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The History of the Mammal Fauna During the Ipswichian/Last Interglacial in England

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Phil. Trans. R. Soc. Lond. B 1976 **276**, 221-250
doi: 10.1098/rstb.1976.0112

THE HISTORY OF THE MAMMAL FAUNA DURING THE IPSWICHIAN/LAST INTERGLACIAL IN ENGLAND

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(*Communicated by R. G. West, F.R.S. – Received* 18 *September* 1975).

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Vol. 276. B 945. 16 [Published 7 December 1976

Changes in the mammal fauna, in relation to climatic and vegetational changes, during the Ipswichian interglacial in England have been followed by using fossil material which has been related to the pollen stratigraphy. The stratigraphy at each site and the climatic, vegetational and archaeological histories of the interglacial are summarized. The faunal records are tabulated.

In response to climatic amelioration the tundra-like flora and fauna (e.g. lemmings, mammoth, horse, woolly rhinoceros, reindeer) of the Wolstonian glacial stage gave way to regional mixed oak forest and a temperate fauna (e.g. wood mouse, straight-tusked elephant, hippotamus, fallow deer) by zone Ip IIb. Locally deforested areas in river valleys, indicated by high herb pollen levels at several sites, in zone Ip IIb probably supported such animals as the rhinoceros *Dicerorhinus hemitoechus* and giant deer. These areas of herb-dominated vegetation may have resulted largely from the activities of herbivorous mammals. The apparent regional thinning of the forest in zone Ip III was accompanied by the reappearance of mammoth and horse. The occurrence of typically cold stage mammals (e.g. lemmings, woolly rhinoceros, musk ox) in company with temperate forms in the Crayford deposits, which are thought to date from the end of the Ipswichian, appears to be related to generally open vegetational conditions and perhaps a more continental climate. In the succeeding Devensian glacial stage the fauna was similar to that of the Wolstonian.

Artefacts, sometimes associated with large mammal remains, are recorded at several sites but the possible influence of man on the faunal history is difficult to assess.

The taxonomy of *Crocidura*, voles, rhinoceroses and elephants is discussed.

1. INTRODUCTION

The changes in the mammal fauna in England in response to the climatic and vegetational changes of the Middle and Upper Pleistocene glacial-interglacial succession are known in outline (Stuart 1974).

The fossil record for the Ipswichian/Last interglacial is sufficiently good for the history of the mammal fauna to be followed in detail through the stage. With the exception of records of the pond tortoise (*Emys orbicularis*), which have climatic implications, the Ipswichian lower vertebrates and birds are poorly-known (see the list in Stuart 1974) and are not discussed here.

Much of the fossil mammal material preserved in museum collections (table 2) was obtained prior to 1920. Many new sites have however been discovered in the past few years and it is to be hoped that further finds will help to fill in the many gaps and clarify some of the problems of interpretation. In particular it would be useful to have sites suitable for more detailed investigations of the taphonomy and palaeo-ecology of their vertebrate faunas.

2. STRATIGRAPHY

(*a*) *Introduction*

The stratigraphy of the important Ipswichian sites and the provenance of the fossil mammal finds are considered here in some detail because of their importance as a basis for reconstructing faunal history. The stratigraphical nomenclature follows that proposed by the Quaternary Era Sub-Committee of the Geological Society of London (Mitchell, Penny, Shotton & West 1973), and accepts the view that the deposits generally regarded as Ipswichian do in fact belong to a single temperate stage, a view consistent with the stratigraphical and palaeontological data.

However, Sutcliffe (1975, 1976) has expressed the view that the actual sequence of climatic changes during the Pleistocene was considerably more complex than proposed by the Quaternary Era Sub-Committee. In particular he has suggested that two or more warm stages are represented by deposits usually assigned to the Ipswichian interglacial. The arguments are based essentially on the interpretation of the relationships of the fossiliferous deposits at Ilford and Aveley to those of Trafalgar Square in the Lower Thames Valley.

Sutcliffe has drawn attention to the fact that the zone IIb organic horizons at Ilford and Aveley are several metres higher than those at Trafalgar Square (see figure 2) and that prior to the work of West, Lambert & Sparks (1964) the deposits had been regarded by many workers as belonging to an older Taplow (Middle) terrace and a younger Flood Plain (Lower) terrace respectively.

