myodes torquatus* Pall. ; Blackmore & Alston : 469–470.
1910a	*Dicrostonyx gulielmi* Sanford ; Hinton : 38–39.
1910a	*Dicrostonyx henseli* Hinton : 37–38.
1960	*Dicrostonyx* sp. ; Bramwell : [10].

Localities : Westbury-sub-Mendip, Somerset (13) (*Dicrostonyx* sp., lower middle Pleistocene) : Bishop 1974.

Erith, Kent (27) : Newton 1890a, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Kennard 1944, Jackson 1947.

Hutton Cave, Somerset (10) : Stevens 1869, Sanford 1870a, b, Blackmore & Alston 1874, Jackson 1909, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Tornewton Cave (Glutton Stratum and Reindeer Stratum), Devon (3) : Kowalski 1967, BM(NH).

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, 1926b, BM(NH).

Chudleigh Fissure, Devon (7) : Hinton 1926b.

Dog Holes Cave, Lancashire (79) : Jackson 1909, 1910, 1929a, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Jackson 1947, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Fisherton, Wiltshire (22) : Stevens 1869, Blackmore & Alston 1874, Jackson 1909, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Great Doward Cave, Herefordshire (17) : Bristol University Spelaeological Society, det. K. K.

Gwaenysgor Cave, Flintshire (68) : Jackson 1932 (*fide* Jackson 1947), Jackson 1947.

Ightham Fissures, Kent (28) : Newton 1894, Jackson 1909, Hinton 1910a, b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Jackson 1929a, 1947, Zimmermann 1959, BM(NH).

Kent's Cavern, Devon (6) : BM(NH).

King Arthur's Cave, Herefordshire (17) : BM(NH) (Hinton collection).

Langwith Cave, Derbyshire (72) : Mullins 1913, Hinton 1910a, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Jackson 1929a, 1947, BM(NH).

Merlin's Cave, Herefordshire (18) : Hinton 1925, 1926b, BM(NH).

Murston, Kent (32) : Newton 1890a, Barrett-Hamilton & Hinton 1910–21.

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Rowberrow Cavern, Somerset (11) : BM(NH) (Hinton collection).

Upton Warren, Worcestershire (20) : Coope *et al.* 1961.

Brean Down, Somerset (9) : Apsimon *et al.* 1961.

Fox Hole Cave, Derbyshire (71) : Bramwell 1970.

Dowel Cave, Derbyshire (71) : Bramwell 1960.

Lynx Cave, Denbighshire (67) : Blore 1966.

Etches' Cave, Derbyshire (71) : Pernetta 1966.

Hackney, London (36) : BM(NH).

Angel Road, Middlesex (36) : Hinton 1912, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Nazeing, Essex (37) : Hinton 1952, BM(NH).

Ponders End, Middlesex (36) : Hinton 1926b.

Corstorphine, nr. Edinburgh, Scotland (81) : Evans 1907, 1913, Barrett-Hamilton & Hinton 1910–21, Jackson 1929b.

Creag nan Uamh Cave, Sutherland (83) : Peach & Horne 1917.

Ballynamintra Cave, Co. Waterford, Ireland (90) : Coleman 1965.

Castlepook Cave, Co. Cork (87) : Ussher *et al.* 1908, Jackson 1910, Ussher 1910, Hinton 1910a, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Jackson 1929b, 1947, Coleman 1965.

Castletownroche Cave, Co. Cork (88) : Coleman 1965.

Edenvale Caves (Alice and Gwendoline, Catacombs, Newhall), Co. Clare (85) : Scharff 1906, Hinton 1926b, Coleman 1965, BM(NH).

Keshcorran Caves (Coffey, Plunkett), Co. Sligo (84) : Jackson 1909, Scharff *et al.* 1903, Scharff, Seymour & Newton 1918, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Jackson 1929b, Coleman 1965, BM(NH).

Kilgreany Cave, Co. Waterford (89) : Jackson 1929b, Coleman 1965.

Red Cellar Cave, Co. Limerick (86) : Coleman 1965.

Brandon, Warwickshire, and Penkridge, Staffordshire, are two additional *Dicrostonyx* localities not marked on Fig. 1, which were notified to us by Mr J. Carreck (*in litt.*) after the compilation of the above list.

Fig. 12. Distribution of fossil remains of *Dicrostonyx torquatus* (Pallas) in the British Isles.

Distribution in the British Isles. *Dicrostonyx* is known in the British Isles from at least three stages of the Pleistocene. The earliest record (*Dicrostonyx* sp.) is from the lower middle Pleistocene site of Westbury-sub-Mendip. The second stage is represented by remains from the *Corbicula* bed at Erith and the Glutton Stratum of Tornewton Cave. At the last-mentioned site *Dicrostonyx* disappeared in the overlying Last Interglacial deposits and reappeared again in the Last Glaciation Reindeer Stratum. During the Last Glaciation it reached its greatest climax, spreading throughout England, Wales, Scotland and Ireland. Its remains are especially abundant in deposits dating from the later part of this stage and it was clearly a dominant element of the tundra faunal assemblage of that time. At Nazeing, Essex, it apparently survived until late Glacial pollen Zone III.

General distribution. The collared lemming is now widely distributed in the tundra belt of the Holarctic, in both Eurasia and North America. The American subspecies are sometimes recognized as specifically different from those of Eurasia. Fossil remains are known from the deposits of four different glaciations in Europe and they are also present in Asia and North America. Pre-Cromerian collared lemmings from Czechoslovakia and Poland are morphologically different from later ones and were named *Dicrostonyx simplicior* Fejfar 1966. During the Last Glaciation *D. torquatus* in Europe reached as far south as Hungary, Switzerland and central France.

Systematic remarks. Hinton (1910a) distinguished two species of fossil collared lemmings in the British Isles, *Dicrostonyx gulielmi* and *D. henseli*. According to him the differences between these were as great as those between different Recent species of the genus *Dicrostonyx*. It is now generally accepted, however, that disregarding the Canadian *D. hudsonius* (which does not concern us here) all living forms belong to one species. The European fossil forms may, at the most, be subspecifically different from Recent ones, but this seems not to be the case as the two forms described by Hinton are present together at nearly all localities. Janossy (1954) found in Hungarian caves not only all possible intermediate forms between *D. gulielmi* and *D. henseli*, but also specimens with left tooth-row of one type and right one of the other. Most palaeontologists are of the opinion that there was only one species of the collared lemming in the Upper Pleistocene of Europe and that it was conspecific with the living *D. torquatus*. Like the Recent population, it was very variable (Mandach 1938). Recently Agadzhanian (1973) has stated that, among the populations of Recent and fossil collared lemmings, there are different morphotypes, differing in the grade of complication of the crown pattern of their molars. He considered that the simpler morphotypes are more numerous among the populations from the Last Glaciation of Eurasia than among Recent animals from north Asia. For this reason he favoured preserving the name *D. gulielmi* as the oldest available designation for the collared lemmings from the time of the Last Glaciation of Eurasia.

Genus *LEMMUS* Link 1795

Lemmus lemmus (Linnaeus 1758)

Norwegian lemming

1870a	*Lemmus norvegicus* (var.) ; Sanford : 51, 56, fig. 4.
1870b	*Lemmus norvegicus* ; Sanford : 125–126, pl. viii, fig. 4.
1874	*Myodes lemmus* (Linn.) ; Blackmore & Alston : 470–471.
1921	*Lemmus lemmus* Linn. ; Hinton : 75–76.
1950	*Lemmus* sp. ; Schreuder : 629, 633–634.

Localities : Westbury-sub-Mendip, Somerset (13) (*Lemmus* sp., lower middle Pleistocene) : Bishop 1974.

Hoxne, Suffolk (54) : Wolff (*in litt.*).

Swanscombe (Barnfield Pit, Upper Middle Gravel), Kent (30) (*Lemmus* sp.) : Schreuder 1950.

Erith, Kent (27) : Newton 1890a, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Kennard 1944, Jackson 1947, BM(NH).

Hutton Cave, Somerset (10) : Sanford 1870a, b, Blackmore & Alston 1874, Jackson 1909, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Tornewton Cave (Glutton Stratum), Devon (3) : Kowalski 1967, BM(NH).

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1926b, BM(NH).

Chudleigh Fissure, Devon (7) : Hinton 1926b.

Dog Holes Cave, Lancashire (79) : Jackson 1909, 1910, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Great Doward Cave, Herefordshire (17) : Bristol University Spelaeological Society, det. K. K.

Ightham Fissures, Kent (28) : Newton 1894, Bate 1901, Jackson 1909, Hinton 1910a, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Zimmermann 1959, BM(NH).

Kent's Cavern, Devon (6) : Kennard 1945–46.

Langwith Cave, Derbyshire (72) : Mullins 1913, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b.

Merlin's Cave, Herefordshire (18) : Hinton 1924, 1926b, BM(NH).

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Uphill Cave, Somerset (9) : Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Dowel Cave, Derbyshire (71) : Bramwell 1960.

Etches' Cave, Derbyshire (71) : Pernetta 1966.

Harborough Cave, Derbyshire (70) : Jackson 1929a.

Nazeing, Essex (37) : Hinton 1952, BM(NH).

Castlepook Cave, Co. Cork, Ireland (87) : Ussher *et al.* 1908, Ussher 1910, Scharff, Seymour & Newton 1918, Barrett-Hamilton & Hinton 1910–21, Jackson 1929b, Coleman 1965, BM(NH).

Castletownroche Cave, Co. Cork (88) : Coleman 1965.

After the compilation of the above list we have been informed by Mr J. Carreck (*in litt.*) that he has also determined remains of *Lemmus lemmus* from deposits of Ipswichian (Zone IIb) age at Wretton, Norfolk (not marked on Fig. 1).

FIG. 13. Distribution of fossil remains of *Lemmus lemmus* (Linn.) in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *L. lemmus* is distributed in Pleistocene sediments of England and southern Ireland. In many localities it has been found together with *Dicrostonyx torquatus*, but it is usually less numerous. Most of the fossil localities with *Lemmus* are of Last Glaciation age. Its occurrence at Nazeing, where it was found in peaty muds lying deeper than the calcareous muds in which

Dicrostonyx torquatus appears for the last time, seems to be the latest well-dated evidence of its presence in Britain. This may indicate that *Lemmus* disappeared slightly earlier than *Dicrostonyx*, though it could also be explained by lack of sufficient specimens.

Lemmus is known from at least four stages of the British Pleistocene. Earlier records are the lower middle Pleistocene site of Westbury-sub-Mendip, the Hoxnian of Hoxne and Swanscombe (Barnfield Pit, Upper Middle Gravel), and the stage or stages represented by the *Corbicula* Bed of Crayford and Erith and the Glutton Stratum of Tornewton Cave.

General distribution. The genus *Lemmus* has a circumpolar distribution ranging in the Old World from Scandinavia to the Bering Strait and including the arctic regions of North America. The differences between the Eurasiatic and American forms do not justify their distinction as different species (Sidorowicz 1964) : they can all be treated as subspecies of a single species, *L. lemmus*. *Lemmus* coexists in a great part of its range with *Dicrostonyx*, but is generally more southerly in distribution : it does not occur in Greenland or on the Canadian islands north of Viscount Melville Sound, where *Dicrostonyx* is abundant.

The genus *Lemmus* appeared very early in Europe. Its remains are known from middle Villafranchian deposits of Hungary, Poland and Germany. During the early Pleistocene it extended further south in eastern Europe than *Dicrostonyx*, and was present, for example, in Romania, where *Dicrostonyx* never penetrated. Its remains have been found at most early and middle Pleistocene fossil localities of central and western Europe and the genus is a characteristic element of the arctic fauna of the last two glaciations.

Systematic remarks. Fossil remains of *Lemmus* from the late Pleistocene of the British Isles and from the continent of Europe are indistinguishable, on the basis of teeth and preserved skeletal remains, from those of Recent *L. lemmus*. Villafranchian to middle Pleistocene remains are specifically different from the Recent form.

Genus ***CLETHRIONOMYS*** Tilesius 1850

Clethrionomys glareolus (Schreber 1780)

Bank vole

1846	*Arvicola pratensis* ; Owen : 208, fig. 78.
1870a	*Arvicola glareolus* (= *pratensis*) ; Sanford : 56.
1870b	*Arvicola glareolus* (Schreber) = *pratensis* (Baillon) = *riparia* (Yarrell) ; Sanford : 124.
1882a	*Arvicola* (*Evotomys* Coues & Allen) *glareolus* Schreber ; Newton : 82–83, pl. xiv, fig. 1–1c.
1900	*Microtus* (*Evotomys*) *glareolus* Schreb. ; Hinton, Kennard & Newton : 347–349.
1901	*Microtus glareolus* ; Hinton : 142.
1910b	*Evotomys* sp. ; Hinton : 492, 494, 497.
1926	*Evotomys harrisoni* Hinton : 216–217, pl. vii, fig. 2.
1926	*Evotomys kennardi* Hinton : 225–226, pl. vii, fig. 3.
1950	*Clethrionomys* sp. ; Schreuder : 629, 634–635.

Localities : West Runton (Upper Freshwater Bed), Norfolk (65) : Blackmore & Alston 1874, Newton 1882a, 1891, Hinton 1910b, Osborn 1922, Hinton 1926b, BM(NH).

Westbury-sub-Mendip, Somerset (13) : Bishop 1974.

Clacton, Essex (43) : Singer *et al.* 1973.

Hitchin, Hertfordshire (39) : Carreck 1959.

Swanscombe (Barnfield Pit, Upper Middle Gravels and Ingress Vale), Kent (30) : Stopes 1904, Hinton 1926b, Schreuder 1950, Sutcliffe 1964, Carreck (*in litt.*).

Aveley, Essex (34) : BM(NH).

Grays Thurrock, Essex (33) : Hinton, Kennard & Newton 1900, Hinton 1901, 1910b, 1926b, BM(NH).

Northfleet, Kent (29) : det. A. J. Stuart (*in litt.*).

Hutton Cave, Somerset (10) : Sanford 1870a, b, Blackmore & Alston 1874.

Tornewton Cave (Glutton Stratum and Reindeer Stratum), Devon (3) : Kowalski 1967, BM(NH).

Alveston Fissure, Gloucestershire (15) : det. G. B. Corbet.

Bacon Hole, Glamorganshire (16) : Stuart (*in litt.*).

Kirkdale Cave, Yorkshire (77) : BM(NH).

Swanton Morley, Norfolk (66) : Stuart 1974.

West Wittering, Sussex (24) : BM(NH).

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, BM(NH).

Brixham Cave, Devon (4) : Lydekker 1885, Hinton 1926b, BM(NH).

Chudleigh Fissure, Devon (7) : BM(NH).

Dog Holes Cave, Lancashire (79) : Jackson 1910, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Great Doward Cave, Herefordshire (17) : BM(NH).

Gwaenysgor Cave, Flintshire (68) : Jackson 1947.

Ightham Fissures, Kent (28) : Newton 1894, Hinton 1910b, 1926b, Zimmermann 1959, BM(NH).

Kent's Cavern, Devon (6) : Owen 1846, Dawkins & Sanford 1866, Blackmore & Alston 1874, Lydekker 1885, Kennard 1945–46, BM(NH).

Langwith Cave, Derbyshire (72) : Mullins 1913.

Merlin's Cave, Herefordshire (18) : Hinton 1925.

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Rowberrow Cavern, Somerset (11) : BM(NH).

Dowel Cave, Derbyshire (71) : Bramwell 1960.

Happaway Cave, Devon (5) : BM(NH).

Nazeing, Essex (37) : Hinton 1952, BM(NH).

Joint Mitnor Cave (layer X, Holocene), Devon (1) : BM(NH).

Distribution in the British Isles. The bank vole appeared in England for the first time during the Cromerian Interglacial. It was also present during the Hoxnian (Hitchin, Swanscombe). Although a few remains were found in the pre-hippopotamus Glutton Stratum of Tornewton Cave, this species is lacking from typical faunal assemblages of this time, for example from Clevedon Cave. It is a common element in deposits of Last Interglacial, Last Glaciation and Holocene age.

Fig. 14. Distribution of fossil remains of *Clethrionomys glareolus* (Schreber) in the British Isles.

Clethrionomys glareolus is an element of the forest fauna. It was probably not present in this country during the maxima of the glaciations, though it was able to reach it very early after the retreat of the ice and invaded the British Isles many times in all the interglacials and in post-glacial time.

General distribution. *C. glareolus* is now distributed throughout Europe, northern and central Asia and probably North America. Remains of the genus *Clethrionomys* are common in faunas of early middle Pleistocene age from continental Europe and have been described under different specific names, though they probably all belong to *C. glareolus*. *C. glareolus* is abundant in the interglacial and interstadial deposits of the late Pleistocene of Europe.

Systematic remarks. Only a few remains of *Clethrionomys* are known from the Norfolk Forest Bed. Although they were determined by Hinton (1926b) as '*Evotomys* sp.', they cannot be distinguished from Recent *C. glareolus*. The bank vole is a primitive, and very conservative, species of vole and its existence in Europe in the early Pleistocene is not unexpected.

Hinton (1926b) described from the Ightham Fissures two new species of *Clethrionomys*, '*Evotomys kennardi*' and '*E. harrisoni*', both from the same faunal assemblage. The material from Ightham is however a mixture of late Glacial and Recent bones and the holotype of *E. harrisoni* is a well-preserved skull of a typical *C. glareolus*. It is the skull of a young individual and its supposed characters (small dimensions, broad inter-orbital region) are related to its juvenile condition; it is probably a Recent specimen. '*E. kennardi*' seems to be of earlier geological age and its dimensions are somewhat larger than those of Recent specimens. According to Hinton (1926b), it belongs to the '*E. nageri*' group. *C. g. nageri* is now generally recognized as an Alpine subspecies (or perhaps only an ecotype) of *C. glareolus*, living under a more severe climate. It seems probable that during the difficult conditions of the Last Glaciation individuals of *Clethrionomys* grew bigger than during interglacial and postglacial times, but there are no reasons to determine them as a new species.

Genus ***PLIOMYS*** Méhely 1914

Pliomys episcopalis Méhely 1914

Vole, extinct

1914 ** *Pliomys episcopalis* Méhely : 195–203, pls 4–5.
1974 *Pliomys episcopalis* Méhely ; Bishop : 309, 314.

LOCALITY : Westbury-sub-Mendip Fissure, Somerset (13) : Bishop 1974, 1975.

FIG. 15. Distribution of remains of *Pliomys episcopalis* Méhely in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *Pliomys* is known from only one British locality, Westbury-sub-Mendip, where it occurs in association with a lower middle Pleistocene fauna.

GENERAL DISTRIBUTION. *P. episcopalis* (type locality Betfia in Romania) appeared in the late Villafranchian of Europe and became widespread in the lower middle Pleistocene. In Italy it probably survived until the Holsteinian. Its remains are distributed from the European part of the Soviet Union to France and Italy. This species is generally recognized as an element of the steppe fauna.

Genus ***MIMOMYS*** Major 1902

Mimomys pliocaenicus Major 1902

Vole, extinct

1874 *Arvicola amphibius* (Linn.) ; Blackmore & Alston : 462–464 (*partim*).
1882a *Arvicola* (*Evotomys*) *intermedius* Newton : 83, pl. 13 (*partim*).
1902 *Mimomys pliocaenicus* Major : 102–107, figs 13–15.

DISTRIBUTION IN THE BRITISH ISLES. Although one rolled microtine tooth from the Red Crag has provisionally been referred to *Mimomys* by Spencer (1964) no remains identifiable at specific level are known from Britain earlier than the Norwich Crag. *M. pliocaenicus* has been found in the Norwich Crag and Weybourne Crag

Fig. 16. Distribution of remains of *Mimomys pliocaenicus* Major in the British Isles.

of Covehithe, Easton Bavents and Sizewell, Suffolk, and Thorpe[1] and Bramerton, Norfolk (51, 50, 49, 48, 55). Its remains are also known from deposits of uncertain age at Kyson, Suffolk (47), and from the Weybourne Crag and probably Pastonian Forest Bed deposits at East Runton, Norfolk (64). All the specimens from this last locality seen by us in the British Museum (Natural History) are rounded, with visible traces of transport by water.

Bibliography. Blackmore & Alston 1874, Newton 1882a, Major 1902, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Cranbrook 1955a, b, Carreck 1966, West 1968. Specimens have been seen in the BM(NH) and Ipswich Museum.

General distribution. *M. pliocaenicus* was first described by C. I. F. Major from the Val d'Arno in Italy. It is known from Late Villafranchian (Tiglian) deposits in France, Holland, Belgium, Germany, Poland, Hungary, Czechoslovakia, Romania and the Soviet Union (including Siberia). It has not been found in Cromerian (s.l.) faunal assemblages outside Britain, where it is of Pastonian age.

Systematic remarks. *M. pliocaenicus* is a characteristic species. It developed from smaller and more primitive ancestors living in the early Villafranchian (*M. polonicus* Kowalski) and disappeared or rather evolved into other species at the end of the Tiglian Interglacial.

[1] There are several places in East Anglia known as Thorpe and the location of the *M. pliocaenicus* site is not proved beyond doubt. The two most likely localities are Thorpe near Norwich, Norfolk, and Thorpe near Aldeburgh, Suffolk. C. I. F. Major (1902) described specimens collected by Mr Fitch from Thorpe, preserved in the Norwich Museum, though he did not indicate the county in which the Thorpe in question is situated. Carreck (1966) assumed that it was the Thorpe near Aldeburgh. Mr Fitch is known to have collected in the Norwich Crag of the Norwich area, however, and as the specimens subsequently found their way to Norwich Museum the possibility that they came from the Thorpe near Norwich must also be considered. Mr H. E. P. Spencer (*in litt.*) favours the last-mentioned locality, since there is a well-documented Crag mammal site there, whereas he points out that Thorpeness in Suffolk is on Coralline Crag. Mr P. Cambridge informs us of a Norwich Crag pit at Shell Cottages, Thorpe, Aldringham, near Aldeburgh, Suffolk. He too thinks the Thorpe near Norwich, where there were formerly several Norwich Crag pits with mammalian remains, is the most likely locality for the remains of *M. pliocaenicus* described by Major. We have tentatively accepted the Norfolk alternative, and this is marked on Fig. 1 as locality 48.

Mimomys reidi Hinton 1910

Vole, extinct

1882a *Arvicola* (*Evotomys*) *intermedius* Newton : 83 (*partim*).
1910b *Mimomys reidi* Hinton : 491.

Distribution in the British Isles. This species is known in Britain from the Weybourne Crag at *Trimingham (61) and from the Norwich Crag at Sizewell (49). In the collections of the British Museum (Natural History) there are specimens from the Savin collection labelled 'West Runton, Upper Freshwater Bed', but they are probably mislabelled or were found in a secondary layer. Hinton (1926b) stated that this species was not found outside the Norwich and Weybourne Crags.

Bibliography. Newton 1882a, Barrett-Hamilton & Hinton 1910–21, Hinton 1910b, 1926b. Specimens have been seen at the BM(NH) and Ipswich Museum.

General distribution. *M. reidi* (probably identical with *M. petenyi* Méhely 1914) is known from many localities of Tiglian age in Holland, France, Germany, Italy, Poland, Czechoslovakia, Hungary and the Soviet Union (including Siberia).

Systematic remarks. The holotype of this species was described from the Weybourne Crag at Trimingham, Norfolk, but the systematic position of the remains determined as *M. reidi* from continental Europe presents a problem: different forms, probably different stages of the same phyletic line, appear to be represented.

Fig. 17. Distribution of remains of *Mimomys reidi* Hinton (▽) and *M. newtoni* Major (●) in the British Isles.

Mimomys newtoni Major 1902

Vole, extinct

1902 *Mimomys newtoni* Major : 102–107, figs 13–15.

Distribution in the British Isles. In Britain *M. newtoni* is known from deposits ranging in age from Norwich Crag to either Weybourne Crag or Forest Bed. The holotype was described by Major (1902 : text-fig. 13, no. 7) as having been found in the 'East Runton Forest Bed'. It is now known that the deposits at East Runton are Pastonian and the holotype is most likely to be of this age. *M. newtoni* is also known from specimens in the British Museum (Natural History) collected by the Earl of Cranbrook from the Norwich Crag of Easton Bavents, Suffolk (50). The specimen in the BM(NH) from the Norwich Crag at Bramerton, Norfolk, (Hinton 1926b : 376, footnote) 'which may be referred to *M. newtoni*' is clearly different from the holotype and probably does not belong to the same species.

Bibliography. Major 1902, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b.

General distribution. *M. newtoni* is known outside Britain from deposits of Tiglian age in Holland, France, Germany, Poland, Czechoslovakia, Hungary and the Soviet Union.

Systematic remarks. Small representatives of the genus *Mimomys* Major are so rare in the Lower Pleistocene strata of East Anglia that it is difficult to decide how many species are represented. Some of the specimens of '*M. newtoni*' from East Runton (M6967, numbers 19, 20 and 23) are visibly larger than the holotype (M_1 2·9 and 3·0 mm long, compared with 2·5 mm) and have cement in the re-entrant angles, absent in the type specimen. There may be two 'chronospecies' of different geological ages. The continental specimens (e.g. from Kadzielnia, Poland) are identical with these larger specimens of '*M. newtoni*' and different from the holotype. Further research will be necessary to determine whether an additional species should be established.

Mimomys savini Hinton 1910

Vole, extinct

1874	*Arvicola amphibius* (Linn.) ; Blackmore & Alston : 462–464 (*partim*).
1881	*Arvicola* (*Evotomys*, Coues) *intermedia* Newton : 258.
1902	*Mimomys intermedius* (Newt.) ; Major : 102–107.
1910b	*Mimomys savini* Hinton : 491.
1910b	*Mimomys majori* Hinton : 491.
1958	*Mimomys milleri* Kretzoi : 55.

Distribution in the British Isles. *M. savini* is a common species in the Upper Freshwater Bed at West Runton (65) and it is also known from East Runton (64). According to Newton (1882a), it has also been found at Cromer (63), Geldeston (53) and Kessingland (52). *Mimomys* cf. *savini* was recorded by Stuart (1974) from Cromerian deposits at Sugworth, near Oxford (21).

Bibliography. Blackmore & Alston 1874, Newton 1881, 1882a, 1891, Reid 1890, Major 1902, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1920, 1926b, Kretzoi 1958, 1965, Pasquier 1972.

General distribution. *Mimomys savini* is widely distributed at localities of 'Cromerian' age in Holland, France, Germany, Italy, Poland, Czechoslovakia, Yugoslavia and the Soviet Union (including Siberia).

FIG. 18. Distribution of remains of *Mimomys savini* Hinton in the British Isles.

SYSTEMATIC REMARKS. *M. savini* was described by Newton (1881) from the Upper Freshwater Bed of *West Runton under the name of *Arvicola intermedia*. Hinton (1910b) described two further species of the same genus, *M. majori* and *M. savini*, from the same deposit. According to him, they differed from *M. intermedius* only in slight differences in the pattern of M_1, the dimensions of all the molars and the patterns of all other teeth being identical. Kretzoi (1958) found that *A. intermedia* is a junior homonym and must therefore be replaced by the name *Mimomys milleri* Kretzoi ; in a later paper (1965) he showed that the three species *M. intermedius*, *M. savini* and *M. majori* really represent only one variable species. The name of it must therefore be *Mimomys savini* Hinton, which is the oldest valid name. In fact all possible intermediate forms between typical *M. intermedius*, *M. savini* and *M. majori* are present in the abundant material from the Upper Freshwater Bed (Pasquier 1972). The presence of three species of one genus with identical dimensions in one and the same layer is also scarcely imaginable from the ecological point of view. Specimens determined as '*M. majori*' and '*M. savini*' have also been found in some Czechoslovak and German fossil localities, always associated with *M. intermedius*.

Genus *ARVICOLA* Lacépède 1799

The systematic study of even the living representatives of this genus presents many difficulties to zoologists. Miller (1912) divided living populations of water voles from western Europe into seven species but later investigators (for bibliography see Reichstein 1963) have demonstrated that nearly all the characters which were used for the diagnosis of these species lie within the limits of individual variation. Variations occur principally in the dimensions and in some proportions of the skull, proportions which may change allometrically with the changes of absolute dimensions.

Cytological studies support the view that there are only two living species in this genus, *A. sapidus* Miller 1908, from the south of France and the Iberian Peninsula, and *A. terrestris* (Linnaeus 1758) distributed throughout the rest of Europe as well as the northern part of Asia and the Middle East. The Recent population in Britain belongs to this last species. Reichstein (1963), after a very thorough analysis, found distinct but small craniological differences between the two species of *Arvicola* and further differences were reported by Corbet *et al.* (1970).

The systematic study of fossil forms, usually possible only from teeth and fragmentary skulls, is still more difficult. Remains from glacial deposits are usually larger than those from the interglacials and interstadials or from the Holocene, and most of the characters which have been used for creating new fossil species of water voles are expressions of individual variability, present also in Recent species. It seems beyond doubt that *Arvicola* developed from a late form of the genus *Mimomys*, most likely *Mimomys savini*, through the progressive reduction of the formation of roots in the molars and acquisition of the continual growth of these teeth. One character, typical of *Mimomys*, is nevertheless retained in geologically older populations of *Arvicola* : the enamel of the cheek-teeth is thinner on the concave and thicker on the convex sides of the salient angles, the reverse being true in the late Pleistocene and Recent populations. The two forms are united by a full series of intermediate specimens. O. Fejfar (in Koenigswald 1970) re-examined the holotype of *Mimomys cantianus* Hinton from the Hoxnian deposits of Ingress Vale, Swanscombe, and found that there is no trace of root-formation. This form must therefore be included in the genus *Arvicola*. *Arvicola cantiana* (Hinton) is the oldest available name for the primitive representatives of *Arvicola* and later names such as *A. bactonensis*, *A. greeni* and *A. praeceptor* must be treated as synonyms.

Koenigswald (1972, 1973) also studied the stratigraphical range of the various stages of the *Mimomys–Arvicola* lineage from European localities and defined a series of faunal groups :

(a) A *Mimomys savini* fauna, including the Upper Freshwater Bed of West Runton.
(b) and (c) *Arvicola* faunas groups 1 and 2, both with *A. cantiana* (Koenigswald included Swanscombe in group 2).
(d) *Arvicola* fauna group 3, with *A. terrestris*.

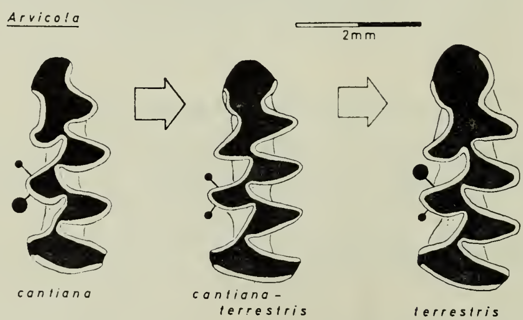


Fig. 19. Development of the enamel layer in Middle European forms of *Arvicola*. *Arvicola cantiana* (Elster–Riss) ; *Arvicola cantiana-terrestris* transition form (Riss–Eem) ; *Arvicola terrestris* (Eem–Holocene). From Koenigswald (1973 : 164).

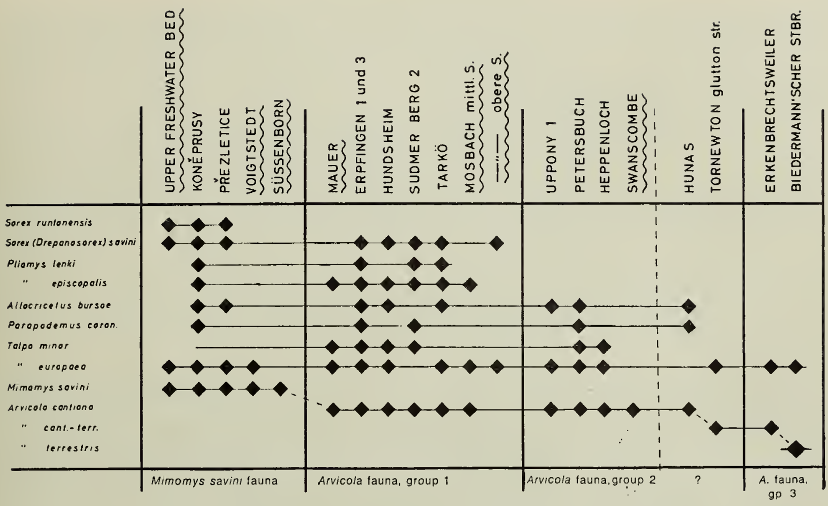


FIG. 20. Chronological distribution of *Arvicola* and other stratigraphically important small mammal species in European Pleistocene faunas. From Koenigswald (1973 : 161).

He referred the Glutton Stratum of Tornewton Cave to an intermediate stage between groups 2 and 3 (Fig. 20).

Koenigswald made a further study of British *Arvicola* remains in 1974 and (pers. comm.) assigned the phylogenetic position, between *A. cantiana* and *A. terrestris*, of the finds from various sites as follows :

A. cantiana ————————→ intermediate forms ————————→ *A. terrestris*

Clacton	Aveley	Barrington	Ightham
Swanscombe (Barnfield Pit and Ingress Vale)	Crayford	Joint Mitnor Cave	Kent's Cavern (Cave Earth)
Ostend	Grays	Swanton Morley	Wye Cave (= Merlin's Cave)
Westbury-sub-Mendip	Stutton	Tornewton Cave (Otter Stratum)	Tornewton Cave (Reindeer Stratum)
		Tornewton Cave (Glutton Stratum)	

These findings are of very far-reaching stratigraphical importance. *A. cantiana* appears for the first time in Britain at the 'late Cromerian' site of Westbury-sub-Mendip, which appears to represent Koenigswald's group 1, and is also present in the Hoxnian deposits of Clacton and Swanscombe. The transition form is represented by remains from the cold stage represented by the Glutton Stratum of

Tornewton Cave, in the Otter Stratum of that cave (where it is apparently slightly more advanced) and in the Last Interglacial hippopotamus faunas of Barrington, Joint Mitnor Cave and Swanton Morley. *A. terrestris* is characteristic of Last Glaciation and Holocene faunas.

It must be noted that Hinton's and Koenigswald's divisions between *A. cantiana* and *A. terrestris* do not exactly coincide. Koenigswald, from a re-examination of the specimens from the Barrington hippopotamus site, considered that the *Arvicola* remains from this locality should be attributed to the *A. cantiana-terrestris* transition form rather than to *A. praeceptor* (= *A. cantiana*), as determined by Hinton (1926b : 393). Stuart (see p. 69) has suggested that both forms are present. The specimens from the Last Interglacial site of Hessle, Yorkshire, attributed by Hinton (in Bisat 1940) to *A. praeceptor*, but which Boylan (1967) considered to lie within the normal range of variability of *A. terrestris*, have not been re-examined during the present investigation.

Surprisingly the remains from Aveley, Grays Thurrock, Harkstead and Stutton (currently widely regarded as Last Interglacial, though most if not all are sites without hippopotamus – the undoubted hippopotamus remains from Grays were collected more than a century ago and their exact provenance within the terrace complex of that area is unknown) are advanced *A. cantiana* and appear to be earlier than the pre-hippopotamus Glutton Stratum of Tornewton Cave.

The Crayford record of *A. cantiana* must be accepted with some reserve. Although *Arvicola* is recorded from this locality by Dawkins & Sanford (1866) and by Whitaker (1889) it was not mentioned by Hinton (1900a, b, 1910b, 1926b). The present determination is based on a single specimen in the British Museum (Natural History).

Arvicola cantiana (Hinton 1910)

Water vole, extinct

1846	*Arvicola amphibia* ; Owen : 201–205 (*partim*).
1882a	*Arvicola amphibius* ? Linnaeus ; Newton : 87–88.
1902	*Microtus intermedius* ; Hinton & White : 414–415.
1910b	*Mimomys cantianus* Hinton : 491.
1926b	*Arvicola bactonensis* Hinton : 386–389.
1926b	*Arvicola greeni* Hinton : 389–391, fig. 106, 1–2.
1926b	*Arvicola praeceptor* Hinton : 391–394, fig. 106, 3–17.
1970	*Arvicola cantiana* (Hinton) ; Koenigswald : 418–420.

LOCALITIES : Ostend, Norfolk (57) : Owen 1846, Newton 1882a, Lydekker 1885, Hinton 1926b, BM(NH).

Westbury-sub-Mendip, Somerset (13) : Bishop 1974, 1975.

Clacton-on-Sea, Essex (43) : Hinton in Warren 1955, Sutcliffe 1964, BM(NH).

*Swanscombe (Ingress Vale and Barnfield Pit, Lower Loam), Kent (30) : Hinton & White 1902, Stopes 1904, Hinton 1910b, 1926b, Barrett-Hamilton & Hinton 1910–21, Sutcliffe 1964, Koenigswald 1970, BM(NH).

Aveley, Essex (34) : BM(NH).

Grays Thurrock, Essex (33) : Hinton, Kennard & Newton 1900, Hinton 1910b, 1926b, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Ilford, Essex (35) : Dawkins & Sanford 1866, Whitaker 1889, Newton 1890a, Johnson & White 1900, Hinton 1900a, b, 1910b, 1926b, BM(NH).

Stutton, Suffolk (44) : Stuart collection and seen in Ipswich Museum.

Harkstead, Suffolk (44) : Ipswich Museum – Stuart (*in litt.*).

Northfleet, Kent (29) : det. A. Stuart.

Crayford, Kent (27) : Dawkins & Sanford 1866, Whitaker 1889, BM(NH).

Arvicola cantiana-terrestris transition form

(see pp. 99–102 above)

LOCALITIES : Tornewton Cave (Glutton Stratum and Otter Stratum), Devon (3) : Kowalski 1967, (BM(NH).

Barrington, Cambridgeshire (40) : Hinton 1926b (but see note on p. 69), BM(NH).

Joint Mitnor Cave (layer IV), Devon (1) : BM(NH).

Minchin Hole, Glamorganshire (16) : det. A. J. Stuart.

Stoke Tunnel Beds, Suffolk (46) : Ipswich Museum.

Swanton Morley, Norfolk (66) : Stuart, pers. comm.

FIG. 21. Distribution of fossil remains of *Arvicola cantiana* (Hinton) (■) and *A. terrestris* (Linn.) (□) in the British Isles. (Transition form ■□, not studied ●.)

Arvicola terrestris (Linnaeus 1758)

Water vole

1846 *Arvicola amphibia* ; Owen : 201–205 (*partim*).
1847 *Hypudaeus spelaeus* Cuv. ; Giebel : 88.
1872 *Arvicola amphibius* Desm. ; Dawkins & Sanford : 180.
1910a *Arvicola abbotti* Hinton : 34–35.
1960 *Arvicola amphibius terrestris* Bramwell : [10].

LOCALITIES : Ightham Fissures, Kent (28) : Newton 1894, Hinton 1910a, b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Zimmermann 1959, BM(NH).

Kent's Cavern (Cave Earth), Devon (6) : Owen 1846, Dawkins & Sanford 1866, Blackmore & Alston 1874, Lydekker 1885, Hinton 1926b, Kennard 1945–46, Carreck 1957, BM(NH).

Tornewton Cave (Reindeer Stratum), Devon (3) : Kowalski 1967.

Wye (= Merlin's) Cave, Herefordshire (18) : Bate 1901, Hinton 1926b, BM(NH).

Arvicola cantiana / A. terrestris complex
(phylogenetic position not studied)

With the exception of Hoxne (Hoxnian) and Bacon Hole, Hessle, Kirkdale Cave and the Hyaena Stratum of Tornewton Cave (which are Last Interglacial) the following sites are all believed to be of Last Glaciation or Holocene age. The *Arvicola* remains are probably mostly advanced forms.

LOCALITIES : Hoxne, Suffolk (54) : Wolff (*in litt.*).

Bacon Hole (16) : Stuart (*in litt.*).

Bobbitshole, Suffolk (46) : Ipswich Museum, det. J. N. Carreck.

Hessle, Yorkshire (74) : Lamplugh 1891, Bisat 1940, Catt & Penny 1966, Boylan 1967, specimen in Institute of Geological Sciences Museum, London, not seen by K. K.

Kirkdale Cave, Yorkshire (77) : Owen 1846, Giebel 1847, Dawkins & Sanford 1866, Lydekker 1885, Hinton 1926b, BM(NH).

Tornewton Cave (Hyaena Stratum), Devon (3) : Kowalski 1967.

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, 1926b, BM(NH).

Brixham Cave, Devon (4) : Hinton 1926b, Carreck 1957, BM(NH).

Chudleigh Fissure, Devon (7) : BM(NH).

Dog Holes Cave, Lancashire (79) : Jackson 1910, 1912, Hinton 1926b, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Gough's Cave, Somerset (12) : BM(NH).

Langwith Cave, Derbyshire (72) : Mullins 1913, BM(NH).

Levaton Cave (2) : Carreck 1957.

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Happaway Cave, Devon (5) : Hinton 1926b, Carreck 1957, BM(NH).

Nazeing, Essex (37) : Hinton 1952, BM(NH).

Cowside Cave No. 3, Yorkshire (78) : BM(NH).

Thatcham, Berkshire (Holocene, 23) : Wymer 1962.

GENERAL DISTRIBUTION of *Arvicola*, and systematic remarks. As stated above, the forms described as *A. greeni*, *A. bactonensis* and *A. praeceptor* must be treated as synonyms of *A. cantiana*. The first two of the above-mentioned species were described by Hinton (1926b) from specimens collected at Ostend, near Bacton, Norfolk, during the first part of the nineteenth century. *A. bactonensis* is known only from the holotype and *A. greeni* is represented only by two isolated teeth. The stratigraphic position of these remains is uncertain. Hinton (1926b) suggested that they were contemporary with the Cromer Forest Bed or only slightly younger. As *Arvicola* is not represented at the Cromerian type locality of West Runton, where the ancestral form *Mimomys savini* is present, it must be supposed that these specimens are from later deposits. They may be equivalent in age to the faunal assemblage of Westbury-sub-Mendip, where *A. cantiana* is present.

A. cantiana is known, under various names, from numerous localities of Holsteinian (Hoxnian) age in continental Europe and Siberia. Remains of *A. terrestris*, to which species it gave rise, are abundant from the Upper Pleistocene of Europe, including England and Wales. Like other voles, *Arvicola* never reached Ireland.

A. terrestris is now widely distributed in nearly all Europe and in cold and temperate parts of Asia, as far south as Persia and Palestine. It lives mostly near water, but under diverse climatic and vegetational conditions, ranging from the taiga belt, through deciduous forest and steppe, to the deserts in the south. As a species of high ecological tolerance it was present during the Pleistocene under both glacial and interglacial conditions.

Genus ***PITYMYS*** McMurtrie 1831

Many zoologists are of the opinion that *Pitymys* is only a subgenus of *Microtus*. *Pitymys* is morphologically similar to *Microtus*, *sensu stricto*, and is rather similar in its ecology, but the living forms are biologically quite different. Chaline (1972), who studied fossil vole remains from the French Pleistocene, came to the conclusion that fossil forms of *Pitymys* are nothing but morphotypes of *Allophaiomys pliocaenicus* Kormos 1932. If this is correct, then *A. pliocaenicus* would be a junior synonym of *Pitymys arvaloides* and its name must be changed accordingly. In his opinion the Recent subgenus *Pitymys* is polyphyletic and its members are more closely related to different forms of *Microtus* than to one another. In the opinion of one of us (K. K.) Chaline underestimates the ecological similarity of Recent species of *Pitymys* and all other zoological evidence, basing his conclusions on the pattern of M_1 only. For this reason he is unable to follow Chaline's suggestions.

Voles of the *Pitymys* group dominated the European vole faunule during the Cromerian Interglacial. They were still common during the Hoxnian, after which they disappeared completely from Britain. Their distribution in Europe and western Asia is now rather discontinuous. The first evidence of the presence of *Pitymys* in Britain was published by Major in 1902. Hinton (1923a) described two different species from the Upper Freshwater Bed of West Runton, *P. gregaloides* and *P. arvaloides*. They are clearly distinct species, though in continental Europe intermediate specimens are present. If *Pitymys* is only a subgenus of *Microtus*, a very prevalent opinion among Recent mammalogists, the name *Pitymys arvaloides* Hinton is a taxonomic homonym and must be replaced by a new name, *Microtus* (*Pitymys*) *arvalidens* Kretzoi 1958. In the opinion of K. K. it is more convenient to treat *Pitymys* as a separate genus and the name given by Hinton is therefore retained here.

Pitymys arvaloides Hinton 1923

Pine vole, extinct

1882a *Arvicola arvalis* Pallas ; Newton : 88–89, pl. xiv, figs 2–5.
1902 *Microtus* (*Pitymys*) sp. ; Major : 107, fig. 15 (28).
1923a *Pitymys arvaloides* Hinton : 541–542.
1958 *Microtius* (*Pitymys*) *arvalidens* Kretzoi : 57 (new name for *Pitymys arvaloides* Hinton 1923, non *Arvicola arvaloides* Pomel).
1972 *Allophaiomys pliocaenicus* Kormos ; Chaline : 104.

Localities : West Runton (Upper Freshwater Bed), Norfolk (65) : Newton 1882a, Major 1902, Hinton 1923a, 1926b, Kretzoi 1958, Chaline 1972, BM(NH).

Hitchin, Hertfordshire (39) : Carreck 1959 : 326 (det. as *P.* cf. *arvaloides*).

Swanscombe (Barnfield Pit, Lower Gravel and Lower Loam), Kent (30) : Carreck 1959 (: 326), Sutcliffe 1964.

Fig. 22. Distribution of remains of *Pitymys arvaloides* Hinton in the British Isles.

Distribution in the British Isles. *P. arvaloides* is abundant in the Cromerian Upper Freshwater Bed at West Runton. It is present also in deposits of the lower part of the Hoxnian Interglacial, but disappears completely before its end. There is at present no evidence of its presence in Britain during the Anglian cold phase and it is probable that it invaded this country from the European continent twice.

General distribution and Systematic remarks. *P. arvaloides* is present at numerous localities of 'Cromerian' age on the continent (Italy, Yugoslavia, Germany, Hungary, Poland, Czechoslovakia, Austria, the European part of the Soviet Union and Georgia). Nearly everywhere it has been found together with *P. gregaloides*. It is not impossible that the two species, different in the morphology of M_1 but of identical dimensions, are only two forms of one polytypic species.