The Ilford and Aveley organic deposits were laid down by tributary streams, whereas those at Trafalgar Square were probably laid down by or close to the main river and this could largely account for the differences in heights. It is also possible that the Ilford–Aveley–Crayford area has since been uplifted relative to Trafalgar Square (West 1972*b*). In this connection it is important to note that in the Romford memoir Dines & Edmunds (1925) specifically stated (page 34) that in the Ilford area the boundaries of the Middle and Lower terraces merge, are to some extent conjectural, and that they are based on the levels where the respective deposits would have been expected to occur.

According to Sutcliffe the marked differences between the faunas, namely, the occurrence at Ilford of horse, mammoth, the rhinoceros *Dicerorhinus kirchbergensis*, and the absence of hippopotamus and fallow deer make it improbable that the fauna dates from the same temperate stage as Trafalgar Square. The Ilford fauna is thought to be older because of the presence of a primitive mammoth, showing affinities to the Middle Pleistocene *Mammuthus trogontherii*, and of *D. kirchbergensis*, otherwise known in Britain only from the preceeding Hoxnian interglacial. The possibility that the faunas date from different times within a single stage is discounted by him on the grounds that neither in river terrace nor in cave deposits has a faunal assemblage of Ilford type ever been observed to overlie an assemblage of Trafalgar Square type, e.g. remains of hippopotamus have not been found in the zone IIb horizon at Aveley.

Sutcliffe (1975, 1976) has further suggested that the two postulated temperate periods occurred close together in time, separated only by a short cold interval, and that the pollen spectra for equivalent zones of these periods have not or cannot be distinguished. This has led, he believes, to confusion of the deposits of the two stages on the basis of palaeobotany when the mammal faunas are clearly distinct.

The investigation of several sites outside the Thames Valley, notably Barrington, Beetley and Stutton by the author, has largely confirmed the faunal distinctions between Trafalgar Square and Ilford described by Sutcliffe. There is however a remarkably good correspondence between faunas and pollen zones (see table 2) e.g. mammoth and horse have never been recorded in association with zone II spectra and similarly hippopotamus is recorded only from zone II and the beginning of zone III, which is consistent with their dating from different zones within a single Ipswichian stage. Moreover the identification of *D. kirchbergensis* is unjustified (see §8 (*f*)), as is the contention that the so-called 'Ilford mammoth' is closely related to *M. trogontherii* (see §8 (*g*)). The faunal evidence that Ilford pre-dates Trafalgar Square is therefore at present unsubstantiated.

The failure to recognize faunal assemblages of Ilford type in caves, either above or below assemblages of Trafalgar Square type, is not remarkable when one considers that only one or two cave sites with deposits of Ipswichian age have been carefully excavated; and that none of the Ilford mammals are characteristic, in contrast to, for example, hippopotamus and fallow deer at Trafalgar Square. Similarly the absence of hippotamus at Ilford is most probably because zone II deposits occur there only locally and the mammalian remains were recovered from the brickpits excavated in the younger brickearths. The fauna from Aveley is rather sparse (table 2) and the fact that hippopotamus has not so far been found in the zone II deposits is surely not significant. More important are the absence of mammoth and presence of straight-tusked elephant in this horizon corresponding with the records from zone II deposits elsewhere.

The contrasting view of Bristow & Cox (in Mitchell *et al.* 1973), that the Hoxnian and Ipswichian deposits belong to the same interglacial stage, separated by a minor cold interval, does not accord very well with the rather marked and consistent differences in the floras

TABLE 1. CHARACTERS AND INFERRED REGIONAL VEGETATION OF IPSWICHIAN POLLEN ZONES (YOUNGEST FIRST) (BASED ON WEST 1972*a*; PHILLIPS 1973)

zone	pollen assemblage zone character	regional vegetation
(Early Devensian)	high n.a.p.	herb-dominated vegetation
Ip IV	*Pinus*	boreal forest (probably open)
Ip III	*Carpinus*	temperate forest with hornbeam
Ip II*b*	m.o.f. *Pinus*, *Acer*, *Corylus*	mixed oak forest
Ip II*a*	*Pinus*-*Quercus*	
Ip I*b*	*Pinus*-*Betula*	boreal forest
Ip I*a*	*Betula*-*Pinus*	
(Late Wolstonian)	high n.a.p.	herb-dominated vegetation

Abbreviations: n.a.p., non-arboreal pollen: Ip, Ipswichian; m.o.f., mixed oak forest genera. *N.B.* The boundary between zone Ip IV and the early Devensian is not easily defined. Here it is based solely on high n.a.p.