Pitymys gregaloides Hinton 1923

Pine vole, extinct

1882a *Arvicola gregalis* Pallas ; Newton : 90–91, pl. xiv, figs 6, 6a.
1891 *Microtus* (*Arvicola*) *gregalis* Pallas ; Newton : 53.
1923a *Pitymys gregaloides* Hinton : 541–542.
1972 *Allophaiomys pliocaenicus* Kormos ; Chaline : 104.

LOCALITIES : West Runton (Upper Freshwater Bed), Norfolk (65) : Newton 1882a, 1891, Hinton 1923a, 1926b, BM(NH).

Westbury-sub-Mendip Fissure, Somerset (13) : Bishop 1974, 1975.

Kent's Cavern, Devon (6) : Hinton 1926b, Kennard 1945–46, BM(NH).

FIG. 23. Distribution of remains of *Pitymys gregaloides* Hinton in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *P. gregaloides* is present in Cromerian deposits at West Runton and at the Westbury Fissure, together with *P. arvaloides*. Two specimens, one preserved in the British Museum (Natural History), the other in Bristol Museum, are known from Kent's Cavern. The stratigraphical position of these specimens is unknown, but the species has not yet been recorded from any British Hoxnian locality and it is likely that they are of pre-Hoxnian age.

GENERAL DISTRIBUTION AND SYSTEMATIC REMARKS. *P. gregaloides* is present, together with *P. arvaloides*, at numerous localities in central and southern Europe dated as Cromerian (*sensu lato*).

Genus ***MICROTUS*** Schrank 1798

The genus *Microtus* now holds the dominant position in the subfamily Microtinae, being both most highly differentiated and most individually numerous. In the fossil state molar teeth make up most of the finds, mandibles occurring less commonly and complete skulls only in exceptional cases. Furthermore, it should not be forgotten that in living populations the variability of the molar pattern is sometimes enormous (Kowalski 1970) and this variability may be discontinuous, representing genetical polymorphism. At the same time there are species, clearly differentiated in external characters and in biological requirements, in which the teeth are nearly identical (e.g. the lower teeth of *M. agrestis* and *M. arvalis* cannot be clearly distinguished, nor can the upper teeth of *M. arvalis* and *M. oeconomus*). All these factors make the correct determination of fossil remains, including the material from Britain described below, very difficult.

The genus *Microtus* appeared rather late in the European Pleistocene, being found first in the Cromerian Interglacial when *Pitymys* was still numerically dominant. In the Hoxnian Interglacial both genera lived together but in later sediments in Britain *Pitymys* disappeared completely and on the European continent it now plays only a subordinate role.

Microtus arvalinus Hinton 1923

Vole, extinct

1902 *Microtus* sp., recalling *M. arvalis* ; Major : 107, fig. 15 (27).
1923a *Microtus arvalinus* Hinton : 541–542.
1972 *Microtus* (*Microtus*) *arvalis* (Pallas) ; Chaline : 106.

Localities : West Runton (Upper Freshwater Bed), Norfolk (65) : Major 1902, Hinton 1923a, 1926b, BM(NH).

Westbury-sub-Mendip, Somerset (13) : Bishop (pers. comm.).

Swanscombe (Lower Loam and Upper Middle Gravel), Kent (30) : Schreuder 1950, Sutcliffe 1964, BM(NH).

Fig. 24. Distribution of remains of *Microtus arvalinus* Hinton in the British Isles.

General distribution. *M. arvalinus* was present in Britain during the Cromerian and Hoxnian interglacials and the intervening Westbury stage. A small form of *Microtus*, with the M_1 pattern of the *M. arvalis/agrestis* group, is present in the Cromerian deposits of France, Germany, Austria, Czechoslovakia, Hungary, Romania and Yugoslavia.

Systematic remarks. *M. arvalinus* is identical in its M_1 pattern with Recent representatives of the *M. arvalis/agrestis* group, and differs from these only in its slightly smaller dimensions. It is probable that *M. arvalinus* is the ancestral form of *M. agrestis*. According to Chaline (1972), *M. arvalinus* is a synonym of *M. arvalis*, but there does not seem to be any good reason for putting it into this synonymy rather than that of *M. agrestis*.

Microtus agrestis (Linnaeus 1761)

Field vole

1846	*Arvicola agrestis* ; Owen : 206–207.
1847	*Hypudaeus bucklandii* Giebel : 88.
1894	*Microtus* (= *Arvicola*) *agrestis* ; Newton : 197.
1910b	*Microtus agrestis neglectus* ; Hinton : 494.
1910b	*Microtus agrestoides* Hinton : 493.
	Microtus arvalis and *Microtus arvalis/agrestis* group (*partim*) ; many authors.

General notes on the *Microtus arvalis/agrestis* group. During the nineteenth century most zoologists did not appreciate the differences between *M. arvalis* and *M. agrestis* and these two names must be regarded as synonyms in papers published at that time. Later on, the presence of the *M. arvalis* group on the Orkney Islands (*M. arvalis* does not survive today on the mainland of Britain and *M. agrestis* does not occur on Orkney) led to the hypothesis that *M. arvalis* was the first *Microtus* to reach Britain in the postglacial period. Under the influence of this hypothesis fossil remains of the *M. arvalis/agrestis* group were usually determined as '*M. arvalis*'. It must nevertheless be born in mind that only the upper M^2 provides diagnostic characters for distinguishing *M. agrestis* and *M. arvalis*. Both lower jaws and other isolated teeth are useless for this purpose (Dienske 1969). An example of the confusion which can occur in this context is provided by the *Microtus* remains from Dog Holes Cave, Lancashire. All the upper dentitions were correctly determined as '*M. agrestis*', but all the lower jaws were labelled '*M. corneri*' (= *M. arvalis*). This illustrates well the tendency to decide in each doubtful case in favour of *M. arvalis*.

In the site list for *M. agrestis* given below all the localities of *M. agrestis*, '*M. agrestoides*', '*M. arvalis/agrestis* group' and '*M. arvalis*' are enumerated.

Localities : Clacton-on-Sea, Essex (43) : Hinton 1923b, Singer *et al.* 1973.

Swanscombe (Upper Middle Gravels), Kent (30) : Schreuder 1950 (*M. arvalis/agrestis* group).

Ilford (Uphall Estate), Essex (35) : Hinton 1900a, b, Johnson & White 1900.

Grays Thurrock, Essex (33) : Hinton, Kennard & Newton 1900, Hinton 1901, 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1924, 1926b, BM(NH) ('*M. agrestoides*').

Harkstead, Suffolk (44) : Ipswich Museum.
Stutton, Suffolk (44) : Ipswich Museum.
Northfleet, Kent (29) : Burchell 1935.
Tornewton Cave (Glutton Stratum, Hyaena Stratum, Reindeer Stratum, Diluvium), Devon (3) : Kowalski 1967, BM(NH).
Water Hall Farm Pit, Hertfordshire (38) : BM(NH).
Alveston Fissure, Gloucestershire (15) : det. G. B. Corbet.
Bacon Hole, Glamorganshire (16) : det. A. J. Stuart.
Bobbitshole, Suffolk (46) : Ipswich Museum, det. J. N. Carreck.
Barrington, Cambridgeshire (40) : BM(NH).
Joint Mitnor Cave, Devon (1) : BM(NH).
Kirkdale Cave, Yorkshire (77) : Owen 1846, Giebel 1847, Dawkins & Sanford 1866, Blackmore & Alston 1874, BM(NH).
Minchin Hole, Glamorganshire (16) : det. A. J. Stuart.
Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, BM(NH).
Bleadon Cave, Somerset (10) : BM(NH).
Brixham Cave, Devon (4) : BM(NH).
Chudleigh Fissure, Devon (7) : BM(NH).
Dog Holes Cave, Lancashire (79) : Jackson 1910, 1912, BM(NH).
Elder Bush Cave, Staffordshire (69) : Bramwell 1964.
Gough's Cave, Somerset (12) : BM(NH).
Great Doward Cave, Herefordshire (17) : BM(NH).
Ightham Fissures, Kent (28) : Newton 1894, 1899b, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1921, 1926b, Jackson 1947, Zimmermann 1959.
Kent's Cavern, Devon (6) : Owen 1846, Dawkins & Sanford 1866, Blackmore & Alston 1874, Lydekker 1885–87, Kennard 1944–45, BM(NH).
King Arthur's Cave, Herefordshire (17) : BM(NH).
Langwith Cave, Derbyshire (72) : Mullins 1913, BM(NH).
Levaton Cave, Devon (2) : Carreck 1957.
Merlin's Cave, Herefordshire (18) : Hinton 1925.
Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.
Brean Down, Somerset (9) : Apsimon, Donovan & Taylor 1961.
Happaway Cave, Devon (5) : BM(NH).
Lynx Cave, Denbighshire (67) : Blore 1966.
Cowside Cave No. 3, Yorkshire (78) : BM(NH).
Corstorphine, nr. Edinburgh, Scotland (81) : Evans 1913.
Creag nan Uamh Cave, Inchnadamph, Scotland (83) : Peach & Horne 1917.

Distribution in the British Isles. *M. agrestis* is now widely distributed in Great Britain and many of the remains cited as fossils are probably of relatively recent age, in any case post-glacial.

The supposed earliest British occurrence of this group or species of rodents is at the Hoxnian locality of Swanscombe, where it is recorded as having been found in the Upper Middle Gravel in association with *M. arvalinus* (Schreuder 1950). The occurrence together of these two forms, which, it has been suggested (p. 109), are members of the same phylogenetic lineage, creates a problem. Schreuder

Fig. 25. Distribution of fossil remains of the *Microtus arvalis/agrestis* group in the British Isles.

distinguished the two forms at Swanscombe on grounds of size and stated that she would not have hesitated to accept as *M. arvalinus* the specimen determined by her as '*Microtus* sp., *arvalis/agrestis* group' had it not been so large. It has been pointed out by Corbet, however (pers. comm.), that there is great variation, which may reflect the age of the animal concerned, in the crown size of teeth of any microtine in which the teeth continue to grow during life. In view of the very small size of the sample studied by Schreuder, the occurrence of both *M. arvalinus* and *M. arvalis/agrestis* together in the same deposit is accepted here with some reserve. The remains are stratigraphically placed at about the time of transition between these two forms and a larger collection of remains is needed for study.

M. agrestis was common during the warm stages represented by both Grays Thurrock and Joint Mitnor Cave, and in the Glutton Stratum of Tornewton Cave, but is absent from the faunas of Crayford and Clevedon Cave. It was common during the Last Glaciation. At most localities where fossil remains have been found only lower jaws were present, but in each case where upper teeth were also found the second upper molar is of the typical *M. agrestis* pattern. There can be no doubt that the field vole was discontinuously present in Britain from at least the time of the Grays Thurrock deposits.

Hinton (1910b) created the name '*M. agrestoides*' for the specimens of *M. agrestis* from Grays Thurrock. He was surely influenced here by the supposition that Grays Thurrock has a very ancient fauna. The only distinctive character of his new species is 'the constant development of a fourth outer angle in the last upper molar'. This 'fourth angle' is present in a great proportion of specimens of Recent *M. agrestis* and its presence is not sufficient for specific determination.

According to Jackson (1929b), a skull of a vole which he regarded as close to *M. arvalis* was found in Kilgreany Cave, Co. Waterford, Ireland. This is the only possible evidence that voles ever reached Ireland; it was a skull with all teeth missing. It was found in the 'Lower Stalagmite' together with *Dicrostonyx* and human remains; '. . . a close examination of the sockets suggests that the species is the continental field vole *Microtus arvalis* or a close ally, and not the common field vole (*M. agrestis*)' (Jackson 1929b : 147).

The specimen has recently been re-examined by Savage (1966), who noted that it is notably fresh and unaltered and who had no doubt that it should be referred to *M. agrestis*. He pointed out that occasional vole remains have been found in north-east Ireland in pellets dropped by passing owls. On the basis of existing evidence, it is unlikely that voles ever reached Ireland.

General distribution. *M. agrestis* is now widely distributed in Europe, as well as in the cold and temperate parts of Asia. In Europe it extends north to include the whole Scandinavian peninsula and Finland. Fossil remains are known in continental Europe beginning with the Riss (penultimate) Glaciation.

Microtus arvalis (Pallas 1779)

Common vole

1910a *Microtus corneri* Hinton : 35–36.
Microtus arvalis (*partim*) ; many authors.

Distribution in the British Isles. Hinton (in Barrett-Hamilton & Hinton 1910–21, **2** : 467) correctly stated that :

> 'On several occasions fossils from various British deposits of Late Pliocene and Pleistocene age have been determined as belonging to *M. arvalis* (e.g. from fissures near Bath, Somerset, by Blackmore and Alston, Proc. Zool. Soc., 1874, 468) ; but in most cases such records imply, because of the fragmentary nature of the material, on which they are based, nothing more than the presence of a "vole" with an arvaloid, i.e. a normal dentition.'

According to Hinton (*loc. cit.*) the cranial remains from the Ightham fissures are 'apparently identical' with *M. arvalis* ; this locality probably marks the date of the arrival of the species in Britain.

Hinton (1910a) described from the Ightham fissures a new species, *M. corneri*, very similar to the Orkney vole, *M. orcadensis*. We now know, however, that *M. orcadensis* is nothing other than an isolated population of *M. arvalis*, possibly developed within historic times.

M. corneri has been recorded from the following localities :

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924.

Brixham Cave, Devon (4) : BM(NH) (det. Hinton).

Dog Holes, Lancashire (79) : BM(NH) (det. Hinton).

Ightham Fissures, Kent (28) : Hinton 1910a, b, Barrett-Hamilton & Hinton 1910–21, Hinton 1921, 1926b, Jackson 1929, Hinton 1952, Zimmermann 1959.

Langwith Cave, Derbyshire (72) : Hinton 1910a, Mullins 1913.

Levaton Cave, Devon (2) : Carreck 1957 ('*Microtus arvalis* group, cf. *corneri* Hinton').

The status of *M. arvalis*, including *M. corneri*, in the British Pleistocene requires extensive further study. Although known today on the Orkney Islands, *M. arvalis* does not occur on the British mainland. There is geological evidence that the Orkney Islands have never been connected to the mainland since the last glacial phase, when ice covered the British Isles as far south as Norfolk and South Wales, and the local population of *M. arvalis* [= *orcadensis*] must therefore be a recent introduction from the continent (Corbet 1961). In Europe, *M. arvalis* is typical of the zone of mild climate, being absent from the Scandinavian peninsula and from northern Denmark. Its distribution as well as ecological data make its presence in the British Isles in the early postglacial period extremely improbable. The majority of fossil records of '*M. corneri*' from Britain are of rather doubtful value. As mentioned above, lower jaws of *Microtus* (which are specifically undeterminable) from Dog Holes Cave have been identified as *M. corneri* whilst all the skulls belong, without exception, to *M. agrestis*. The skull from Brixham Cave determined as belonging to *M. corneri* is probably a specimen of *M. oeconomus*.

One of the most potentially important collections for the study of *M. arvalis* is that from Ightham Fissures, Kent, where many excellently preserved vole skulls were collected. It is evident, however, that remains of both Pleistocene (Last Glaciation) and Holocene age have been mixed together. In such circumstances it is possible that sometimes a single species is represented in the fossil material by two different subspecies or by two different populations of different dimensions. Among the *Microtus* material from this locality, besides the typical skulls of *M. gregalis* and *M. agrestis*, there are two groups of larger and smaller skulls. Some of them may belong to *M. oeconomus*, and the skull selected as the holotype of *M. corneri* probably belongs here. Other specimens could be young individuals of this species, or they may really belong to *M. arvalis*.

Recently two small further collections of rodents have been studied by Corbet (pers. comm.) which suggest that *M. arvalis* may indeed have been present in England during the Last Glaciation. These are from Marlow, Buckinghamshire (25, Treacher Collection), and Beckford, Worcestershire (19, Briggs and Coope Collection), all in the British Museum (Natural History). The Marlow remains were apparently predominantly *M. arvalis*. There was also one first lower molar of *M. oeconomus*. Corbet considers that the lack of any second upper molars of *M. agrestis*, and the occurrence of only one lower molar of *M. oeconomus* among the many first lower molars (the teeth which distinguish these last two closely related species from *M. arvalis*), suggest that *M. arvalis* is the principal species present. The age of the Marlow rodents is uncertain, but is likely to be Last Glaciation.

Corbet considers that the Beckford specimens, if all one species, must be *M. arvalis*. They could be a mixture of *M. agrestis* and *M. oeconomus*, but the absence of the diagnostic second upper molar of *M. agrestis* or the first lower molar of *M. oeconomus* makes this improbable. Beckford is of Last Glaciation age, with a cold insect-fauna and ^{14}C dates of 27 650 ± 250 (Birmingham 293) and 27 300 ± 500 years (Birmingham 595).

At the present state of our knowledge neither the status of *M. arvalis* in the British Pleistocene nor the systematic position of '*M. corneri*' is clear. Craniometric analysis of the whole collection of *Microtus* from Ightham would be of great value. If *M. arvalis* was present in the British Isles it was an invasion of short duration during one of the phases of the Last Glaciation.

Microtus nivaloides Major 1902

Vole, extinct

1902 *Microtus nivaloides* Major : 106, fig. 19.
1923a *Microtus nivalinus* Hinton : 541–542.

LOCALITY : West Runton (Upper Freshwater Bed), Norfolk (65) : Major 1902, Barrett-Hamilton & Hinton 1910–21, Hinton 1923a, 1926b.

FIG. 26. Distribution of remains of *Microtus nivaloides* Major in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *M. nivaloides* is present in the Cromerian of Norfolk.

GENERAL DISTRIBUTION. Small representatives of the genus *Microtus* with the M_1 resembling that of *M. nivalis*, determined as *M. nivalinus* Hinton, *M. nivaloides* Major or *M. subnivalis* Pasa, have been recorded in 'Cromerian' deposits in Germany, Czechoslovakia, Hungary, Romania, Yugoslavia, Italy and the Ukraine.

SYSTEMATIC REMARKS. In addition to the well-defined form *M. nivaloides*, another from the same layer and locality was described as *M. nivalinus* by Hinton (1923a). Intermediate specimens between these two forms also occur and it is probable that only one species is represented. *M. nivaloides*, widely distributed in deposits of 'Cromerian' age in Europe, is probably the ancestor of *M. nivalis*, a common species in late Pleistocene localities. In Chaline's opinion (1972 : 151) *M. nivaloides* and *M. nivalinus* are synonyms of *M. nivalis*. This is in contradiction to the picture of evolution in the *M. nivalis* line as presented by the same author who considered that *M. nivalis* developed from *M. malei* not earlier than the penultimate glaciation.

Microtus nivalis (Martins 1842)

Snow vole

1907a *Microtus nivalis* (Martins) ; Hinton : 39–48 ; pl. 1, figs 5–23.
1907a *Microtus malei* Hinton : 49 ; pl. 1, figs 24–27.

Localities : Crayford and Erith (27) : Hinton 1907a, b, 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Kennard 1944, Jackson 1947, Chaline 1972, BM(NH).

Clevedon Cave, Somerset (14) : Hinton 1907a, b, 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Chaline 1972, BM(NH).

Cow Cave, Chudleigh (7) : det. G. B. Corbet.

Gough's Cave, Somerset (12) : BM(NH).

Tornewton Cave (Glutton Stratum), Devon (3) : Kowalski 1967, BM(NH).

Water Hall Farm Gravel Pit, Hertfordshire (38) : BM(NH).

East Wickham, Plumpstead, London : Hinton 1907b, 1926b, BM(NH).

Some additional records of *M. nivalis* exist in early papers. This species has been mentioned from a cave in the Forest of Dean, from Fisherton, Grays Thurrock and Swanscombe. Hinton (1926b) did not mention these localities in his monograph as containing *M. nivalis* and no remains of the snow vole have been seen by the writers among material collected from these sites.

Fig. 27. Distribution of fossil remains of *Microtus nivalis* (Martins) in the British Isles.

Distribution in the British Isles. *M. nivalis* seems to be a typical element of the fauna of the period represented by Crayford and the Tornewton Cave Glutton Stratum. There was a stage when the genus *Microtus* was represented in the British Isles by two species only, *M. nivalis* and *M. oeconomus*. It is entirely absent from Devensian localities in Britain.

General distribution. *M. nivalis* is now distributed in mountain ranges, mostly in the Mediterranean area, from the Pyrenees in the west to Lebanon, the Caucasus and Kopet-Dag in the east. It inhabits treeless, mostly rocky or stony localities, not necessarily cold ones. During the Pleistocene it was more widely distributed.

Systematic remarks. *M. nivalis* has a very variable tooth-pattern. Its presence in Britain is beyond doubt, but the existence of a second species from this group, *M. malei*, does not seem probable. The teeth determined by Hinton (1907a) as belonging to *M. malei* were found exclusively in localities where *M. nivalis* is numerous, and all intermediate forms between typical *nivalis* and typical *malei* can be found. *M. malei* must therefore be taken as a synonym of *M. nivalis*. But according to Chaline (1972) *M. malei* is a valid species, and he designates as its lectotype the specimen M26481 in the British Museum (Natural History) from Clevedon Cave. In his opinion all the specimens from Clevedon Cave, determined by Hinton as belonging to *M. nivalis*, *M. malei* and *M. ratticeps*, represent only one variable species, *M. malei*. *M. nivalis* developed, according to Chaline, from *M. malei* during the late Pleistocene and was not present in Britain. His hypothesis, as stated above, seems to be contradictory, but it is possible that the representatives of the group of *M. nivalis* present in the lowland of Europe, including Britain, were different from the Recent *M. nivalis* from the European mountains. In such a case they must be named *Microtus malei* Hinton.

Microtus ratticepoides Hinton 1923

Vole, extinct

1923a *Microtus ratticepoides* Hinton : 541–542.

LOCALITIES : West Runton (Upper Freshwater Bed), Norfolk (65) : Hinton 1923a, 1926b, BM(NH).

Swanscombe (Lower Loam and Upper Middle Gravel), Kent (30) : Schreuder 1950, Sutcliffe 1964, BM(NH).

FIG. 28. Distribution of remains of *Microtus ratticepoides* Hinton in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *M. ratticepoides* is known from deposits of Cromerian and Hoxnian age.

GENERAL DISTRIBUTION. *M. ratticepoides* has been recorded, mostly in 'Cromerian' faunal assemblages, in Holland, Germany, Romania, Czechoslovakia, Poland, Hungary and the European part of the Soviet Union including Georgia.

SYSTEMATIC REMARKS. The tooth-pattern of *M. ratticepoides* is nearly identical to that of *M. oeconomus*, but the dimensions of the fossil form are slightly smaller than those of the Recent one. *M. ratticepoides* may be the ancestor of the Middle Pleistocene and Recent *M. oeconomus.*

Microtus oeconomus (Pallas 1776)

Root vole

1870b *Arvicola ratticeps* (Blasius) ; Sanford : 124–125, pl. viii, figs 1, 1a–1d.
1890a *Microtus* (*Arvicola*) *ratticeps* Key. and Bl. ; Newton : 453–456, figs 1–2.
1901 *Microtus ratticeps* ; Bate : 103–104.

LOCALITIES : Crayford and Erith (27) : Whitaker 1889, Newton 1890a, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Kennard 1944, Jackson 1947, Hinton 1952, BM(NH).

Harkstead, Suffolk (44) : Ipswich Museum.

Clevedon Cave, Somerset (14) : Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Tornewton Cave (Glutton Stratum, Reindeer Stratum, Diluvium), Devon (3) : Kowalski 1967, BM(NH).

Bacon Hole, Glamorganshire (16) : det. A. J. Stuart.

Water Hall Farm Pit, Hertfordshire (38) : BM(NH).

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, BM(NH).

Bleadon Cave, Somerset (10) : Palmer 1934, BM(NH).

Chudleigh Fissure, Devon (7) : BM(NH).

Dog Holes Cave, Lancashire (79) : Jackson 1910, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Fisherton, Wiltshire (22) : Blackmore & Alston 1874, Bate 1901, Jackson 1910, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Gough's Cave, Somerset (12) : BM(NH).

Great Doward Cave, Herefordshire (17) : BM(NH).

Ightham Fissures, Kent (28) : Newton 1894, Bate 1901, Jackson 1910, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Zimmermann 1959, BM(NH).

Isleworth, Middlesex (26) : BM(NH).

Kent's Cavern, Devon (6) : Sanford 1870b, Kennard 1945–46, BM(NH).

King Arthur's Cave, Herefordshire (17) : BM(NH).

Langwith Cave, Derbyshire (72) : Barrett-Hamilton & Hinton 1910–21, Mullins 1913.

Levaton Cave, Devon (2) : Carreck 1957.

Marlow, Buckinghamshire (25) : BM(NH).

Merlin's Cave, Herefordshire (18) : Hinton 1924.

Picken's Hole, Somerset (10) : Stuart 1974.

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Dowel Cave, Derbyshire (71) : Bramwell 1960.

Etches' Cave, Derbyshire (71) : Pernetta 1966.

Lynx Cave, Denbighshire (67) : Blore 1966.
Nazeing, Essex (37) : Hinton 1952, BM(NH).
Cowside Cave No. 3, Yorkshire (78) : BM(NH).
Hay Wood Rockshelter, Somerset (10) : BM(NH).
Somerset levels, Huntspill Cut (8) : Hinton 1952.
Nornour, Isles of Scilly (91) : Pernetta & Handford 1970.
Creag nan Uamh Cave, Sutherland (83) : Peach & Horne 1917.

Fig. 29. Distribution of fossil remains of *Microtus oeconomus* (Pallas) in the British Isles.

Distribution in the British Isles. *M. oeconomus* is a widely distributed fossil species in England and Wales, which also reached northern Scotland. It is a dominant element of the Crayford fauna and is numerous in the sediments of the Last Glaciation. It was still present at the end of this period (Nazeing) and disappeared during postglacial times.

General distribution. *M. oeconomus* is now widely distributed in the northern parts of Europe, Asia and North America. In Europe its westernmost localities are in Holland and Germany and isolated colonies are known in Hungary and Austria. Fossil remains are common in the Late Pleistocene and Holocene layers of central Europe including France, Hungary and Switzerland.

Systematic remarks. In Chaline's opinion (1972) *M. ratticepoides* is a synonym of *M. oeconomus*, which developed during the Last Glaciation, its ancestor being *M. malei*. This hypothesis is rather contradictory and lacks evidence, at least as far as material from the British Isles is concerned.

Microtus gregalis (Pallas 1779)

Narrow-skulled vole

1894 *Microtus* (= *Arvicola*) *gregalis* ; Newton : 197–198, pl. xi, fig. 12.
1910a *Microtus anglicus* Hinton : 36–37.

Localities : Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, BM(NH).

Bleadon Cave, Somerset (10) : BM(NH).
Brixham Cave, Devon (4) : BM(NH).
Chudleigh Fissure, Devon (7) : BM(NH).
Great Doward Cave, Herefordshire (17) : BM(NH).
Ightham Fissures, Kent (28) : Newton 1894, Hinton 1910a, b, Barrett-Hamilton & Hinton 1910–21, Hinton 1924, 1926b, 1952, Zimmermann 1959, Chaline 1972, BM(NH).
Isleworth, Middlesex (26) : BM(NH).
Kent's Cavern, Devon (6) : Kennard 1945–46, BM(NH).
King Arthur's Cave, Herefordshire (17) : BM(NH).
Langwith Cave, Derbyshire (72) : Hinton 1924, Mullins 1913.
Levaton Cave, Devon (2) : Carreck 1957 ('*Microtus* cf. *anglicus*').
Merlin's Cave, Herefordshire (18) : Hinton 1925.
Picken's Hole, Somerset (10) : Stuart 1974.
Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.
Tornewton Cave (Reindeer Stratum), Devon (3) : Kowalski 1967, BM(NH).
Uphill Cave, Somerset (9) : Hinton 1926b.
Dowel Cave, Derbyshire (71) : Bramwell 1960.
Happaway Cave, Devon (5) : BM(NH).
Nazeing, Essex (37) : Hinton 1952, BM(NH).

FIG. 30. Distribution of fossil remains of *Microtus gregalis* (Pallas) in the British Isles.

Although *M. anglicus* (= *M. gregalis*) is recorded from Dog Holes Cave (Jackson 1912) four specimens from this locality preserved in the British Museum (Natural History) and labelled by Hinton as *M. anglicus* do not belong to this species but to *M. agrestis*.

DISTRIBUTION IN THE BRITISH ISLES. *M. gregalis* was present in the southern parts of England during the Last Glaciation, but is absent in all earlier sediments. It probably reached Britain only once and disappeared before the end of the last glacial period.

General distribution. *M. gregalis*, the unique representative of the subgenus *Stenocranius* Kastschenko, is now distributed widely in northern and central Asia and in arctic Europe from the White Sea in the west to the Bering Strait in the east. In the western parts of its range it is associated with the tundra belt but in the east, where the climate is more continental, it is present also in the steppe and desert zone in eastern and central Asia.

In Europe it was common in the time of the Last Glaciation, reaching France and Britain in the west and Switzerland and Hungary in the south. According to Chaline (1972), it was present in France during both the last and penultimate glaciations.

Systematic remarks. *M. gregalis* was recorded in the Pleistocene of Europe by Nehring (1875 : 7). According to Hinton (1924), fossil remains from Europe are specifically distinct from *M. gregalis* and approach *M. tianschanicus* Büchner (now regarded as synonym of *M. eversmanni* Poljakov). In the modern systematics of this group *M. eversmanni* is recognized as a subspecies of *M. gregalis*. The morphology and dimensions of the European fossil specimens lie completely within the range of variability of the polytypic species *M. gregalis*. According to Chaline (1972) the name *anglicus* can be preserved to designate the subspecies of *M. gregalis* from the Last Glaciation localities of Europe.

Genus ***LAGURUS*** Gloger 1841

Lagurus lagurus (Pallas 1773)

Steppe lemming

1967 *Lagurus lagurus* (Pallas) ; Kowalski : 115–119, figs 1–24.

Fig. 31. Distribution of fossil remains of *Lagurus lagurus* (Pallas) in the British Isles.

Distribution in the British Isles. Remains of *Lagurus lagurus* have been found at only one locality, in the Glutton Stratum of Tornewton Cave, Devon (3) (Kowalski 1967). Sixty-three first lower molars (3·8 per cent of the total number of rodent remains in this layer) and many other teeth were found in this deposit, which dates from the cold stage preceding the interglacial hippopotamus-bearing Hyaena Stratum of this cave.

General distribution. *L. lagurus* developed during the Middle Pleistocene from more primitive forms of the genus *Lagurus*. It is now distributed in the steppe zone of Eurasia from the River Dnepr to Mongolia and Chinese Turkestan. Its fossil remains are relatively common in Upper Pleistocene localities in central and eastern Europe, but less so in western Europe. In France (Chaline 1973) it has been found in strata of the penultimate ('Riss') and early last (Würm) glaciations.

Systematic remarks. The fossil British *Lagurus* remains are identical in dimensions and molar pattern with recent specimens of this species. The only character not observed in contemporary material is a tendency among the Tornewton specimens towards the fusion of the two anterior enamel triangles on the first lower molar (Kowalski 1967).

IV. HISTORY OF THE RODENT FAUNA OF THE BRITISH ISLES DURING THE PLEISTOCENE

In the earlier parts of this work rodent localities and rodent species were considered individually. In conclusion, let us attempt to construct from this information a generalized table of the rodent faunas of the various stages of the British Pleistocene. The construction of such a table must nevertheless be carried out with reserve. Rodent faunas were not uniform throughout the British Isles. Cold-adapted species in the north were able to coexist with more temperate species in the south, and during every glacial and interglacial stage there occurred a shifting of the vegetational zones which would have caused corresponding movements of the rodent populations.

Sometimes sea barriers prevented the movement of rodents. The known rodent faunas of the Lower Pleistocene and of the later glaciations of England are similar to those of the continent of Europe, suggesting land connections, whereas only a few rodent species are known from the later interglacials, suggesting separation. There is no evidence that any rodents crossed to Ireland until some stage during the Last Glaciation.

Fossil rodent material is seldom rich enough to demonstrate local or temporal differentiation within particular divisions of the Pleistocene of the British Isles and there are some stages, especially the earlier glaciations, from which no rodent remains are yet known. The incompleteness of the record of British rodents was strikingly demonstrated by the recent discovery of previously unrecognized rodent faunas in the Westbury Fissure and in Tornewton Cave. Further discoveries can be expected to provide an ever more detailed sequence for a long time to come.

The most likely stratigraphical relationship of the principal British rodent localities, at our present incomplete state of knowledge, and the known range of the various rodent species, is shown in Table 12. A series of faunal stages can be recognized. In ascending order these are as follows.

RED CRAG. The study of rodents from the earliest Pleistocene deposit of the British Isles, the Red Crag, is very difficult because of the mixing in this marine deposit of contemporary and derived fossils. *Castor fiber* is apparently a contemporary species. *Trogontherium minus*, known from Pliocene sediments on the continent of Europe, and *Hystrix* are apparently derived remains of pre-Pleistocene age.

ICENIAN CRAG AND PASTONIAN FOREST BED. The next faunal assemblage is that of the Icenian Crag and the earlier (Pastonian) part of the Forest Bed Series at East Runton. *Mimomys pliocaenicus* (from both deposits) and *M. reidi* (from the Icenian Crag) are species of great stratigraphic importance. On the continent of Europe they are limited to the Upper Villafranchian or Tiglian. There is no evidence of any difference between the British and European continental rodent faunas at this stage. *Trogontherium boisvilletti* and *Castor fiber* are two long-ranging rodents also present in both series of deposits.

CROMERIAN *sensu stricto*. The rodent fauna from the Cromerian type locality at West Runton is unusually rich, there being at least eleven species. *Trogontherium boisvilletti* and *Castor fiber* reappear. *Mimomys savini* replaces *M. pliocaenicus*; *Apodemus sylvaticus, Cricetus cricetus, Clethrionomys glareolus, Pitymys arvaloides, P. gregaloides, Microtus arvalinus, M. nivaloides* and *M. ratticepoides* make an appearance. *Sciurus whitei* occurs in the overlying marine 'Monkey Gravel'.

The West Runton fauna is predominantly of forest and meadow type, testifying to a mild climate, though *Cricetus cricetus* could point to colder or more continental conditions. No arctic elements are present. *Allophaiomys pliocaenicus* and lemmings, already present on the continent at the time of the earliest glaciations, are so far unrecorded from West Runton.

'WESTBURY STAGE'. The rich mammalian fauna from Westbury Fissure, described by Bishop (1974), does not at present fit into the generally accepted Pleistocene sequence of the British Isles. Bishop has presented evidence of a previously unrecognized stage later than the Cromerian *sensu stricto* of West Runton and possibly equivalent to Mosbach and other continental sites.

Although the richest rodent-bearing level at Westbury (the 'Rodent Earth') is the latest deposit in the fissure and may be slightly younger than the main bone deposit (the 'Calcareous Series') five rodent species are nevertheless represented in the latter. *Apodemus sylvaticus, Pitymys gregaloides* and *Microtus arvalinus* reappear; *Arvicola cantiana* and *Lemmus* sp. appear for the first time. All these forms persist into the 'Rodent Earth' which also contained *Dicrostonyx* sp., the earliest record in the British Pleistocene, and the only record from the British Pleistocene of *Pliomys episcopalis*. *Clethrionomys glareolus* reappears. Of special interest is the first appearance in the British Pleistocene of *Arvicola cantiana*, which apparently replaces *Mimomys savini*, believed to be an earlier stage in the same phylogenetic lineage, and which is so common at West Runton.

Castor fiber is represented in the lowest water-laid deposits of the cave. The lowest deposits of Kent's Cavern and the 'Forest Bed' deposit of Ostend, Norfolk, may also belong to this stage.

TABLE 12

Probable chronological distribution of fossil rodent localities and rodent species from the British mainland and Ireland, according to ava

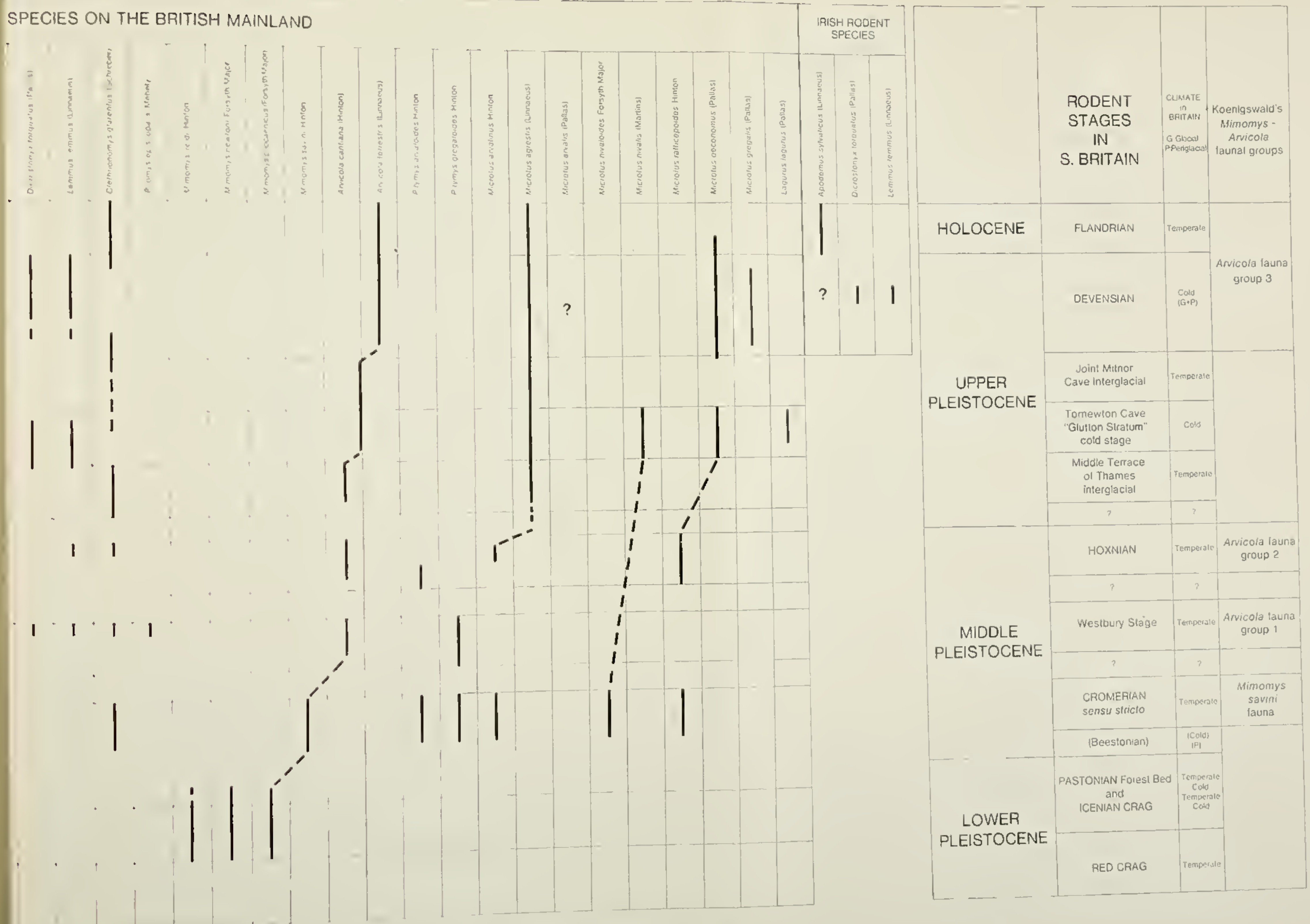
	RODENT STAGES IN S. BRITAIN	CLIMATE in BRITAIN (G Glacial, P Periglacial)	Koenigswald's *Mimomys* - *Arvicola* faunal groups	BRITISH DEPOSITS	RODENT LOCALITIES ON THE BRITISH MAINLAND	IRISH RODENT LOCALITIES
HOLOCENE	FLANDRIAN	Temperate		CAVE, TERRACE & ALLUVIAL DEPOSITS; KENT'S CAVERN; TORNEWTON CAVE ('CAVE EARTH', REINDEER STRATUM, HYAENA STRATUM, OTTER STRATUM, GLUTTON STRATUM)	Cambridge Fens, ?Cowside Cave No 3, Hayward Rockshelter, Huntspill Cut, Staple Howe (Iron Age A, c 2,400 years ago), Star Carr (Mesolithic, c. 9,500 years ago), Thatcham (Mesolithic c 9,900-9,500 years ago), Nornour, Isle of Scilly (Bronze Age)	
UPPER PLEISTOCENE	DEVENSIAN	Cold (G+P)	*Arvicola* fauna group 3		↕ Dowel Cave, Etche s Cave, Fox Hole Cave, Nazeing; Aveline's Hole, Bleadon Cave, Brixham Cave, Chudleigh Fissure, Dog Holes Cave, Elderbush Cave, Fisherton, Great Doward Cave, Gwaenysgor Cave, Harborough Cave, Ightham Fissure, King Arthur's Cave, Langwith Cave, Levaton Cave, Marlow, Merlin's Cave, Murston, Picken's Hole, Pin Hole Cave, Rowberrow Cave, Uphill Cave; LATE GLACIAL: Angel Road, Brean Down, Hackney, Happaway Cave, Lynx Cave, Ponders End; C 14 DATED SITES: Beckford 27,650 ± 250 years ago, Upton Warren c.41,000 years, Isleworth 43,140 $^{+1520}_{-1280}$ years; SCOTLAND: Loch of Marlee, Middlesfots Bog, Corstorphine, Creag nan Uamh Cave; ↕ Minchin Hole, Alveston Fissure, Hessle	Ballynamintra Cave, Castlepook Cave, Castletownroche Cave, Edenvale Caves, Keshcorran Caves, Kilgreany Cave, Red Cellar Cave
	Joint Mitnor Cave interglacial	Temperate			Barrington, Joint Mitnor Cave, Kirkdale Cave, Swanton Morley, Upnor; "IPSWICHIAN" *sensu lato*: Bobbitshole, Selsey, Stoke Tunnel Beds, ?West Wittering	
	Tornewton Cave "Glutton Stratum" cold stage	Cold			↕ Water Hall Farm Pit; Banwell Cave, Clevedon Cave, Cow Cave (part), ?Goughs Cave (part), ?Hutton Cave	
	Middle Terrace of Thames interglacial	Temperate			↕ Crayford and Erith; ? Northfleet; Aveley, Grays Thurrock, Ilford, Stutton, Harkstead	
	?	?				
MIDDLE PLEISTOCENE	HOXNIAN	Temperate	*Arvicola* fauna group 2		Clacton-on-Sea, Copford, Hitchin, Hoxne, Swanscombe (Ingress Vale and Barnfield Pit)	
	?	?		?BRECCIA	Mundesley Arctic Bed (alternative positions)	
	Westbury Stage	Temperate	*Arvicola* fauna group 1		Westbury-sub-Mendip, ?Ostend	
	?	?		CROMER FOREST BED SERIES		
	CROMERIAN *sensu stricto*	Temperate	*Mimomys savini* fauna		West Runton; CROMERIAN *sensu lato*: Bacton, Cromer, Kessingland, Overstrand, Paston, Sugworth	
	(Beestonian)	(Cold) (P)				
LOWER PLEISTOCENE	PASTONIAN Forest Bed and ICENIAN CRAG	Temperate Cold Temperate Cold		ICENIAN CRAG	East Runton, Happisburgh; Bramerton, Covehithe, Easton Bavents, Sizewell, Thorpe, Trimingham	
	RED CRAG	Temperate		RED CRAG	Sutton, Woodbridge	

RODENT

Stage	*Sciurus whitei* Hinton	*Sciurus vulgaris* Linnaeus	*Spermophilus primigenius* Kormos	*Spermophilus superciliosus* (Kaup)	*Muscardinus avellanarius* (Linnaeus)	*Trogontherium boisvilletti* Laugel	*Castor fiber* Linnaeus	*Apodemus sylvaticus* (Linnaeus)	*Apodemus flavicollis* (Melchior)	*Micromys minutus* (Pallas)	*Mus musculus* Linnaeus	*Rattus rattus* Linnaeus	*Rattus norvegicus* (Berkenhout)	*Cricetus cricetus* Linnaeus	cf *Allocricetus bursae* Schaub
FLANDRIAN		|			|		|	|	|	|	|	|	|		
DEVENSIAN				|	|		|	|							
Joint Mitnor Cave interglacial							|	|							
Tornewton Cave "Glutton Stratum" cold stage								|						|	|
Middle Terrace of Thames interglacial			|				|	|							
HOXNIAN						|	|	|							
Westbury Stage			| (Alternative positions)				|	|							
CROMERIAN *sensu stricto*	|		| (Alternative positions)		?	|	|	|						|	
PASTONIAN and ICENIAN CRAG						|	|								
RED CRAG							|								

lable information

(*for* Hayward *read* Hay Wood)



Mundesley Arctic Bed. The *Spermophilus* described by Newton (1882b) from a deposit with remains of arctic plants at Mundesley, Norfolk, provides the only known instance of a fossil rodent from a British Lower or Middle Pleistocene non-interglacial deposit. According to Newton the deposit was immediately overlain by thick glacial deposits which West & Wilson (1966) attributed to the Lowestoftian (Anglian) Glaciation. They referred underlying interglacial deposits to the Cromerian *sensu stricto*.

For the time being the exact relationship between the Mundesley Arctic Bed and the Westbury deposits must remain uncertain. If, as might be expected, Mundesley is later than Westbury then it is necessary to explain why the Westbury stage has not been recognized, except possibly at Ostend, in the Forest Bed sequence of East Anglia. If, on the other hand, it is earlier then it is necessary to postulate a hitherto unrecognized cold stage between the Cromerian *sensu stricto* and the 'Westbury' stage.

Hoxnian deposits. The best sequence of deposits with rodent remains of Hoxnian age is that of Barnfield Pit, Swanscombe. A considerable time interval is believed to have occurred within this sequence, between the Lower Loam and the Middle Gravel (see p. 52). From the lowest deposit, the Lower Gravel, only *Pitymys arvaloides* has been recorded. In the overlying Lower Loam this species is accompanied by *Castor fiber*, *Arvicola cantiana*, *Microtus arvalinus* and *M. ratticepoides*.

These last two species continue into the Upper Middle Gravel, where they are joined by *Clethrionomys glareolus* and *Lemmus* sp. Although *Trogontherium boisvilletti* and *Apodemus sylvaticus* have not been recorded from Barnfield Pit, they are known from a nearby pit in the same terrace deposits at Ingress Vale. *Trogontherium boisvilletti* appears to have been common during the Hoxnian, being recorded also from Clacton, Copford and Hoxne. It is unknown from later deposits.