(West 1972*a*) and vertebrate faunas (Stuart 1974). The Ipswichian stage is subdivided in a series of pollen assemblage zones (table 1).

Where sediments have yielded pollen they can usually be confidently assigned to pollen assemblage zones. Although pollen-dated sites provide the main framework of this study, deposits which can be correlated using stratigraphical and/or faunal evidence have also been utilized.

With the exception of those now on the coast all of the sites are in existing river valleys (figure 1). At some sites fine clastics and organic deposits accumulated in small lakes connected to streams and rivers, e.g. at the type site Bobbitshole (West 1957). The majority of deposits are

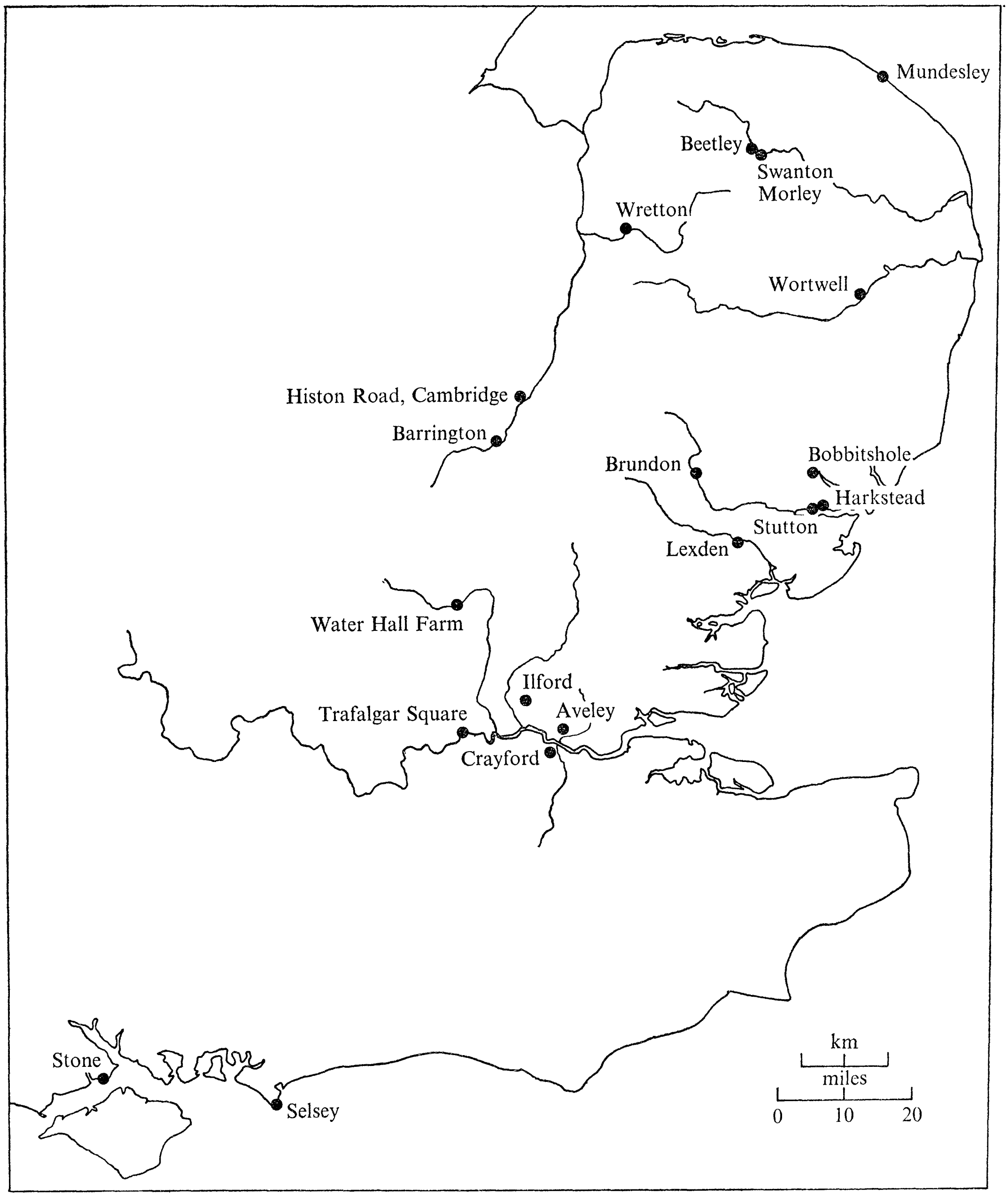

FIGURE 1. Location map of sites in relation to modern rivers (only relevant rivers shown).

fluviatile including both channel and overbank facies. At many sites fine, inorganic, sediments, usually oxidized ('brickearths'), occur overlying sediments with floras and faunas of zone Ip IIb age (figures 2, 3). Where preserved the pollen indicates deposition in zones Ip III and Ip IV. The widespread deposition of this type of sediment in the second half of the Ipswichian may result in part from aggradation in response to rising sea level or perhaps from soil erosion related to decreasing tree cover.

Marine and brackish water horizons, indicated by the molluscan faunas, at Stone, Wretton, Selsey (zone Ip IIb) and Stutton (zone Ip III) are probably related to the interglacial eustatic rise in sea level and to the coastal or estuarine position of the sites.

The vertebrate fossil record for the Ipswichian stage is fairly good but much better for some zones than others. The rarity of pollen in 'brickearths' means that few faunal assemblages can be accurately related to the vegetational changes of zones Ip III and I p IV. Very little is known about the vertebrates of zone Ip I. This may be in part due to lack of adequate stratigraphical control when the material was collected, so that some of the vertebrates from Bobbitshole, Mundesley and Selsey may be of this age. It is interesting to note however that at the 5 sites where it is represented zone Ip I is relatively thin, suggesting that it was of correspondingly short duration. The shortness of zone I is also strongly indicated by Continental diagrams, e.g Hollerup, Denmark (Andersen 1965).

(*b*) *Lower Thames Valley sites*