Comparison of the rodent faunas of West Runton, Westbury-sub-Mendip and Swanscombe. Although the geological evidence indicates at least one major glaciation between the time of accumulation of the deposits at West Runton and at Swanscombe, and although there are very great differences between the large mammals of the three sites mentioned above, changes in the rodent fauna were remarkably gradual. The distribution of the various rodent species is shown in Table 13.

Whilst incomplete collecting probably accounts for many of the gaps in the table a gradual replacement of species is nevertheless apparent. *Mimomys savini*, abundant at West Runton, appears to be replaced at Westbury by *Arvicola cantiana*. This species persists at Swanscombe and in slightly later deposits. *Microtus arvalinus* and *M. ratticepoides* are present at both West Runton and Swanscombe (the former occurs also at Westbury), but apparently disappear from the British Pleistocene after the Upper Middle Gravel. *Trogontherium boisvilletti* and *Pitymys arvaloides* are of similar distribution, last seen at Ingress Vale and in the Lower Loam of Barnfield Pit respectively. *Pitymys gregaloides* occurs at West Runton and Westbury but does not reappear at Swanscombe. *Microtus nivaloides* is not at present known from deposits later than West Runton. *Pliomys* is at present known

TABLE 13

Comparison of rodent species represented at West Runton, Westbury-sub-Mendip (Bishop 1974 and pers. comm.) and Swanscombe

	West Runton	Westbury-sub-Mendip			Swanscombe			
					Barnfield Pit			
	Upper Freshwater Bed	'Siliceous Group'	'Calcareous Group'	'Rodent Earth'	Lower Gravel	Lower Loam	Upper Middle Gravel	Ingress Vale
Sciurus whitei	×							
Trogontherium boisvilletti	×							×
Castor fiber	×	×				×		
Apodemus sylvaticus	×		×	×				×
Cricetus cricetus	×							
Dicrostonyx sp.				×				
Lemmus sp.			×	×			×	
Clethrionomys glareolus	×			×			×	
Pliomys episcopalis				×				
Mimomys savini	×							
Arvicola cantiana			×	×		×		×
Pitymys arvaloides	×				×	×		
P. gregaloides	×		×	×				
Microtus arvalinus	×		×	×		×	×	
M. nivaloides	×							
M. ratticepoides	×					×	×	

only from the youngest deposit at Westbury. *Dicrostonyx* and *Lemmus*, so common in British Upper Pleistocene deposits, appear for the first time at Westbury. *Lemmus* reappears in the Upper Middle Gravel of Swanscombe.

No major break is discernible in the above sequence of rodent faunas. The Westbury fauna has some characters in common with both West Runton and Swanscombe, confirming Bishop's supposition that it is of intermediate age. The rodent faunas of the three localities are similar to Koenigswald's *Mimomys savini* fauna, *Arvicola* fauna group 1 and *Arvicola* fauna group 2 of the continent of Europe (see p. 101) and suggest land connections during the periods concerned. A similarity of the large mammals of Swanscombe and those from the Holsteinian site of Steinheim an der Murr in Germany has previously been observed by Sutcliffe (1964).

NOTES ON THE WOLSTONIAN–IPSWICHIAN PART OF THE SUCCESSION. Although palaeobotanical evidence provides support for only one further interglacial in the

British Isles after the Hoxnian it is difficult to fit all the known Upper Pleistocene rodent faunas into such a simple sequence of events. The generally accepted Wolstonian–Ipswichian part of the succession appears, from the rodent and other evidence previously described, to be composite. The so-called 'Ipswichian' interglacial is here interpreted as double, with the Middle Terrace of the Thames representing a warm stage earlier than the Joint Mitnor Cave warm stage.

Middle Terrace of the Thames interglacial. Reasons for regarding the deposits of the Middle Terrace of the Thames (type locality Grays Thurrock) as representing the earlier of these two warm periods have been given on pp. 55–58. Ilford, Aveley, Harkstead, and Stutton in Suffolk are also included here. The known rodent fauna of this stage is very sparse. *Arvicola cantiana* reappears; other species include *Castor fiber*, *Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis*. Consideration needs to be given to the possibility that this stage is Hoxnian (Zeuner (1945) believed that Grays was of Penultimate Interglacial = Hoxnian age) but the occurrence of *Arvicola cantiana* in other Middle Terrace localities such as Aveley and Stutton, both of which have been claimed on palaeobotanical grounds to be Ipswichian, makes it unnecessary to resort to such an early date.

Tornewton Cave Glutton Stratum cold stage. The *Arvicola* from the Glutton Stratum of Tornewton Cave is the transition form between *A. cantiana* and *A. terrestris*, suggesting that this deposit is later than the Middle Terrace of the Thames where the species is *A. cantiana*. We know that this stage was followed by a further interglacial, since these deposits were immediately overlain by the Hyaena Stratum, with remains of hippopotamus. Other species from the Glutton Stratum are *Microtus oeconomus* and *M. nivalis*, which make up the bulk of the rodent fauna, and also *M. agrestis*, *Lagurus lagurus* (the only British record of this species), cf. *Allocricetus bursae* and *Cricetus cricetus*. *Dicrostonyx torquatus* and *Lemmus lemmus* are present, but not abundant.

This assemblage closely resembles that of the Late Middle Terrace of Crayford and Erith, regarded by Hinton (1926b) as later than that of the Middle Terrace of Grays Thurrock. Rodents common to both Crayford and the Tornewton Cave Glutton Stratum are *Microtus oeconomus*, *M. nivalis*, *M. agrestis*, *Arvicola* sp., *Lemmus lemmus* and *Dicrostonyx torquatus*. Most of the species that are not common to both deposits are so rare in the British Pleistocene that stratigraphic comparison with other localities cannot be made. *Spermophilus primigenius* from Crayford and *Cricetus cricetus* from Tornewton Cave are unknown from any other post-Hoxnian British sites; cf. *Allocricetus bursae* (Tornewton Cave) is known from only one other British locality, Hutton Cave, which is of uncertain age. *Lagurus lagurus* is known only from Tornewton Cave.

The mollusc evidence suggests that the *Corbicula* Bed at Crayford, in which most of the rodent remains were found, is still interglacial, though absence of forest species of land mollusca indicates open grassland. The living representatives of the subgenus *Urocitellus*, to which *Spermophilus primigenius* belongs, are also open-country species. On the continent *S. primigenius* is unknown later than the 'penultimate' glaciation.

From the available evidence the most likely stratigraphic position for Crayford would seem to be the end of the Grays–Ilford–Aveley interglacial. *S. primigenius* prevents us from attributing a date late in the Pleistocene to the Crayford deposits. Crayford apparently heralds the arrival of the Tornewton Cave Glutton Stratum rodent fauna and marks the beginning of the arrival of a great wave of eastern species of rodents from the European continent. Characteristic of this particular invasion of continental forms are *Spermophilus primigenius, Cricetus cricetus, Allocricetus bursae, Lagurus lagurus* and *Microtus nivalis*. In addition, there arrived three other boreal species, *Dicrostonyx torquatus, Lemmus lemmus* and *Microtus oeconomus*. During the coldest phase of this period all rodents connected with forest environment, including such adaptable species as *Clethrionomys glareolus* and *Apodemus sylvaticus*, apparently disappeared from the British Isles. The absence of *Microtus gregalis*, so common in Last Glaciation deposits, is a characteristic feature of the fauna of this stage.

The apparent occurrence of this cold stage between two interglacial stages with 'Ipswichian' floras is not in accordance with current palaeobotanical opinion, which identifies only one Ipswichian. The severity of this cold stage requires further assessment. The occurrence of both reindeer and wolverine, in addition to the above-mentioned rodent species, suggests more than a minor cool phase within an interglacial. Intense disturbance of the Glutton Stratum and the mixing of it with a vast quantity of fragments of broken stalagmite formations could be interpreted as evidence of very intense frost disturbance later than the Glutton Stratum but earlier than the deposition of the overlying layers. The relationship of this apparent cold stage to known glacial stages of the Upper Pleistocene (ice of the penultimate glaciation is believed to have reached north Devon) must remain, for the time being, unknown.

Other localities which Hinton (1926b) considered, from the rodent evidence, to be contemporaneous with Crayford are Clevedon and Banwell Caves. Cow Cave (part), Gough's Cave (part), Northfleet and Water Hall Farm (each with *Microtus nivalis*), and Hutton Cave (with cf. *Allocricetus bursae*) may be further examples of deposits approximately contemporaneous with the Glutton Stratum of Tornewton Cave.

Microtus nivalis apparently disappears from the British Pleistocene after this stage.

JOINT MITNOR INTERGLACIAL. The occurrence of a further interglacial stage with hippopotamus is reliably demonstrated at Tornewton Cave where the interglacial Hyaena Stratum overlies the Glutton Stratum. The occurrence of remains of *M. nivalis* and *M. oeconomus*, apparently underlying hippopotamus-bearing deposits, at Water Hall Farm gravel pit provides a further example of this relationship.

Important hippopotamus sites dating from this interglacial probably include Barrington, Joint Mitnor Cave and Swanton Morley. The rodent fauna of this stage is very sparse. The *Arvicola cantiana-terrestris* transition form and *Microtus agrestis* are the most common species. *Clethrionomys glareolus, Apodemus sylvaticus* and *Castor fiber* also occur. The Otter Stratum of Tornewton Cave (with the clawless otter, *Cyrnaonyx*, and white-toothed shrew, *Crocidura*, unknown elsewhere in the British Pleistocene) may represent the beginning of this stage, before the arrival of hippopotamus ; Minchin Hole appears to represent the end, after it had disappeared. The sparseness of this fauna suggests isolation of the British Isles from the European continent at that time.

Before leaving discussion of this interglacial, represented also by other sites such as Trafalgar Square with plant remains, we must refer once more to the Middle Terrace of the Thames interglacial, indistinguishable from it on palaeobotonical evidence. Evidence from the rodent remains nevertheless makes it difficult to explain the sequence other than with two post-Hoxnian interglacial stages separated by the Tornewton Glutton Stratum cold stage. The sequence becomes even more complicated if we consider the significance of the Baker's Hole cold stage. Was this the same as the Tornewton Cave Glutton Stratum cold stage or (if, as Carreck (*in litt.*) has suggested, it occurred between the Ilford and Crayford stages) does it represent yet another earlier cold stage within the 'Ipswichian', *sensu lato?*

There is at present no means of knowing to which of these warm stages the Ipswichian type locality of Bobbitshole belongs, although recent studies by Coope (1974) have showed very close similarities between the insects of this site and of Trafalgar Square, suggesting that it could be the later one. This is in agreement with the view of Evans (1971) who assigned the Ipswichian *sensu stricto* to his half-cycle 3W (see pp. 40–42).

Last Glaciation. The Last (Devensian) Glaciation opened the way for a new immigration. This time the immigrants included not only both species of lemmings but also two new arrivals, the ground squirrel *Spermophilus superciliosus* and the vole *Microtus gregalis*. *Cricetus*, *Lagurus* and *Allocricetus*, though present at this time in France, did not find their way back to Britain. *Arvicola* had by this time evolved to *A. terrestris* (Koenigswald's *Arvicola* fauna group 3, see pp. 100–101). *Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis* are other species recorded and *M. arvalis* may have been present for a short time. *Castor fiber* apparently disappeared.

This fauna differs substantially from that of the preceding cold phase represented by the Glutton Stratum of Tornewton Cave, from which it is readily distinguishable. Diagnostic criteria include the absence of *Spermophilus primigenius* (found at Crayford), *Cricetus*, *Allocricetus*, *Microtus nivalis* and *Lagurus* and the appearance of *Spermophilus superciliosus* and *Microtus gregalis*. *Arvicola* had evolved from the *A. cantiana-terrestris* transition form to true *A. terrestris*. *Dicrostonyx*, *Lemmus* and *Microtus oeconomus* were present during both stages.

It is impossible at present to reconstruct in detail all the changes of the rodent fauna of the Last Glaciation. We have nevertheless now reached the most recent stage within the Quaternary, except for the Holocene, and the later part of it lies within the range of radiocarbon dating. Some changes of the rodent fauna are apparent, which offer a basis for more detailed study in the future, when more and better-dated material becomes available for study.

During the coldest part of the Last Glaciation *Apodemus sylvaticus* and perhaps also *Clethrionomys glareolus* disappeared from a large part or perhaps all of Britain. During the warmest interstadial the two lemmings were apparently absent, at least in the south of England.

Three sites with ^{14}C dates are of special importance. These are:

1. Willment's Pit, Isleworth, west London. 43 140 + 1520 or − 1280 years B.P. *Microtus oeconomus* and *M. gregalis* (possibly the earliest record of this species in Britain) occur; no lemmings.
2. Upton Warren, Worcestershire. 41 000 years B.P. *Dicrostonyx* present.
3. Beckford, Worcestershire. 27 650 ± 250 years B.P. Probably with *Microtus arvalis*.

Coope, who is making a detailed study of the insect faunas of the Last Glaciation, has named the period of time covered by the above sites the Upton Warren Interstadial complex. He found evidence (pers. comm.) of an intense and short amelioration of climate at about 43 000 years ago, followed by climatic deterioration with increase of continentality at about 41 000 years. The lack of lemmings at Isleworth is in accordance with the evidence provided by the insects. The Beckford insect fauna (pers. comm.) indicates cold conditions.

Other important Last Glaciation sites in the south of England, which lack lemmings, are Levaton Cave and Picken's Hole. The deposits of this last-mentioned site are interpreted by Stuart (1974) as possibly Early Devensian (layer 5, with *Microtus* cf. *oeconomus* and *M.* cf. *gregalis*) and Middle Devensian (layer 3, with *Citellus* sp. (= *Spermophilus* sp.) and *Microtus* cf. *gregalis*).

The best evidence of the rodent faunas of the end of the Last Glaciation and early Holocene is provided by the deposits of the Lea Valley and by the Peakland Archaeological Society's excavations in Dowel Cave, Etches' Cave and Fox Hole Cave. The end of the Pleistocene is marked by a special abundance of lemmings. Late Glacial deposits in the Lea Valley (dated on palaeobotanical evidence) contained both *Lemmus lemmus* and *Dicrostonyx torquatus* and also *Arvicola terrestris*, *M. oeconomus* and *M. anglicus* (= *M. gregalis*). Of these *Dicrostonyx torquatus* was still present in pollen Zone III (the last stage of the Pleistocene, ending about 10 000 years ago) and *M. oeconomus* survived into the Holocene. The cave sites mentioned above also indicate an abundance of lemmings in the Late Pleistocene. Other species present were *Arvicola terrestris*, *M. gregalis* and *M. oeconomus*, the last-mentioned species surviving there too into the Holocene.

At the end of the Last Glaciation arctic species of rodents began to disappear, though both *Lemmus* and *Dicrostonyx* seem to have survived at Nazeing until near the end of this period, the latter species still being present in pollen Zone III. *M. gregalis* does not appear to have persisted into post-Pleistocene times.

HOLOCENE. The postglacial rodent fauna is poorer than that of the neighbouring continent of Europe, but two species of rodents, now extinct in the British Isles, persisted. These are *Microtus oeconomus* and *Castor fiber*. *M. oeconomus* apparently continued in the Lea Valley until pollen Zone V, Mesolithic, about 9000 years ago. It also survived until Mesolithic times at Dowel Cave and was apparently present on the Isles of Scilly during the Bronze Age.

Castor fiber, apparently absent during the Last Glaciation, had already reappeared by about 9500 years ago (pollen Zone IV–V transition, Mesolithic, Star Carr), surviving until possibly the thirteenth century. Although the date of the Scottish finds is uncertain, *Castor fiber* may have reached Scotland during this stage.

Arvicola terrestris persisted from the Pleistocene and still occurs in Britain at the present day. In the Lea Valley *Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis* reappeared in pollen Zone V–VI (about 9000 years ago) after an apparent interval at the end of the Pleistocene.

Sciurus vulgaris was probably a post-Pleistocene arrival. Others were *Apodemus flavicollis*, *Muscardinus avellanarius* and *Micromys minutus*. It is difficult to decide whether these last three species reached Britain with or without participation of human activity. Geological and ecological data suggest rather the second possibility. *Glis glis*, *Mus musculus*, *Rattus rattus* and *Rattus norvegicus* are evidently recent human introductions.

IRELAND. At some stage during the Last Glaciation the two species of lemmings, but no voles nor any steppe elements, managed to cross to Ireland. A ^{14}C date of 33 000 years for an associated mammoth bone from Castlepook Cave suggests that *Lemmus* and *Dicrostonyx* were probably established in Ireland at that time. Both are northern species which might be expected to reach Ireland in advance of other rodents. On the basis of existing evidence, the availability of lemmings for immigration from the British mainland appears entirely plausible.

Apodemus sylvaticus, recorded from the Pleistocene levels of Castlepook Cave, may also have arrived in Ireland during the Pleistocene, although it has been observed that at some cave sites this species was most abundant in the upper levels, suggesting a later date. Other rodent species which occur in Ireland today are probably post-Pleistocene arrivals.

V. ACKNOWLEDGEMENTS

The writers gratefully acknowledge help with the compilation of this Bulletin from many sources.

Dr W. von Koenigswald, of Tübingen University, advised on British representatives of the *Mimomys–Arvicola* lineage, and commented on the typescript.

Mr M. J. Bishop, of University College, London, provided us with full details of his determinations of the rodent remains from the Middle Pleistocene fissure deposit at Westbury-sub-Mendip and allowed us to see the typescript of his report on this site before publication.

Mr J. N. Carreck (Queen Mary College) read the typescript and provided many valuable suggestions. He also allowed us to mention important findings from his own unpublished studies in the Thames estuary.

Dr G. B. Corbet, of the British Museum (Natural History), provided determinations of rodent remains from Alveston Fissure, Beckford and Marlow and commented on the typescript.

Dr A. J. Stuart, of the University of Cambridge, provided determinations of rodent remains excavated in Minchin Hole in 1973 and much other help. He commented on our typescript and allowed us to see that of his review of British Pleistocene vertebrates before publication.

Dr J. d'A. Waechter provided an important collection of rodent remains excavated from the Lower Loam of Barnfield Pit, Swanscombe, during 1968–72.

Dr G. R. Coope, of Birmingham University, provided rodent remains from Beckford and advice on the events of the Last Glaciation in Britain.

Dr R. G. Wolff, of the University of Florida, provided details of rodent remains collected from Hoxne, Norfolk, by the University of Chicago under grants GS41435 and GS2907 of the National Science Foundation to Dr R. Singer.

Stratigraphic and other information was received from Mr D. Bramwell (Peakland Archaeological Society), Dr A. S. Clarke (Royal Scottish Museum, Edinburgh), Dr J. Jewell (British Museum (Natural History)), Mr D. Mayhew (Cambridge), Professor G. F. Mitchell (Trinity College, Dublin), Mr H. E. P. Spencer (Ipswich), Dr R. G. West and Mrs G. Wilson (University of Cambridge).

Mr J. J. Hooker sieved Pleistocene sediment from Aveley, Essex, for rodent remains, Mr J. Simons sediment from Willments Gravel Pit, Isleworth, London, and from Water Hall Farm Pit, Hertfordshire, all with important results.

Mr A. P. Currant (British Museum (Natural History)) prepared Figs 1, 5–18 and 21–31 and Mrs A. J. Sutcliffe drew Figs 2–4.

Mr D. L. F. Sealy provided much editorial help, including preparing the index, and Mrs M. N. M. Bhukhureea prepared the typescript with great patience.

VI. REFERENCES

An asterisk (*) distinguishes those papers cited in the text which are not directly concerned with Quaternary rodents of the British Isles.

Abbot, W. J. L. 1917. The ossiferous fissures of the valley of the Shode. Appendix I *in* : Bennett, F. J. *Ightham, The Story of a Kentish Village and its Surroundings* : 101–119, 1 pl., 2 tables, 1 fig. London.

* Agadzhanian, A. K. 1973. (Collared lemmings of the Pleistocene). *Nov. tekt. nov. otlozhi i chelovek*, Moscow, **5** : 320–355. [In Russian.]

ApSimon, A. M., Donovan, D. T. & Taylor, H. 1961. The stratigraphy and archaeology of the late-glacial and post-glacial deposits at Brean Down, Somerset. *Proc. speleol. Soc.*, Bristol, **9** : 67–136.

* Azzaroli, A. 1953. The deer of the Weybourne Crag and Forest Bed of Norfolk. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **2** : 1–96.

Barrett-Hamilton, G. E. H. & Hinton, M. A. C. 1910–21. *A History of British Mammals* (unfinished). **1** (1910) : xvi+263 pp., 20 pls. **2** (1911–21) : 748 pp., 37 pls. London.

Bate, D. M. A. 1901. A short account of a bone cave in the Carboniferous Limestone of the Wye Valley. *Geol. Mag.*, London, (n.s. 4) **8** : 101–106.

Beirne, B. P. 1947. The history of the British Land Mammals. *Ann. Mag. nat. Hist.*, London, (11) **14** : 501–514.

Bisat, W. S. 1940. Older and Newer Drift in East Yorkshire. *Proc. Yorks. geol. Soc.*, Leeds, **24** : 137–151.

Bishop, M. J. 1974. A preliminary report on the Middle Pleistocene mammal bearing deposit of Westbury-sub-Mendip, Somerset. *Proc. speleol. Soc.*, Bristol, **13** : 301–318.

—— 1975. Earliest record of Man's presence in Britain. *Nature, Lond.* **253** : 95–97.

Blackmore, H. P. & Alston, E. R. 1874. On Fossil Arvicolidae. *Proc. zool. Soc. Lond.* **1874** : 460–471, 3 figs.