Representative sections at sites in the Lower Thames Valley in relation to O.D. are given in figure 2. The fact that the Ilford and Aveley organic deposits appear to have been laid down by tributary streams, whereas those at Trafalgar Square were probably laid down by or close to the main river may partly account for the considerable differences in heights of the zone Ip IIb horizons, although it is possible that the Ilford–Aveley–Crayford area has since been uplifted relative to Trafalgar Square (see West 1972*b*).

(i) *Trafalgar Square, London* (TQ 300804)

Mammalian remains were recovered from the organic deposits and the sands and gravels of zone Ip IIb (Franks, Kerney, Sutcliffe & Coope 1958; Franks 1960; West *et al.* 1964).

(ii) *Ilford, Essex* (*e.g. Seven Kings:* TQ 453871)

During the 19th century many mammalian remains were recovered from several pits in the complex sequence of gravels, sands and 'brickearths' of the Ilford area (Cotton 1847; Woodward & Davies 1874). The discovery of organic deposits covering zones l Wo to Ip IIb below 'brickearth' at Seven Kings (West *et al.* 1964) suggests, that the mammal remains date from zones Ip III and Ip IV.

(iii) *Crayford and Erith, Kent* (*e.g. Rutters New Pit:* TQ 519764)

The Pleistocene deposits of this area broadly comprise 'brickearths' overlying gravels (Kennard 1944). As at Ilford the vertebrate material was collected in the last century. The height relationships of the Lower Brickearth at Crayford are comparable with the heights of the 'brickearths' at other localities in the same area, e.g. at Ilford, Aveley only 5 km (3 miles) away, Ebbsfleet and Northfleet. At Ilford and Aveley these 'brickearths' overlie and therefore postdate Ipswichian zone IIb deposits. At Ebbsfleet (Burchell in Zeuner 1959, fig. 40) and

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Northfleet (Burchell 1933, fig. 2) 'brickearths' rest on an eroded surface of the Main Coombe Rock formed under permafrost conditions, probably during the Wolstonian cold stage and with a fauna (Northfleet) of *Mammuthus primigenius* (mammoth), *Coelodonta antiquitatis* (woolly rhinoceros) and *Equus caballus* (horse). The Crayford gravel also overlies chalk rubble (Kennard 1944, fig. 13). The top of the Lower Brickearth at Crayford and the top of the 'brickearths' elsewhere exhibit involutions presumably resulting from permafrost in the Devensian cold stage. The Upper Brickearth at Crayford appears to have been soliflucted onto the Lower Brickearth (Kennard 1944) during the Devensian and contains a 'cold' fauna comprising *M. primigenius*, *C. antiquitatis* and *E. caballus*.

The broad stratigraphical relationships therefore suggests that the Crayford Lower Brickearth is of Ipswichian or Devensian age. The late Hoxnian and early Wolstonian deposits at Swanscombe, only 7 km ($4\frac{1}{2}$ miles) away are considerably higher (Kerney 1971, fig. 4) and the erosional contact of the 'brickearths' with the Main Coombe Rock and evidence of widespread post zone Ip IIb 'brickearth' aggradation argue strongly against a Wolstonian or early

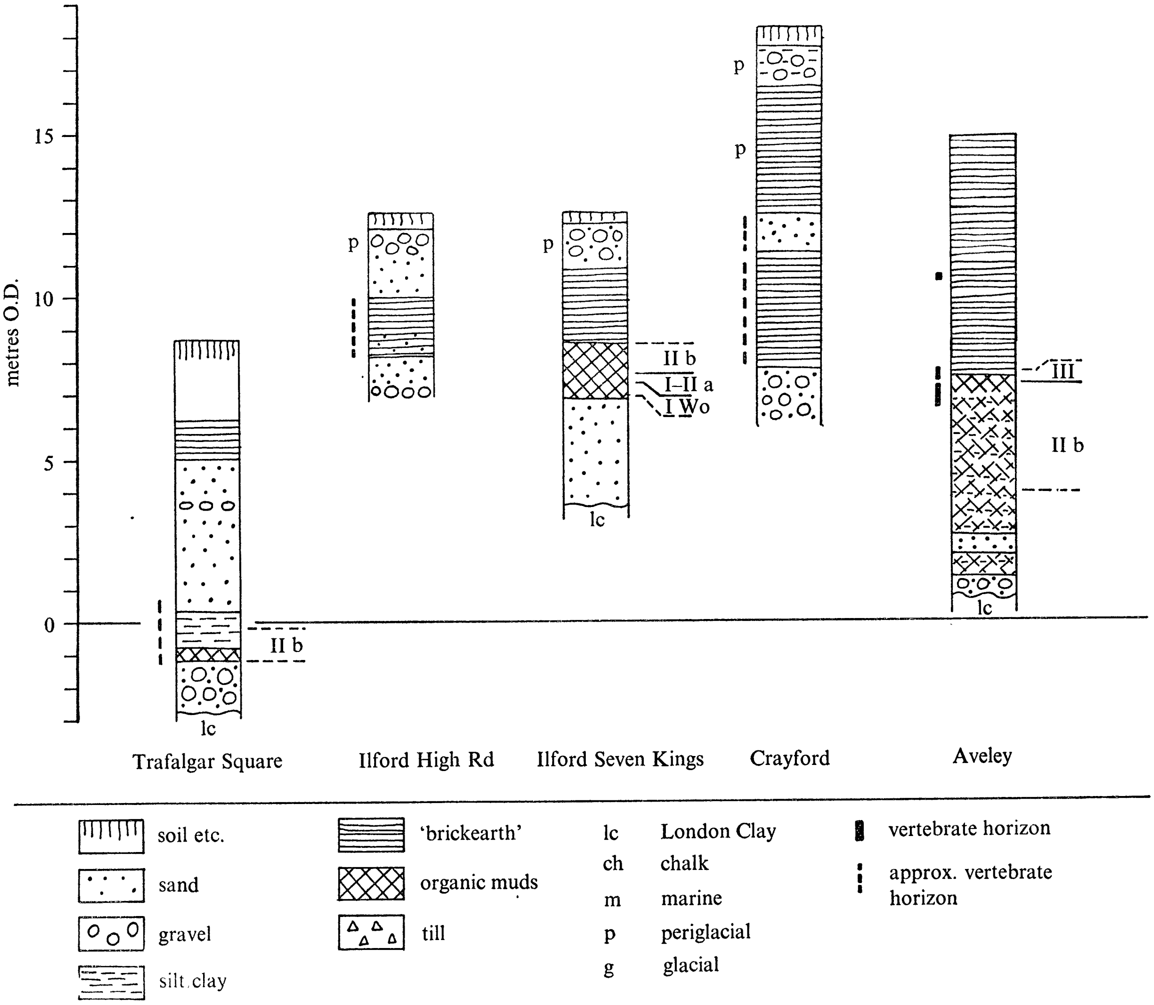

FIGURE 2. Representative sections at Lower Thames Valley sites in relation to O.D. Pollen stratigraphy where known is indicated on the right hand side of each section, fossil mammal horizons on the left. After West, Lambert & Sparks (1964) (Trafalgar Square, Ilford); Kennard (1944) (Crayford); West (1969) (Aveley).

Ipswichian age. The mammal fauna of the Lower Brickearth at Crayford (table 2) differs from the Ipswichian Ilford (probably zones Ip III-IV) and Stutton (zones Ip III-IV) faunas in the presence of additional characteristically cold stage species, namely, *Lemmus lemmus* (Norway lemming) *Dicrostonyx torquatus* (arctic lemming) *Microtus oeconomus* (northern vole) *C. antiquitatis* and *Ovibos moschatus* (musk ox). It should be pointed out that there appear to be no marked faunal changes within the Lower Brickearth and overlying *Corbicula* Bed (Kennard 1944). For example a mandible of *C. antiquitatis* is recorded from the very base of the Lower Brickearth, a skull of *O. moschatus* was recovered from beneath the *Corbicula* Bed and remains of *L. lemmus* and *D. torquatus* occur throughout.

Although the fauna includes these typically cold stage mammals it is by no means identical to faunas of Devensian age, including an early Devensian fauna from Wretton, Norfolk (West *et al.* 1974; Stuart 1974). At Crayford the temperate forms *Bos primigenius* (aurochs) and *Dicerorhinus hemitoechus* (a rhinoceros), both unknown from the Devensian, still occur and one characteristic cold stage animal *Rangifer tarandus* (reindeer), abundantly represented in Devensian faunas, is not recorded from Crayford. The absence of the latter is almost certainly genuine in view of