BLORE, J. D. 1966. The excavation of Lynx Cave, 1962–1964. A preliminary report. *Newsl. Peakland archaeol. Soc.*, Stockport, **21** : 17–19, 35.
BOYLAN, P. J. 1967. The Pleistocene mammalia of the Sewerby–Hessle buried cliff, East Yorkshire. *Proc. Yorks. geol. Soc.*, Leeds, **36** : 115–125.
BRAMWELL, D. 1960. The vertebrate fauna of Dowel Cave – final report. *Newsl. Peakland archaeol. Soc.*, Stockport, **17** : [9–12, 23] (pages unnumbered).
—— 1964. The excavations at Elder Bush Cave, Wetton, Staffs. *North Staffs. J. Fld Studs*, Keele, **4** : 46–60.
—— 1970. The tenth report on Fox Hole Cave, High Wheeldon. *Bull. Peakland archaeol. Soc.*, Stockport, **25** : 8–10.
BREWSTER, T. C. M. 1963. *The Excavation of Staple Howe.* Malton, E. Riding Arch. Res. Cttee.
BROWN, J. 1852. On the Upper Tertiaries at Copford, Essex. *Q. Jl geol. Soc. Lond.* **8** : 184–193.
BURCHELL, J. P. T. 1935. Evidence of a further glacial episode within the valley of the Lower Thames. *Geol. Mag.*, London, **72** : 90–91.
* BURLEIGH, R. 1972. Carbon 14 dating with application to dating of remains from caves. *Stud. Speleol.*, London, **2** : 176–190.
CAMPBELL, J. B. & SAMPSON, C. G. 1971. A new analysis of Kent's Cavern, Devonshire, England. *Univ. Ore. anthrop. Pap.*, Eugene, Oregon, **3** : 1–40.
CARRECK, J. N. 1957. A late Pleistocene rodent and amphibian fauna from Levaton, near Newton Abbot, South Devon. *Proc. Geol. Ass.*, London, **68** : 304–308.
—— 1959. *In* : KERNEY, M. P. An interglacial tufa near Hitchin, Herts. *Proc. Geol. Ass.*, London, **70** : 322–337.
—— 1966. Microtine remains from the Norwich Crag (Lower Pleistocene) of Easton Bavents, Suffolk. *Proc. Geol. Ass.*, London, **77** : 491–496.
CATT, J. A. & PENNY, L. F. 1966. The Pleistocene deposits of Holderness, East Yorkshire. *Proc. Yorks. geol. Soc.*, Leeds, **35** : 375–420.
CHALINE, J. 1972. *Les Rongeurs du Pléistocène Moyen et Supérieur de France.* 410 pp., 17 pls. Paris.
CHEADLE, R. W. 1876. On mammalian bones recently found at Crayford and Erith. *Proc. W. Lond. scient. Ass. Fld Club* **1** : 70–71.
COLEMAN, J. C. 1965. *The Caves of Ireland.* 88 pp., 21 figs, 8 pls. Tralee.
* COOPE, G. R. 1974. Interglacial Coleoptera from Bobbitshole, Ipswich, Suffolk. *J. geol. Soc. Lond.* **130** : 333–340.
* —— 1975. An ecological study of a temperate interlude in the middle of the Last Glaciation, based on Coleoptera from Isleworth, Middlesex. *J. anim. Ecol.*, London. **44** : 365–391.
——, SHOTTON, F. W. & STRACHAN, I. 1961. A late Pleistocene fauna and flora from Upton Warren, Worcestershire. *Phil. Trans. R. Soc.*, London, B **244** : 379–421.
* CORBET, G. B. 1961. Origin of the British insular races of small mammals and of the 'Lusitanian' fauna. *Nature, Lond.* **191** : 1037–1040.
* —— 1966. *The Terrestrial Mammals of Western Europe.* xi + 264 pp. London.
* ——, CUMMINS, J., HEDGES, S. R. & KRZANOWSKI, W. 1970. The taxonomic status of British water voles, genus *Arvicola*. *J. Zool., Lond.* **161** : 301–316.
CRANBROOK, LORD 1955a. Fossil Voles. *Trans. Suffolk Nat. Soc.*, Ipswich, **9** : 48–49, 3 figs [published anonymously].
—— 1955b. Records of *Mimomys*. *Trans. Suffolk Nat. Soc.*, Ipswich, **9** : 58 [published anonymously].
DAVIES, J. A. 1921. Aveline's Hole, Burrington Combe. *Proc. speleol. Soc.*, Bristol, **1** : 61–68.
DAWKINS, W. B. & SANFORD, W. A. 1866–72. British Pleistocene Mammalia, **1** (Felidae). l + 194 pp., 26 pls. *Palaeontogr. Soc.* (*Monogr.*), London.
* DIENSKE, H. 1969. Notes on difference between some external and skull characters of *Microtus arvalis* (Pallas, 1778) and of *Microtus agrestis* (Linnaeus, 1761) from the Netherlands. *Zöol. Meded. Leiden* **44** (6) : 83–108.

* ELLERMAN, J. R. & MORRISON-SCOTT, T. C. S. 1966. *Checklist of Palaearctic and Indian Mammals*. 2nd ed. 810 pp., map. London, British Museum (Natural History).

* EVANS, P. 1971. Towards a Pleistocene time-scale. *In*: The Phanerozoic Time-scale – a Supplement. *Spec. Publs geol. Soc. Lond.* **5**: 123–351.

EVANS, W. 1907. Mammals of the Edinburgh or Forth area. *Proc. R. phys. Soc. Edinb.* **16**: 387–405.

—— 1913. Lemming remains in south-east Scotland. *Scott. Nat.*, Edinburgh, **17**: 97–100, 1 fig.

* FAHLBUSCH, V. 1969. Pliozäne und Pleistozäne Cricetinae (Rodentia, Mammalia) aus Polen. *Acta zool. cracov.* **14** (5): 99–137, pls 8–18.

FALCONER, H. See Murchison, C. 1868.

* FRANKS, J. W. 1960. Interglacial deposits at Trafalgar Square, London. *New Phytol.*, Oxford, **59**: 145–152.

FRASER, F. C. & KING, J. E. 1954. Faunal remains. Ch. 3 *in*: CLARK, J. G. D. *Excavations at Star Carr*: 70–95. Cambridge.

FRIANT, M. 1962. Sur le *Castor plicidens* F. Maj. de l'époque des Palafittes. *Jb. naturh. Mus. Bern* **1960–62**: 117–125, pls 1–2.

* GIEBEL, C. G. A. 1847. *Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere* **1** (1), Die Säugethiere. 467 pp. Leipzig.

* GROMOV, I. M. 1965. *In*: GROMOV, I. M., BIBIKOV, D. I., KALABUKHOV, N. I. & MEIER, M. N. Nezemnye belichi (Marmotinae). *Fauna SSSR*, Moscow & Leningrad, **3** (2): 1–466.

HINTON, M. A. C. 1900a. On the Pleistocene deposits of the Ilford and Wanstead district, Essex. *Essex Nat.*, Buckhurst Hill, **11**: 161–165.

—— 1900b. The Pleistocene deposits of the Ilford and Wanstead district. *Proc. Geol. Ass.*, London, **16**: 271–281.

—— 1901. Excursion to Grays Thurrock. *Proc. Geol. Ass.*, London, **17**: 141–144.

—— 1907a. On the existence of the alpine vole (*Microtus nivalis* Martins) in Britain during Pleistocene times. *Proc. Geol. Ass.*, London, **20**: 39–58.

—— 1907b. Note on the occurrence of the alpine vole (*Microtus nivalis*) in the Clevedon Cave deposit. *Proc. Bristol Nat. Soc.* (4) **1**: 190–191.

—— 1910a. Some new late Pleistocene voles and lemmings. *Ann. Mag. nat. Hist.*, London, (8) **6**: 34–39.

—— 1910b. A preliminary account of the British fossil voles and lemmings; with some remarks on the Pleistocene climate and geography. *Proc. Geol. Ass.*, London, **21**: 489–507.

—— 1912. Note on the lemming remains from the Arctic Bed at Angel Road. *In*: WARREN, S. H. A Late Glacial stage in the valley of the River Lea. *Q. Jl geol. Soc. Lond.* **68**: 249.

—— 1914. On some remains of rodents from the Red Crag of Suffolk. *Ann. Mag. nat. Hist.*, London, (8) **13**: 186–195, 1 pl.

—— 1915. Note on British fossil species of Apodemus. *Ann. Mag. nat. Hist.*, London, (8) **15**: 580–584.

—— 1920. Description of the rodent teeth. *In*: TRECHMANN, C. T. On a deposit of interglacial loess and some transported pre-glacial clays on the Durham Coast. *Q. Jl geol. Soc. Lond.* **75**: 201.

—— 1921. Note on the remains of small mammals obtained from Aveline's Hole, Burrington Combe, Somerset. *Proc. speleol. Soc.*, Bristol, **1**: 74–78.

—— 1923a. Diagnoses of species of *Pitymys* and *Microtus* occurring in the Upper Freshwater Bed of West Runton, Norfolk. *Ann. Mag. nat. Hist.*, London, (9) **12**: 541–542.

—— 1923b. Note on the rodent remains from Clacton-on-Sea. *Q. Jl geol. Soc. Lond.* **79**: 626.

—— 1924. Notes on the rodent remains from Aveline's Hole. *Proc. speleol. Soc.*, Bristol, **2**: 34–37.

—— 1925. Preliminary note upon the mammalian remains from Merlin's Cave. *Proc. speleol. Soc.*, Bristol, **2**: 156–158.

—— 1926a. The Pleistocene mammalia of the British Isles and their bearing upon the date of the glacial period. *Proc. Yorks. geol. Soc.*, Leeds, (n.s.) **20**: 325–348.

Hinton, M. A. C. 1926b. *Monograph of the Voles & Lemmings (Microtinae) Living and Extinct.* **1** : xvi+488 pp., 15 pls, 110 figs. London, British Museum (Natural History).
—— 1952. *In* : Allison, J., Godwin, H. & Warren, S.H. Late-glacial deposits at Nazeing in the Lea Valley, North London. *Phil. Trans. R. Soc.*, London, B **236** : 169–240.
——, Kennard, A. S. & Newton, E. T. 1900. Contributions to the Pleistocene geology of the Thames Valley. I. The Grays Thurrock area, part 1. *Essex Nat.*, Buckhurst Hill, **11** : 336–370.
—— & White, G. 1902. Note on the occurrence of *Microtus intermedius* in the Pleistocene deposits of the Thames Valley. *Proc. Geol. Ass.*, London, **17** : 414–415.
Jackson, J. W. 1909. On the discovery of the remains of lemmings in Dog Holes, Warton Crag. *Lancs. Nat.*, Darwen, **2** : 227–229.
—— 1910. On the vertebrate fauna found in the cave-earth at Dog Holes, Warton Crag. *Lancs. Nat.*, Darwen, **2** : 323–332.
—— 1912. Additional notes on the Pleistocene fauna of Dog Holes, Warton Crag. *Lancs. Nat.*, Darwen, **4** : 420–422.
—— 1929a. Remains of lemmings in Derbyshire caves. *Naturalist, Hull* **1929** : 105–107.
—— 1929b. Report on the animal remains found in Kilgreany Cave, Co. Waterford. *Proc. speleol. Soc.*, Bristol, **3** : 137–152.
—— 1932. [*Dicrostonyx* in Welsh caves.] *Proc. Dyserth Distr. Fld Club*, Llanfairfechan, **54** [not seen].
—— 1934. The rodent remains from the Pin Hole Cave. *Rep. Br. Ass. Advmt Sci.*, Aberdeen : 256–257.
—— 1947. The Upper Pleistocene fauna and its relation to the Ice Age. *Proc. Lpool geol. Soc.* **19** : 165–183.
* Janossy, D. 1954. Fossile Microtinen aus dem Karpathenbecken. I. Lemminge. *Annls hist.-nat. Mus. natn. hung.*, Budapest, n.s. **5** : 39–48, 1 pl.
* —— 1961. Die Entwicklung der Kleinsäugerfauna im Pleistocän (Insectivora, Rodentia, Lagomorpha). *Z. Säugetierk.*, Berlin, **26** : 1–11.
* —— 1962. Vorläufige Mitteilung über die Mittelpleistozäne Vertebratenfauna der Tarkö-Felsnische (NO-Ungarn, Bükk-Gebirge). *Annls hist.-nat. Mus. natn. hung.*, Budapest, **54** : 155–176.
Johnson, J. P. & White, G. 1900. Some new sections in, and contributions to, the fauna of the river drift of the Uphall estate, Ilford, Essex. *Essex Nat.*, Buckhurst Hill, **11** : 157–160.
* Kaup, J. J. 1839. *Description d'Ossements Fossiles de Mammifères* (&c.) **5** : 91–119. Darmstadt.
Kennard, A. S. 1944. The Crayford brickearths. *Proc. Geol. Ass.*, London, **55** : 121–169.
—— 1945–46. The early digs in Kent's Hole, Torquay, and Mrs Cazalet. *Proc. Geol. Ass.*, London, **56** : 156–213.
Kerney, M. P. 1971. Interglacial deposits in Barnfield Pit, Swanscombe, and their molluscan fauna. *J. geol. Soc.*, London, **127** : 69–93.
* King, W. B. R. & Oakley, K. P. 1936. The Pleistocene succession in the lower parts of the Thames Valley. *Proc. prehist. Soc.*, Cambridge, (n.s.) **2** : 52–76.
* Koenigswald, W. von 1970. Mittelpleistozäne Kleinsäugerfauna aus der Spaltenfüllung Petersbuch bei Eichstätt. *Mitt. bayer. St. Paläont. Hist. Geol.*, Munich, **10** : 407–432.
—— 1972. Sudmer-Berg-2, eine Fauna des frühen Mittelpleistozäns aus dem Harz. *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **141** : 194–221.
—— 1973. Veränderungen in der Kleinsäugerfauna von Mitteleuropa zwischen Cromer und Eem (Pleistocän). *Eiszeitalter Gegenw.*, Ohringen, **23–24** : 159–167.
* Kormos, T. 1934. Neue Insectenfresser, Fledermäuse und Nager aus dem Oberpliocän der Villányer Gegend. *Földt. Közl.*, Budapest, **64** : 296–321.
Kowalski, K. 1966. Stratigraphic importance of rodents in the studies on European Quaternary. *Folia quatern.*, Krakow, **22** : 1–16.
—— 1967. *Lagurus lagurus* (Pallas 1773) and *Cricetus cricetus* (Linnaeus 1758) (Rodentia, Mammalia) in the Pleistocene of England. *Acta zool. cracov.* **12** : 111–122, 24 figs.
* —— 1970. Variation and speciation in fossil voles. *Symp. zool. Soc. Lond.* **26** : 149–160.

Kretzoi, M. 1958. New names for Arvicolid homonyms. *Annls hist.-nat. Mus. natn. hung.*, Budapest, **50** : 55–58.
—— 1965. Die Nager und Lagomorphen von Voigstedt in Thüringen und ihre chronologische Aussage. *Paläont. Abh. Berl.* A **11** : 585–660, 2 pls, 2 figs.
* Kurtén, B. 1969. *Pleistocene Mammals of Europe.* viii + 317 pp. London.
Lamplugh, G. W. 1891. Final report of the Committee . . . appointed for the purpose of investigating an ancient sea-beach near Bridlington Quay. *Rep. Br. Ass. Advmt Sci.*, Leeds : 375–377.
Lankester, E. R. 1864. On new mammalia from the Red Crag. *Ann. Mag. nat. Hist.*, London, **14** : 353–360, pl. 8.
* Laugel, A. 1862. La faune de Saint-Prest près Chartres (Eure et Loire). *Bull. Soc. géol. Fr.*, Paris, (2) **19** : 709–718, 3 figs.
* Lehmann, U. 1953. Eine Villafranchiano-Fauna von der Erpfingen Höhle (Schwäb. Alb). *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, B **1953** : 437–464.
* —— 1957. Weitere Fossilfunde aus dem ältesten Pleistocän der Erpfingen Höhle (Schwäbische Alb.). *Mitt. geol. StInst. Hamb.* **26** : 60–99.
Lydekker, R. 1885–87. *Catalogue of the Fossil Mammalia in the British Museum (Natural History).* **1** (Primates, Chiroptera, Insectivora, Carnivora and Rodentia), 1885, xxx + 268 pp. **5** (Tillodontia, Sirenia, Cetacea, Edentata, Marsupialia, Monotremata and Supplement), 1887, xxxv + 345 pp. London.
Lyell, C. 1840. On the Boulder Formation or drift and associated freshwater deposits composing the mud cliffs of eastern Norfolk. *Lond. Edinb. phil. Mag.*, London, (3) **16** : 345–380, 18 figs.
Major, C. I. F. 1902. [Exhibition of, and remarks upon, some jaws and teeth of Pliocene voles (*Mimomys*, gen. nov.).] *Proc. zool. Soc. Lond.* **1902** (1) : 102–107.
—— 1908a. The mammalian fauna of the Forest Bed. *Geol. Mag.*, London, (5) **5** : 329–330.
—— 1908b. On species of *Castor*, fossil and recent. *Proc. zool. Soc. Lond.* **1908** : 630–635.
* Mandach, E. V. 1938. Skelettreste von *Dicrostonyx groenlandicus* Trail als Inhalt von Raubvogelgewöllen. *Meddr Grønland*, Copenhagen, **112** (4) : 1–54, 22 pls.
* Matthews, L. H. 1952. *British Mammals.* xii + 410 pp., 16 + 48 pls. London.
* Méhely, L. v. 1914. Fibrinae Hungariae. Die ternären und quartären Wurzelzähnigen Wühlmause Ungarns. *Annls hist.-nat. Mus. natn. hung.*, Budapest, **12** : 155–243.
* Miller, G. S. 1912. *Catalogue of the Mammals of Western Europe.* xv + 1019 pp. London, British Museum.
Mitchell, G. F. 1969. Pleistocene mammals in Ireland. *Bull. Mammal Soc. Br. Isl.*, Birmingham, **31** : 21–25.
* ——, Penny, L. F., Shotton, F. W. & West, R. G. 1973. A correlation of Quaternary deposits in the British Isles. *Spec. Rep. geol. Soc. Lond.* **4** : 99 pp.
Montagu, I. 1924. On the remains of Fen Beaver in the Sedgwick Museum. *Proc. zool. Soc. Lond.* **1924** : 1081–1086.
Mullins, E. H. 1913. The ossiferous cave at Langwith. *J. Derbysh. archaeol. nat. Hist. Soc.*, Derby, **35** : 137–153, 6 pls.
Murchison, C. (ed.) 1868. *Palaeontological memoirs and notes of the late Hugh Falconer.* **1** : lvi + 590 pp., 34 pls. **2** : xiii + 675 pp., 38 pls. London.
Nehring, A. 1875. Fossile Lemminge und Arvicolen aus den Diluviallehm von Thiede bei Wolfenbüttel. *Z. ges. Naturw.*, Berlin, **45** : 1–28, pl. I.
Newton, E. T. 1881. Notes on the Vertebrata of the pre-glacial Forest Bed Series of the East of England. *Geol. Mag.*, London, (2) **8** : 256–259.
—— 1882a. The Vertebrata of the Forest Bed Series of Norfolk and Suffolk. viii + 143 pp., 19 pls. *Mem. geol. Surv. U.K.*, London.
—— 1882b. On the occurrence of *Spermophilus* beneath the glacial till of Norfolk. *Geol. Mag.*, London, (n.s. 2) **9** : 51–54, pl. 2.
—— 1890a. On the occurrence of lemmings and other rodents in the brick-earth of the Thames Valley. *Geol. Mag.*, London, (n.s. 3) **7** : 452–455, 8 figs.

NEWTON, E. T. 1890b. On some new mammals from the Red and Norwich Crags. *Q. Jl geol. Soc. Lond.* **46** : 444–453, pl. 18.

—— 1891. The Vertebrata of the Pliocene deposits of Britain. xi + 137 pp., 10 pls. *Mem. geol. Surv. U.K.*, London.

—— 1892. On a skull of *Trogontherium cuvieri* from the Forest Bed of East Runton, near Cromer. *Trans. zool. Soc. Lond.* **13** : 165–175, pl. 19.

—— 1894. The vertebrate fauna collected by Mr Lewis Abbot from the fissure near Ightham, Kent. *Q. Jl geol. Soc. Lond.* **50** : 188–210, pls 10–12.

—— 1899a. [Exhibition of remains of *Mus Lewisi* from Ightham.] *Proc. zool. Soc. Lond.* **1899** : 381.

—— 1899b. Additional notes on the vertebrate fauna of the rock-fissure at Ightham (Kent). *Q. Jl geol. Soc. Lond.* **55** : 419–429, pl. 28.

—— 1902. *Trogontherium* from a Pleistocene deposit in the Thames Valley. *Geol. Mag.*, London, (n.s. 4) **9** : 385–388.

—— 1909. Hamster remains from the Norfolk Forest Bed. *Geol. Mag.*, London, (5) **6** : 110–113.

—— 1916. *Trogontherium* from the Pleistocene of Copford, Essex. *Geol. Mag.*, London, (6) **3** : 322–323, 4 figs.

* NORTON, P. E. P. 1967. Marine Mollusca in the Early Pleistocene of Sidestrand and the Royal Society borehole at Ludham, Norfolk. *Phil. Trans. R. Soc.*, London, B **253** : 161–200.

* OKEN, L. 1815–16. *Okens Lehrbuch der Naturgeschichte. III Zoology* **1** : xxviii + 842 + xviii + iv pp., 40 pls. **2** : xvi + 1270 + (2) pp., 1 tab.; pp. 843–50 (suppl. to **1**).

OSBORN, H. F. 1922. Pliocene (Tertiary) and early Pleistocene (Quaternary) mammalia of East Anglia, Great Britain, in relation to the appearance of Man. *Geol. Mag.*, London, **59** : 433–441.

* OVEY, C. D. (ed.) 1964. The Swanscombe Skull. *Occ. Pap. R. anthrop. Inst.*, London, **20** : xii + 215 pp., 25 pls.

OWEN, R. 1846. *A History of British Fossil Mammals, and Birds.* xlvi + 560 pp., 236 figs. London.

—— 1869. On the distinction between *Castor* and *Trogontherium*. *Geol. Mag.*, London, **6** : 49–56, pl. 3, 4 figs.

PALMER, L. S. 1934. Some Pleistocene breccias near the Severn Estuary. *Proc. Geol. Ass.*, London, **45** : 145–161.

PASQUIER, L. 1972. Étude d'une population de *Mimomys savini* Hinton, 1910 (Arvicolidae, Rodentia) provenant de l'Upper Freshwater Bed (Quaternaire Ancien d'Angleterre). *Mammalia*, Paris, **36** : 214–225.

PEACH, B. N. & HORNE, J. 1917. The bone cave in the valley of Allt nan Uamh (Burn of the Caves) near Inchnadamph, Assynt, Scotland. *Proc. Roy. Soc. Edinb.* **37** : 327–349.

PERNETTA, J. C. 1966. Report on the findings at Etches' Cave, Dowel Dale, Derbyshire. *Newsl. Peakland archaeol. Soc.*, Stockport, **21** : 11–16, 35.

—— & HANDFORD, P. T. 1970. Mammalian and avian remains from possible Bronze Age deposits on Nornour, Isles of Scilly. *J. Zool., Lond.* **162** : 534–540.

* PIKE, K. & GODWIN, H. 1952. The interglacial at Clacton-on-Sea. *Q. Jl geol. Soc. Lond.* **108** : 261–272.

* POMEL, A. 1848. Description de la tête du Castoroides Ohioensis Forster par Wyman. *Archs Sci. phys. nat.*, Geneva, **9** : 165–167.

* REICHSTEIN, H. 1963. Beitrag zur systematischen Gliederung des Genus *Arvicola* Lacépède 1799. *Z. Zool. Syst. EvolForsch.*, Frankfurt a.M., **1** : 155–204.

REID, C. 1890. The Pliocene deposits of Britain. viii + 326 pp., 5 pls, 48 figs. *Mem. geol. Surv. U.K.*, London.

* RZEBIK, B. 1968. *Crocidura* Wagler and other Insectivora (Mammalia) from the Quaternary deposits of Tornewton Cave in England. *Acta zool. cracov.* **13** : 251–263.

SANFORD, W. A. 1870a. On the rodentia of the Somerset caves. *Proc. Somerset archaeol. nat. Hist. Soc.*, Taunton, **1868–69** : 51–57, 1 pl.

SANFORD, W. A. 1870b. On the rodentia of the Somerset caves. *Q. Jl geol. Soc. Lond.* **26** : 124–131.

SAVAGE, R. J. G. 1963. Martin Alister Campbell Hinton, 1883–1961. *Biogr. Mem. Fellows R. Soc.*, London, **9** : 155–170, 1 pl.

—— 1966. Irish Pleistocene mammals. *Ir. Nat. J.*, Belfast, **15** : 117–130.

SCHARFF, R. F. 1906. The exploration of the caves of County Clare. *Trans. R. Ir. Acad.*, Dublin, B **33** : 1–76.

——, COFFEY, G., COLE, G. A. J. & USSHER, R. J. 1903. The exploration of the Caves of Kesh, County Sligo. *Trans. R. Ir. Acad.*, Dublin, B **32** : 171–214, pls 9–11.

——, SEYMOUR, H. J. & NEWTON, E. T. 1918. The exploration of Castlepook Cave, County Cork. *Proc. R. Ir. Acad.*, Dublin, B **34** : 33–72 + map.

* SCHAUB, S. 1930. Quartäre und jungtertiäre Hamster. *Abh. schweiz paläont. Ges.*, Basel, **49** (6) : 1–49, 2 pls.

SCHLOSSER, M. 1902. Beiträge zur Kenntniss der Säugetierreste aus den süddeutschen Bohnerzen. *Geol. palaeont. Abh.*, Berlin, **9** : 117–258, 5 pls.

SCHREUDER, A. 1929. *Conodontes* (*Trogontherium*) and *Castor* from the Tegelen Clay, compared with Castoridae from other localities. *Archs Mus. Teyler*, Haarlem, (3) **6** : 99–320, 16 pls, 16 figs.

—— 1931. *Conodontes, Trogontherium* and other Castoridae. *Palaeont. Z.*, Berlin, **13** : 148–176, 6 figs.

—— 1950. Microtinae from the Middle Gravels of Swanscombe. *Ann. Mag. nat. Hist.*, London, (12) **3** : 629–635.

—— 1951. The three species of *Trogontherium* with a remark on *Anchitheriomys*. *Archs néerl. Zool.*, Leiden, **8** : 400–433, pls 20–23.

* SIDOROWICZ, J. 1964. Comparison of the morphology of representatives of the genus *Lemmus* Link, 1795, from Alaska and the Palaearctic. *Acta theriol.*, Białowieża, **8** : 217–226.

SINGER, R., WYMER, J., GLADFELTER, B. G. & WOLFF, R. G. 1973. Excavation of the Clactonian industry at the golf course, Clacton-on-Sea, Essex. *Proc. prehist. Soc.*, Cambridge, **39** : 6–74.

* SOUTHERN, H. N. (ed.) 1964. *The Handbook of British Mammals.* xxi + 465 pp., 60 pls. Oxford.

* SPARKS, B. W. & WEST, R. G. 1972. *The Ice Age in Britain.* xvii + 302 pp., 44 pls, figs. London.

SPENCER, H. E. P. 1956. The Hoxne mammalian remains. *In* : WEST, R. G. The Quaternary deposits at Hoxne, Suffolk. *Phil. Trans. R. Soc.*, London, B **239** : 265–365.

—— 1964. The contemporary mammalian fossils of the Crags. *Trans. Suffolk Nat. Soc.*, Ipswich, **12** : 333–344.

—— 1966. New mammalian fossils from the Red Crag. *Trans. Suffolk Nat. Soc.*, Ipswich, **13** : 154–156.

STEVENS, E. T. 1869. Drift series – mammalian remains. *In* : *Some Account of the Blackmore Museum* **2** : 109–115. Devizes.

STOPES, C. 1904. Palaeolithic implements from the Shelly Gravel Pit at Swanscombe, Kent. *Rep. Br. Ass. Advmt Sci.*, Southport : 803–804.

STRINGER, C. B. 1975. A preliminary report on new excavations at Bacon Hole Cave. *Gower*, Swansea, **26** : 32–37.

STUART, A. J. 1974. Pleistocene history of the British vertebrate fauna. *Biol. Rev.*, Cambridge, **49** : 225–266.

* SUTCLIFFE, A. J. 1960. Joint Mitnor Cave, Buckfastleigh. *Trans. Torquay nat. Hist. Soc.* **13** (1) : 1–26.

—— 1964. The mammalian fauna. *In* : OVEY, C. D. (ed.), The Swanscombe Skull. *Occ. Pap. R. anthrop. Inst.*, London, **20** : 85–111.

—— & BOWEN, D. Q. 1973. Preliminary report on excavations in Minchin Hole, April–May 1973. *Newsl. Pengelly Cave Stud. Trust* **21** : 12–25.

SUTCLIFFE, A. J. & COLLINGS, H. D. 1972. Gnawed bones from the Crag and Forest Bed of East Anglia. *Suffolk nat. Hist.*, Ipswich, **15** : 497–498.

—— & ZEUNER, F. E. 1962. Excavations in the Torbryan Caves, Devonshire. I. Tornewton Cave. *Proc. Devon archaeol. Explor. Soc.*, Torquay, **5** : 127–145, pls 26–27.

* TURNER, C. 1970. The Middle Pleistocene deposits at Marks Tey, Essex. *Phil. Trans. R. Soc.*, London, B **257** : 373–440.

USSHER, R. J. 1910. Cave hunting. *Ir. Nat.*, Dublin, **19** : 37–43.

——, SEYMOUR, H. J., NEWTON, E. T. & SCHARFF, R. F. 1908. On the Cave of Castlepook, near Doneraile, Co. Cork. *Rep. Br. Ass. Advmt Sci.*, Dublin : 697 ; *Geol. Mag.*, London (5) **5** : 462–463 ; *Ir. Nat.*, Dublin, **17** : 231–232.

* VIRET, J. 1954. Le loess à bancs durcis de Saint-Vallier. *Nouv. Archs Mus. Hist. nat. Lyon* **4** : 1–200, 33 pls.

WARREN, S. H. 1916. Further observations on the Late Glacial, or Ponders End, stage of the Lea Valley. *Q. Jl geol. Soc. Lond.* **71** : 164–182.

—— 1955. The Clacton (Essex) Channel deposits. *Q. Jl geol. Soc. Lond.* **111** : 283–307.

* WEST, R. G. 1961. The Glacial and Interglacial deposits of Norfolk. *Trans. Norfolk Norwich Nat. Soc.* **19** : 365–375.

—— 1968. *Pleistocene Geology and Biology* (&c.). xiii + 377 pp., 16 pls, figs. London.

* —— 1969. Pollen analyses from interglacial deposits at Aveley and Grays, Essex. *Proc. Geol. Ass.*, London, **80** : 271–282.

* —— 1972. Land–sea-level changes during the Pleistocene. *In* : A discussion on problems associated with the subsidence of southeastern England. *Phil. Trans. R. Soc.*, London, A **272** : 87–98.

* ——, LAMBERT, A. & SPARKS, R. W. 1964. Interglacial deposits at Ilford, Essex. *Phil. Trans. R. Soc.*, London, B **247** : 185–212.

* —— & WILSON, D. G. 1966. Cromer Forest Bed Series. *Nature, Lond.* **209** : 497–498.

WHITAKER, W. 1889. The geology of London and of part of the Thames Valley **1**. ix + 556 pp. *Mem. geol. Surv. U.K.*, London.

* WYMER, J. 1957. A Clactonian flint industry at Little Thurrock, Grays, Essex. *Proc. Geol. Ass.*, London, **68** : 159–177.

—— 1962. Excavations at the Maglemosian sites at Thatcham, Berkshire, England. *Proc. prehist. Soc.*, Cambridge, **28** : 329–361.

* —— 1974. Clactonian and Acheulean industries in Britain – their chronology and significance. *Proc. Geol. Ass.*, London, **85** : 391–421.

ZEUNER, F. E. 1945–59. *The Pleistocene Period, its Climate, Chronology and Faunal Successions.* 1st edition (1945), 322 pp. London (Ray Society). 2nd edition (1959), 447 pp., 80 figs. London.

* —— 1954. Riss or Würm? *Eiszeitalter Gegenw.*, Ohringen, **4–5** : 98–105.

ZIMMERMANN, K. 1959. Über eine Kreuzung von Unterarten der Feldmaus *Microtus arvalis*. *Zool. Jb.*, Jena, (Abt. Syst.) **87** : 1–12.

VII. INDEX

The page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure. Tab. 12 faces p. 122.

Acheulean industry 50–1
Africa 82
alder 52
Alice and Gwendoline Caves 68 ; see Edenvale
Allocricetus 66, 86–7, 127
  cf. *bursae* 63–4, 66, **86–7**, 101, tab. 12, 125–6
Allophaiomys pliocaenicus 105–7, 122
alluvial deposits 41, 53, 74, tab. 12 ; see localities
Alopex see fox (arctic)
Alston, E. R. 37
Alveston Fissure 45, 67, 93, 110, tab. 12, 129
amphibia 59
Angel Road 45, 59, 88, tab. 12
Anglian 41–2, 47–8, 76, 106, 123
Antian 41, 43

Apodemus 81–4
flavicollis 62, 67, 70–1, **83–4**, tab. 12, 129
lewisi 83–4
sylvaticus 48, 52–3, 59, 61, 63–72, **81–3**, tab. 12, 122–7, 129
whitei **52**, 81–3
sp. 69, 81, 83
Arctic Freshwater Bed 48
Arvicola 37–9, 52–3, 64, 69, **99–102**, 103–5; see *Mimomys–Arvicola* lineage
faunas 61, 100–1, tab. 12, 124, 127
abbotti 103
agrestis 109
amphibia 37, 102–3
amphibius 95, 98, 102–3
terrestris 103
arvalis 37, 106
arvaloides 106
bactonensis 48, 100, 102, 104
cantiana 48, 51–3, 57, 60–2, 69, 72, 100*, 101, **102–3**, 104–5, tab. 12, 122–5
cantiana-terrestris transition form 60, 64–5, 67, 69, 72, 100*, 101–2, **103**, 125–7
cantiana/terrestris complex **104–5**
glareolus 92
greeni 48, 62, 100, 102, 104–5
gregalis 107, 118
gulielmi 37, 87
intermedia 37, 95, 98–9
praeceptor 53, 100, 102, 104
pratensis 92
ratticeps 117
riparia 92
sapidus 99
terrestris 37, 59, 62, 64–5, 69–71, 99, 100*, 101–2, **103–4**, 105, tab. 12, 127–9
sp. 54, 63–7, 69, 72, 125
Asia 76, 80, 82, 84–5, 87, 89, 94, 100, 105, 112, 118, 120–1
Asia Minor 78
Astian 41, 43, 78, 81
Austria 106, 109, 118
Aveley 45, 49–50, 53, 55–7, 69, 93, 101–2, tab. 12, 125–6, 130
Aveline's Hole 45, 70–1, 81, 83–4, 88, 90, 93, 104, 110, 112, 117–8, tab. 12
Avon, Warwickshire 72
Azov Sea 79

Bacon Hole 45, 67, 81, 93, 104, 110, 117
Bacton 45, 46*, 48, 78–9, 104, tab. 12
Baker's Hole 49–50, **59–60**
cold stage 127
Ballymote 45
Ballynamintra Cave 45, 68, 82, 88, tab. 12
bank vole see *Clethrionomys*
Banwell Cave 45, 66, tab. 12, 126
Barnfield Pit 51–3, 80, 90, 92–3, 101–2, tab. 12, 123–4, 130; see Swanscombe
Barntick Cave 68, 82; see Edenvale
Barrington 45, 69, 72, 101–3, 110, tab. 12, 126
Bath 112
Baventian 41, 43
Beaker Age 71
bear 60, 62–3, 65
brown 63–4, 68
Bear Stratum (Tornewton Cave) 63–4, 66
beaver 37, 39, 81; see *Castor*, *Trogontherium*
Beccles 45
Beckford 45, 72, 113, tab. 12, 128–30
Beestonian 41, 47–8, tab. 12
Belgium 83, 96
Bering Strait 92, 120
Berkshire 45; see Thatcham
Berwickshire 45; see Middlestots Bog
Betfia, Romania 95
Bhukhureea, Mrs M. N. M. 130
Biedermann'scher Stbr. 101
birch 56
birds of prey 60, 69; see owls
Bishop, M. J. 108, 129
bison 56
Black Mould (Kent's Cavern) 62
Blackmore, H. P. 37
Bleadon Cave 45, 70–1, 76–7, 110, 117, 119, tab. 12
Bobbitshole 45, 69, 72, 104, 110, tab. 12, 127
Bos see ox, giant
bovids 62–3
Bramerton 43, 45, 46*, 95, 98, tab. 12
Bramwell, D. 130
Brandon 89
Brassington 45
Brean Down 45, 72, 88, 110, tab. 12
Breccia (Kent's Cavern) 62, tab. 12
brickearth 48, 50, 53–4, 56–8
Briggs, D. J. 72, 113
Bristol Museum 107
Bristol University Spelaeological Society 81, 88, 91
British Museum (Natural History) 36, 58, 60–1, 66, 72, 97–8, 102, 107, 113, 116, 119
Brixham Cave 45, 70–1, 93, 104, 110, 112–3, 119, tab. 12
Bronze Age 128; see Nornour

Buckfastleigh 45
Buckinghamshire 45 ; see Marlow
Burchell, J. P. T. 60
Burrington 45
Burwell 45
Buxton 45

Calcareous Group (Westbury) 60–1, 122, 124
Cambridge Fens 45, 72, 80, tab. 12
Cambridge, P. 96 (footnote)
Cambridgeshire 45 ; see localities
Canada 92 ; see North America
Canis see wolf
lupus mosbachensis 61
Cappagh 45
carbon-14 (^{14}C) dated sites 36, 58, 68–9, 72, 113, tab. 12, 127–9
Carnforth 45
Carrant Brook 72
Carreck, J. N. 50, 54, 56, 59–60, 69, 89, 91, 93, 104, 110, 127, 129
Castlepook Cave 45, 68–9, 82, 88, 91, tab. 12, 129
Castletownroche Cave 45, 68–9, 88, 91, tab. 12
Castor 39, 54, 69, 79–81
europaeus 79
fiber 37, 43, 47–8, 52–3, 61–2, 70–3, **79–81**, tab. 12, 122–8
plicidens 81
plicidens 79–81
trogontherium 78
veterior 79–80
sp. 53, 79
Castoridae 78–81
Catacombs 68 ; see Edenvale
Caucasus 83, 115
cave deposits 41–2, 56, 58, 60–9, tab. 12 ; see localities
disturbed 67
Cave Earth (Kent's Cavern) 62, 101, 104, tab. 12
Cervus see red deer
Chaline, J. 39
channels, buried 48–9
Cheddar 45
China 82, 87
Chinese Turkestan 121
Chudleigh (Fissure) 45, 70–1, 88, 90, 93, 104, 110, 117, 119, tab. 12
Citellus 75, 128 ; see *Spermophilus*
erythrogenoides 75
erythrogenys 75
eversmanni 75
nogaici 75
(*Colobotis*) *superciliosus* 75, 77
(*Urocitellus*) *polonicus* 75–6
primigenius 75
sp. 76
Clacton-on-sea 45, 49*, **52–3**, 78–80, 93, 101–2, 109, tab. 12, 123
Clactonian industry 50–1, 53
Clare, Co. 45 ; see Edenvale Caves
Clarke, Dr A. S. 130
classification 73–121
'clay pebbles' 47
Clethrionomys 92–4
glareolus 37, 48, 52–3, 59–67, 70–2, **92–4**, tab. 12, 122–7, 129
nageri 94
sp. 53, 67, 92
Clevedon Cave 45, 66, 93, 111, 115–7, tab. 12, 126
Coelodonta see rhinoceros, woolly
Coffey Cave see Keshcorran
Colchester 45
Colobotis see *Spermophilus superciliosus*
Connaberry 45
Conodontes Boisvilletti 78
coombe rock 50, 59–60 ; see solifluxion deposits
Coope, G. R. 72, 113, 127–8, 130
Copford 45, 69, 78–9, tab. 12, 123
Coralline Crag 41, 96 (footnote)
Corbet, Dr G. B. 58, 72, 93, 110–1, 113, 115, 129
Corbicula Bed 54, 89, 92, 125
Cork, Co. 45 ; see localities
Corstorphine 45, 73, 88, 110, tab. 12
Covehithe 43, 45, 46*, 96, tab. 12
Cow Cave 45, 66, 115, tab. 12, 126
Cowside Cave No. 3 45, 70–1, 104, 110, 118, tab. 12
Cranbrook, Earl of 98
Crags 37, 41–2, 60 ; see Coralline, Icenian, Norwich, Red, Shelly and Weybourne Crags
Crayford 38, 45, 49*, 50, **54**, 60, 64, 66, 75, 92, 101–3, 111, 115, 117–8, tab. 12, 125–7
Gravel 50
Creag nan Uamh Cave 45, **68**, 88, 110, 118, tab. 12
Cresswell 45 ; see Pin Hole Cave
Cricetidae 85–121
Cricetulus migratorius 87
Cricetus 48, 85–6, 127

cricetus 48, 63–6, **85–6**, tab. 12, 122, 124–6
major 86
runtonensis 86
runtonensis 86
songarus 37, 86–7
vulgaris Runtonensis 37, 85
Crocidura 64, 126
Crocuta see hyaena
Cromer 45, 46*, 78, 98, tab. 12
Cromer Forest Bed Series (Norfolk) 36–7, 40–1, 43, **46–8**, 74, 77, 79, 85, 94, 97–8, 105, tab. 12
Cromerian stage 40–1, 47, 60–2, 69, 78, 82–3, 85, 93, 96, 98, 101, 105–8, 114, 116, tab. 12
sensu stricto 47–8, 52, 61–2, 73, tab. 12, 122–3
Currant, A. P. 130
Cyrnaonyx 64, 126
Czechoslovakia 76, 86–7, 89, 96–9, 106, 109, 114, 116

Dama see fallow deer
deep-sea cores 40
deer see fallow, giant, red deer, reindeer, &c.
Denbighshire 45 ; see Lynx Cave
Denmark 113
Derbyshire 45 ; see localities
Devensian 41–2, 115, tab. 12, 127–8
Devon 45, 126 ; see localities
Diabroticus Schmerlingi 78
Dicerorhinus see rhinoceros, narrow-nosed
etruscus 61, 69
hemitoechus 56
kirchbergensis 56
Dicrostonyx 67, 69, 72–3, 87–90, 92, 111, 122–3, 127–9
gulielmi 87, 90
henseli 87, 90
hudsonius 90
simplicior 89
torquatus 37, 54, 59, 62–8, 70–2, **87–90**, 91–2, tab. 12, 125–6, 128
sp. 61, 87, 89, 124
Dierden's Pit 51 ; see Swanscombe
'Diluvium' (Tornewton Cave) 62–4, 66, 110, 117
Dipoides Lydekkeri 78
Diss 45 ; see Hoxne
distribution 73–121
Dnepr, river 121
Dog Holes Cave 45, 70–1, 77, 81, 88, 90, 93, 104, 109–10, 112–3, 117, 119, tab. 12
domestic animals 84
Domnitz 42
Doneraile 45
dormouse see *Muscardinus, Glis*
Dove Holes 60
Dowel Cave 45, 70–1, 74, 82–3, 88, 91, 93, 117, 119, tab. 12, 128
Dowel Dale 45 ; see Dowel Cave, Etches' Cave
Drepanosorex savini 101
Droitwich 45

Earl Sterndale 45
East Anglia 42, 46*, 98 ; see localities
deposits in 42–8, 69, 72
East Runton 38, 45, 46*, **47–8**, 78–80, 96, 98, tab. 12, 122
East Wickham 115
Easton Bavents 43, 45, 46*, 95, 98, tab. 12
Ebbsfleet 49–50, **59–60**
Eburonian 41, 43
Edenvale Caves 45, 68, 82, 88, tab. 12
Edinburgh 45 ; see Corstorphine
Edmonton 48, 49*, **59**
Edrom Parish 45 ; see Middlestots Bog
Eemian 40–2, 100
Elder Bush Cave 45, 70–1, 88, 91, 93, 104, 110, 117, tab. 12
elephant, straight-tusked 56–7
Elsterian 41, 61, 100
Ennis 45
Eocene 43
Eppelsheim 76
Equus see horse
mosbachensis 61
Erith 38, 45, 49*, 50, **54**, 75, 87, 89–90, 92, 115, 117, tab. 12, 125
Erkenbrechtsweiler 101
Erpfingen 1 and 2 101
Essex 45 ; see localities
Etches' Cave 45, 70–1, 83, 88, 91, 117, tab. 12, 128
Europe, continent of 36, 39, 43, 54, 74, 76–8, 80, 82–5, 87, 89, 92, 94, 97, 99, 105–8, 112–4, 116, 118, 120–2, 124, 126–8
Evans, P., half-cycles 40, 42, 127
Evotomys glareolus 92
harrisoni 92, 94
intermedius 95, 97–8
kennardi 92, 94
nageri 94
sp. 92, 94

Falconer, H. 37
fallow deer 56, 63

Felis see lynx
gombaszoegensis 61
Felixstowe 45, 46*, 78
field-vole see Arvicola
Finland 112
fir cones, gnawed 74
Fisherton 45, 72, 76, 88, 115, 117, tab. 12
Fitch, Mr 96 (footnote)
Flandrian 41, 59, tab. 12
Flint bed 47
Flintshire 45 ; see Gwaenysgor Cave
Floodplain Terrace complex (Thames) **54**, 55–8
footprints 51
Forest Bed 42, 46*, 48, 53 ; see Cromer
Forest of Dean 115
fox, arctic 72
Fox Hole Cave 45, 70–1, 88, tab. 12, 128
France 74, 76, 78–9, 83, 87, 89, 95–9, 105, 109, 118, 120–1, 127

Geldeston 45, 46*, 98
geological background 40–2
Geological Society of London 40, 50, 55
Georgia 106, 116
Germany 76, 79, 87, 92, 96–9, 106, 109, 114, 116, 118, 124
giant beaver see *Trogontherium*
giant deer 68
Gippingian, Gipping cold stage 41, 56
glacial till 48
Glamorganshire 45 ; see Penard
Gliridae, glirids 43, 77–8
Glis glis 129
Gloucestershire see Alveston Fissure
glutton 63, 126
Glutton Stratum (Tornewton Cave) 63–6, 82, 85–6, 88–90, 92–3, 101–3, 110–1, 115, 117, 120, tab. 12, 125–6
cold stage tab. 12, 125, 127
Gough's Cave 45, 66, 104, 110, 115, 117, tab. 12, 126
Grays Thurrock 38, 45, 49*, 50, 53–4, 57, 69, 80–1, 93, 101–3, 109, 111, 115, tab. 12, 125–6
Great Doward Cave 45, 70–1, 77, 81, 88, 91, 93, 110, 117, 119, tab. 12
Green, Rev. C. 48
Greenland 92
Gromov, I. M. 75, 77
ground squirrels see *Spermophilus*
Gulo see glutton, wolverine
Günz, Günz–Mindel 76
Gwaenysgor Cave 45, 70–1, 81, 88, 93, tab. 12

Hackney (Marshes) 45, 48, 49*, **59**, 88, tab. 12
hamster see *Cricetus*, *Allocricetus*
Happaway Cave 45, 70–1, 82–3, 93, 104, 110, 119, tab. 12
Happisburgh 45, 46*, **47–8**, tab. 12
Harborough Cave 45, 70–1, 91, tab. 12
Harkstead 45, 69, 72, 102–3, 110, 117, tab. 12, 125
harvest mouse see *Micromys*
Hay Wood Rockshelter 45, 70–1, 80, 118, tab. 12
Helmsley 45
Heppenloch 101
herbivores, large, trampling by 54
Herefordshire 45 ; see localities
Hertfordshire 45 ; see localities
Hessle 45, 69, 102, 104, tab. 12
High Wheeldon Hill 45 ; see Fox Hole Cave
hillwash 49 ; see Northfleet
Hinton, M. A. C. 35–40
rodent faunas 40–1
hippopotamus, *Hippopotamus* 50, 56–9, 63, 67, 69, 86, 93, 102, 121, 125–7
history of rodent faunas 121–9
Hitchin 45, 69, 81, 93, tab. 12
Holland 43, 79, 83, 96–8, 116, 118
Holocene 41, 59–60, 62–4, 67, 70–3, 77, 80, 82–3, 93, 100, 102, 104, 113, tab. 12, 128–9
Holsteinian Interglacial 40–2, 79, 83, 95, 105, 124
Homo, hominids 51 ; see industries, man
Homotherium 62
latidens 61
Hooker, J. J. 130
hornbeam 56
horse 56, 63, 72
Hoxne 42, 45, 69, 78–9, 81, 90, 92, 104, tab. 12, 123, 130
Hoxnian Interglacial 40–2, 52–3, 55–6, 65, 69, 78–80, 82, 92–3, 100–1, 104–8, 110, 116, tab. 12, **123**, 125
Hull see Kingston-upon-Hull
Hunas 101
Hundsheim 61, 101
Hungary 74, 76, 87, 89–90, 92, 95–8, 106, 109, 114, 116, 118, 120
Huntspill Cut 45, 73, 118, tab. 12 ; see Somerset
Hutton Cave 45, 58, 66–7, 86–7, 90, 93, tab. 12, 125–6
hyaena 62–3, 67, 69
Hyaena Stratum (Tornewton Cave) 63–6, 104, 110, 121, tab. 12, 125–6

Hypudaeus bucklandii 109
  spelaeus 103
Hystrix 43, 122

Iberian peninsula 99 ; see Spain
ice covering Britain 113
ice wedges 58
Icenian Crag 41, **43**, tab. 12, **122**
Ightham Fissures 37–8, 41, 45, 67, 76–7, 81, 83–4, 88, 91, 93–4, 101, 104, 110, 112–3, 117, 119, tab. 12
Ilford 45, 49–50, 53, 55–8, 60, 69, 80, 103, 109, tab. 12, 125–7
Inchnadamph 45, 67 ; see Creag nan Uamh Cave
Ingress Vale 51–2, 79, 81, 93, 100–2, tab. 12, 123–4 ; see Swanscombe
insects 36, 58, 72, 113, 127–8
Institute of Geological Sciences Museum 104
Ipswich 45, 72
Ipswich Museum 72, 97, 103–4, 110, 117
'Ipswichian' 57, 63, **67**, 69, 72, tab. 12, 125–7
Ipswichian stage (interglacial) 40–2, 50, 53–7, 82, 91, 124–5, 127
Ireland 42, 91, 129 ; see counties
  caves 68–9
  rodents in 121
  voles in 111–2
Iron Age 84 ; see Staple Howe
Isleworth 45, 48, 49*, **58**, 117, 119, tab. 12, 128
Italy 95, 97–8, 106, 114 ; see Val d'Arno

Jewell, Dr J. 130
Joint Mitnor Cave 45, 56, 67, 82, 93, 101–3, 110–1, tab. 12, 126
  interglacial tab. 12, 125–6

Kadzielnia 98
Kalkberg, Nagyhársanyberg 76
Kent 45, 50 ; see localities
Kent's Cavern 45, 60, **61–2**, 80, 83, 88, 91, 93, 101, 104, 107, 110, 117, 119, tab. 12, 122
Kerney, M. P. 51, 60, 63
Keshcorran Caves 45, 68, 82, 89, tab. 12
Kessingland 45, 46*, 78–9, 98, tab. 12
Kilgreany Cave 45, 68–9, 82, 84, 89, 111, tab. 12
King Arthur's Cave 45, 70–1, 88, 110, 117, 119, tab. 12
Kingston-upon-Hull 45 ; see Hessle
Kinlock 45
Kirkdale Cave 45, 56, 67, 81, 93, 104, 110, tab. 12
Koenigswald, W. von 36, 39, 64, 67, 69, 101, 129
  Mimomys–Arvicola faunal groups of 100–1, tab. 12, 124, 127
Koněprusy 101
Kopet-Dag 115
Kyson 45, 96

Lagurus 120–1, 127
  lagurus 63–6, **120–1**, tab. 12, 125–6
Lancashire 45 ; see Dog Holes Cave
Langwith Cave 45, 70–1, 74, 76, 82, 84, 88, 91, 93, 104, 110, 112, 117, 119, tab. 12
Last Glaciation 50, 54, 56, 58–60, 62–4, 67–72, 76, 82, 89–94, 102, 104, 111, 113, 118–21, 126, **127–8**, 129
Last Interglacial 40, 42, 50, 54–5, 56*, 59, 80, 89, 93, 102, 104
last interglacial 65, 78
Lea Valley 38, 41, 48–60, 49*, **58–9**, 128–9 ; see Nazeing, Ponders End, Water Hall Farm, &c.
Lebanon 115
lemming 54, 64, 67, 122, 127–9 ; see *Lemmus*, *Dicrostonyx*, *Lagurus*
Lemmus 37, 67–8, 90–2, 123–4, 127–9
  lemmus 54, 59, 62–6, 68, 70–1, **90–2**, tab. 12, 125–6, 128
  norvegicus 37, 90
  torquatus 87
  sp. 52, 61, 69, 90, 122–4
Levallois industries 49–50, 54
Levaton Cave 45, 67, 70–1, 82, 104, 110, 112, 117, 119, tab. 12, 128
Limerick, Co. 45 ; see Red Cellar Cave
lion 56, 63
Little Thurrock 50
localities with fossil rodents 42–73, 44–5*
Loch of Marlee 45, 73, 80, tab. 12
London 48, 58 ; see Hackney, Angel Road, &c.
Lough Gur 45
Lower Crayford Brickearth 50
Lower Loam (Swanscombe) 42, 52, 102, 108, 116, 123–4, 130
Lower Thames Valley province 48
Lowestoftian 41, 123
Ludhamian 41
lynx 68
Lynx Cave 45, 70–1, 82, 88, 110, 118, tab. 12

MacEnery, J. 62
Macoma balthica 43
Main Chamber see Tornewton Cave
Major, C. I. Forsyth 75
Male, H. C. 66
mammals other than rodents 56, 60, 72 ; see names
mammoth 50, 56-60, 62, 67-9, 72, 87, 129
Mammuthus 59 ; see mammoth
primigenius 50
trogontherii 50, 56
man, introductions to Britain by 83-4, 129
remains, human 111
Marlow 45, 48, **58**, 113, 117, tab. 12, 129
mastodon 43
Mauer 61, 101
Mayhew, D. 130
Mediterranean 115
Medway, Upper Floodplain Terrace of 54
Megaceros see giant deer
melt-water deposits 59-60
Menapian 41
Mendips see Bleadon Cave, &c.
Merlin's Cave (=Wye Cave) 45, 70-1, 88, 91, 93, 101, 104, 110, 117, 119, tab. 12
Mesolithic 62, 128 ; see Star Carr, Thatcham
Micromys 66, 84
minutus 65, **84**, tab. 12, 129
sylvaticus 81
Microtinae 37-8, 43, 107, 111
Microtius (*Pitymys*) *arvalidens* 106
Microtus 69, 105, **107-8**, 108-20
agrestis 37, 53-4, 58-9, 62-9, 72, 108, **109-12**, 113, 119, tab. 12, 125-7, 129
neglectus 109
of *agrestis* group 53
agrestoides 109, 111
anglicus 60, 118-20, 128
arvalinus 48, 52, 61, **108-9**, 110-1, tab. 12, 122-4
arvalis 58, 60, 72, 108-9, **112-3**, tab. 12, 127-8
sp. (*arvalis/agrestis* group) 52, 60, 70-1, 108, **109**, 111
corneri 109, 112-3
eversmanni 120
glareolus 92
gregalis 58-60, 62-4, 66, 70-1, 107, 113, **118-20**, tab. 12, 126-8
intermedius 102
malei 114-6, 118
nivalinus 114
nivalis 37, 54, 59-60, 63-6, 72, **114-6**, tab. 12, 125-7
nivaloides 48, **114**, tab. 12, 122-4
oeconomus 37, 54, 58-9, 62-3, 65-8, 70-3, 108, 113, 115-6, **117-8**, tab. 12, 125-8
orcadensis 112-3
ratticepoides 48, 52, **116-7**, 118, tab. 12, 122-4
ratticeps 68, 116-7
subnivalis 114
tianschanicus 120
sp. 66, 69
(*Pitymys*) *arvalidens* 105-6
sp. 106
Middle East 100
Middle Terrace of Thames interglacial tab. 12, 125, 127
Middlesex 45 ; see Isleworth, Angel Road, Ponders End
Middlestots Bog 45, 73, 80, tab. 12
Midlothian 45 ; see Corstorphine
Mimomys 60, 95-100
cantiana, cantianus 100, 102
intermedius 98-9
majori 98-9
milleri 98-9
newtoni 43, 47, **97-8**, tab. 12
petenyi 97
pliocaenicus 43, 47, **95-6**, tab. 12, 122
polonicus 96
reidi 43, **97**, tab. 12, 122
savini 47-8, 52, 69, **98-9**, 100-1, 105, tab. 12, 122-4
fauna tab. 12, 124 ; see *Arvicola*
sp. 43
Mimomys–Arvicola lineage 36, 100, tab. 12, 129
Minchin Hole 45, 67, 103, 110, tab. 12, 127, 129
Mindel 76
Miocene 43
Mitchell, Professor G. F. 130
mollusca 43, 51-2, 54, 56, 58, 63, 125
Monastirian, Late 40, 42, 50, 55
Main 42, 50, 55
Mongolia 121
'monkey gravel' 48, 73, 122
Mosbach 61, 101, 122
multituberculate origin of rodents 38
Mundesley 45, 46*, 48, 75-6, 78-9, tab. 12, 122
Arctic Bed tab. 12, **123**
Muridae, murids 43, 81-4
Murston 45, 88, tab. 12
Mus 84
Abbotti 83
Lewisi 83

musculus 81, **84**, tab. 12, 129
songarus 86
sylvaticus 81
sp. 81
Muscardinus 48, 77–8
avellanarius 67, 70–1, **77–8**, tab. 12, 129
Myodes lemmus 90
torquatus 87

narrow-skulled vole see *Microtus gregalis*
Nazeing 45, 48, 49*, **59**, 82, 88–9, 91, 93, 104, 118–9, tab. 12, 128
Neolithic 62, 83
Netherlands see Holland
Newhall Caves 68 ; see Edenvale
Newton, E. T. 37
Norfolk 38, 42, 45–6, 113 ; see localities
Nornour 45, 73, 118, tab. 12
North America 89–90, 92, 94, 118
Northfleet 45, 49*, 50, **59–60**, 93, 103, 110, tab. 12, 126
Norwich Crag 38, 41, 43, 46*, 47, 78, 95–8 ; see Icenian Crag
Norwich Museum 96 (footnote)

oak 56
Orkney Islands 109, 112–3
Orkney vole 112 ; see *Microtus arvalis*
Orsett Road 50, 53
Ostend (Norfolk) 45, 46*, 48, 53, 74, 101–2, 104, tab. 12, 123
Forest Bed 47–8, 53, 74–5, 92, 122–3
otter, clawless 64, 126 ; see *Cyrnaonyx*
Otter Stratum (Tornewton Cave) 36, 64–5, 101–3, tab. 12, 126
Overstrand 45, 46*, 78, tab. 12
Owen, R. 37
owls 69, 112
ox, giant 56
Oxfordshire 45 ; see Sugworth

palaeobotany 39–40, 46–8, 55, 57, 59, 124–7 ; see pollen, plants
Palaeolithic 62–3, 66, 71
Palaeoloxodon antiquus 59 ; see elephant, straight-tusked
Palestine 105
Panthera see lion
Parapodemus coron. 101
Paston 45, 46*, 78, tab. 12
Pastonian (Forest Bed) 41, 43, **47–8**, 78–9, 96, 98, tab. 12, **122**
Peak District 36
Peakland Archaeological Society 67, 128, 130
Penard 45
Penkridge 89
Penultimate Glaciation 42
'penultimate' Glaciation 54, 56, 59, 64–5, 112, 114, 121, 125
Perpignan 78
Persia 105
Perthshire 45 ; see Loch of Marlee
Petersbuch 101
Phodopus 87
sanfordi 86
songorus 86–7
Picken's Hole 45, 70–1, 76, 117, 119, tab. 12, 128
Pin Hole Cave 45, 70–1, 76–7, 82–3, 88, 91, 93, 104, 110, 117, 119, tab. 12
pine 52, 56
pine vole see *Pitymys*
Pitymys 105–8
arvalidens 105
arvaloides 48, 52, 105, **106**, 107, tab. 12, 122–4
gregaloides 48, 61–2, 105–6, **107**, tab. 12, 122–4
sp. 69
plants 53, 58, 122, 127 ; see palaeobotany
Pleistocene 67, 74, 82–5, 87, 91–2, 112, 121–9, tab. 12
generalized British sequence 41
Lower 43, 60, 98, 121
lower middle 80, 87, 89, 92, 94–5
Upper 83
Pliocene 41, 43, 112, 122 ; 'Pliocene' 37, 40
Pliomys 95, 123
episcopalis 61, **95**, 101, tab. 12, 122, 124
lenki 101
Plumpstead 115
Plunkett Cave 68 ; see Keshcorran
Poland 76, 87, 89, 92, 96–8, 106, 116
pollen 36, 52, 55–6, 89, 128–9 ; see palaeobotany
zonation of 'Ipswichian' sites 56*, 57–8
Ponders End 45, 48, 49*, 50, **59**, 88, tab. 12
post-Ipswichian 67
post-Pleistocene 68, 73 ; see Holocene
'preglacial' deposits 37
pre-'Ipswichian' 65–7
Prestatyn 45
Přezletice 101
Pyrenees 115

radiocarbon dating see carbon-14
Rangifer see reindeer
rat see *Rattus*
Rattus 84
norvegicus **84**, tab. 12, 129
rattus 67, 70–1, 74, **84**, tab. 12, 129
Red Cellar Cave 45, 68, 89, tab. 12
Red Crag 41, **43**, 46*, 78–80, 95, tab. 12, **122**
basal nodule bed 43
red deer 56, 63, 67
reindeer 58, 63, 67–9, 72, 126
Reindeer Stratum (Tornewton Cave) 63–6, 88–9, 93, 101, 104, 110, 117, 119, tab. 12
Reuverian 41
rhinoceros 56, 59, 63
narrow-nosed 63
woolly 62, 67, 69, 72
Riss 42, 76, 100, 112, 121
Rodent Earth (Westbury) 60–1, 122, 124
rodent localities on British mainland tab. 12
Romania 92, 95–6, 109, 114, 116
Romano-British 71
root vole see *Microtus oeconomus*
Rowberrow Cavern 45, 70–1, 82, 88, 93, tab. 12
Russia 76, 87, 95–8, 106, 116

Saale 42, 50
Saalian 41
sabre-toothed cat 62 ; see *Homotherium*
Saint-Prest, Chartres 79
St Vallier, France 81
Salisbury 45
Salwarpe river 72
Sanford, W. A. 37
Savin collection 97
Scandinavia 92, 112–3 ; see Sweden, &c.
Scarborough 45
Scarcliffe 45 ; see Langwith Cave
Scilly Isles 45, 73, 118, tab. 12, 128 ; see Nornour
Sciuridae 73–7
Sciurus 73–4 ; see squirrel
vulgaris 67, 70–1, **74**, tab. 12, 129
whitei 48, **73–4**, tab. 12, 122, 124
hungaricus 74
Scotland 73, 80, 128 ; see localities
caves in 67–8, 118
Sealy, D. L. F. 130
Selsey 45, 69, 80, tab. 12
Settle 45
Seven Kings Station 55–6, 58
Severn river 72
Shell Cottages, Thorpe, Aldringham 96 (footnote)
Shelly Crag (East Runton) 38, 41, 47
shrew, white-toothed 64–5, 126 ; see *Crocidura*
Siberia 96–8, 105
Sieveking, G. de G. 60
Siliceous Group (Westbury) 60–1, 124
silver fir 56
Simons, J. 58, 66, 130
Singer, Dr R. 130
Sizewell 43, 45, 46*, 78, 95, 97, tab. 12
Sligo, Co. 45 ; see Keshcorran Caves
snow vole see *Microtus nivalis*
solifluxion deposits 59–60
Somerset 45 ; see localities
caves 37
Levels see Huntspill Cut
Sorex runtonensis 101
savini 101
Soviet Union see Russia
Spain 87
Spencer, H. E. P. 96 (footnote), 130
Spermophilus 48, 54, **75**, 76
altaicus 75–6
citillus 76
eversmanni 75–6
erythrogenoides 37, 75–7
erythrogenys 75
sp. 75, 128
(*Colobotis*) *superciliosus* 70–2, 75, **76–7**, tab. 12, 127
(*Urocitellus*) *parryi* 76
primigenius 54, **75–6**, 77, tab. 12, 125–7
undulatus 76
squirrels 48, 74 ; see *Sciurus*
Staffordshire 45 ; see Elder Bush Cave
Stalagmite (Kent's Cavern) 62
Staple Howe 45, 72, 80, tab. 12
Star Carr 45, 73, 80, tab. 12, 128
Steinheim an der Murr 124
Stenocranius 120 ; see *Microtus gregalis*
steppe lemming see *Lemmus lemmus*
Stoke Tunnel Beds 45, 72, 103, tab. 12
Stuart, A. J. 39, 60, 69, 72, 81, 93, 102–4, 110, 117, 129
studies, history of 37–40
Stutton 45, 69, 72, 81, 101–3, 110, tab. 12, 125
Sudmer Berg 2 101
Suffolk 42–3, 45 ; see localities
Sugworth 45, 69, 98, tab. 12
Süssenborn 101
Sussex 45 ; see West Wittering, Selsey

Sutcliffe, Mrs A. J. 130
Sutherland 45 ; see Creag nan Uamh Cave
Sutton 43, 45, 46*, 79, tab. 12
Swaffley 45
Swanscombe 36, 38–9, 42, 45, 49*, 50, **51–2**, 53, 59, 78–81, 83, 90, 92–3, 100–2, 108–11, 115–6, tab. 12, 123–4
Swanton Morley 45, 69, 72, 81, 93, 101–3, tab. 12, 126
Sweden 78, 83
Switzerland 87, 89, 118, 120
Symond's Yat 45

Talpa europaea 101
  minor 101
Taplow terrace 55
Tarkö 61, 74, 101
terrace deposits 41–2, 48–60, tab. 12 ; see Thames
Thames 48–60, 49*, 62
  High Terrace 38, 41, 49, 51–3 ; see Swanscombe
  Lower **51–8**
  Middle Terraces 36, 38, 41, 49, 55, 57, 125
    early **53**
    interglacial see Middle Terrace of Thames interglacial
    late **54**, 125
  Middle Terrace/Floodplain Terrace problem **55–8**
  Third Terrace 38, 41, 54, 55
  Upper **58**
  Upper Floodplain Terrace 55–8
Thatcham 45, 73, 80, 104, tab. 12
Thorpe, Aldeburgh, Suffolk 96 (footnote)
Thorpe, Norfolk 43, 45, 46*, 78, 96 (incl. footnote), tab. 12
Thorpeness 96 (footnote)
Thurnian 41, 43
Tiglian 41, 43, 78, 83, 96–8, 122
tooth-enamel 81, 100
Torbryan 45
Tornewton Cave 36, 45, **62–5**, 66–7, 81, 84–90, 92–3, 101–4, 110–1, 115, 117, 119–21, tab. 12, 125–6
Torquay 45
Trafalgar Square 55–8, 127
Treacher collection 58, 113
Trimingham 43, 45, 46*, 97, tab. 12
Trogontherium boisvilletti 43, 47–8, 52–3, 69, **78–9**, tab. 12, 122–4
  cuvieri 37, 53, 78–9
  minus 37, 43, **78**, 122
  sp. 78
Turner, C. 54

Ukraine 74, 76, 114
Uphall Estate 109
Uphill Cave 45, 70–1, 91, 119, tab. 12
Upnor 45, 49*, 54, 80, tab. 12
Upper Freshwater Bed (West Runton) 38, 41, 48, 52, 73, 81, 83, 85, 93, 97–101, 105, 107–8, 114, 116, 124
Upper Langwith 45
Upper Rodent Stratum (Tornewton Cave) 64–6
Uppony 101
Upton Warren 45, 69, 72, 88, tab. 12, 128
  interstadial complex 128
Urals 83
Urocitellus 125 ; see *Spermophilus primigenius*
Ursus see bear
  deningeri 61

Val d'Arno, Italy 80–1, 96
Vejlby I and II mild stages (Denmark) 40, 42
Villafranchian 41, 43, 47, 76, 81, 92, 95–6, 122
Viscount Melville Sound 92
Voigtstedt 101
voles 38–9, 47, 51, 69 ; see *Arvicola*, *Mimomys*, *Microtus*
  in Ireland ? 69, 129

Waalian 41, 43
Waechter, J. d'A. 51, 130
Wales, south 113
Waltonian 41
Warthe 42
Warton Crag 45 ; see Dog Holes Cave
Water Hall Farm (Pit) 45, 48, 49*, **58–9**, 110, 115, 117, tab. 12, 126, 130
Waterford, Co. 45 ; see localities
water-rat, water-vole see *Arvicola*
Weichsel 42
Weichselian 41
West, R. G. 47, 130
West Runton 38, 41, 45, 46*, 47–8, 52, 60–1, 73, 78–9, 81, 83, 85, 93, 97–100, 105–8, 114, 116, tab. 12, 122–4
West Thurrock 50

West Wittering 45, 93, tab. 12
Westbury-sub-Mendip (fissure) 36, 45, **60–1**, 80–1, 87, 89–90, 92–3, 95, 101–2, 105, 107–8, 121, tab. 12, 122–4, 129
Westbury stage 108, tab. 12, **122**, 123
Wetton 45
Weybourne Crag 38, 41, 43, 46*, 47, 95–7 ; see Icenian Crag
Whitchurch 45
White Sea 120
Whitechurch 45
Willment's Gravel Pit 58, 128, 130
Wilson, Mrs G. 130
Wiltshire 45 ; see Fisherton
Wintringham 45
wolf 62–3
Wolff, R. G. 69, 81, 90, 104, 130
Wolstonian stage 40–2, 50, 52, 54–5, 124–5
wolverine 126 ; see glutton
wood mouse see *Apodemus sylvaticus*
Woodbridge 43, 45, 46*, 78–9, tab. 12
Worcestershire 45 ; see localities
Wretton 91
Würm 42, 76, 121
Wye Cave see Merlin's Cave

Xenocyon lycaonoides 61

yellow-necked mouse see *Apodemus flavicollis*
Yorkshire 45 ; see localities
Yugoslavia 98, 106, 109, 114

A. J. Sutcliffe, Ph.D.
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

K. Kowalski
Institute of Systematic and Experimental Zoology
Polish Academy of Sciences
Krakow
Poland

Accepted for publication 28 October 1975