the large amount of fossil material recovered from this locality. *Spermophilus undulatus* (Siberian long-tailed suslik) is recorded from Crayford, and from the early Anglian of Mundesley, Norfolk, whereas the only suslik so far recorded from the Devensian (at a few sites only) is *S. major* (red-cheeked suslik) (Mayhew 1975). Moreover the Crayford Lower Brickearth throughout contains abundant temperate and southern Mollusca, notably *Corbicula fluminalis* which indicates that summer temperatures were still high.

The Crayford Lower Brickearth fauna therefore appears to be later than that of Ilford and Stutton and earlier than that of Wretton. In view of the uncertainty of defining a precise late Ipswichian–early Devensian boundary (see table 1) the age of the fauna is probably best considered as late zone Ip IV or possibly earliest Devensian.

Sutcliffe (1976) has suggested that the Crayford fauna is intermediate in age between those of Ilford and Trafalgar Square, and that its closest affinities are with the 'pre-hippopotamus' Glutton Stratum of Tornewton Cave, Devon, rather than with the Devensian levels of that cave. The latter view is based on the identification by Kowalski of *Microtus nivalis* (snow vole) at both Crayford (Sutcliffe & Kowalski 1976) and Tornewton Cave, Glutton Stratum (Kowalski 1967). The taxonomic studies presented here (§8(*c*)) however indicate that only one species of *Microtus*, namely, *M. oeconomus* (northern vole) actually occurs at Crayford and the specimens referred by Kowalski to *M. nivalis* are variants of *M. oeconomus*. Gromov's opinion, quoted by Sutcliffe & Kowalski (1976), that the Crayford and middle or late Devensian susliks are specifically different is substantiated by the detailed work of Mayhew (1975), who, however, unlike Gromov, referred both of them to living species (see above). This difference alone however does not imply that the Crayford deposit is vastly older, especially taking into account the considerable climatic and vegetational changes which occurred through the late Ipswichian and Devensian.

(iv) *Aveley, Essex* (TQ 552807)

Of particular interest is the discovery at this site in 1964 of two elephant skeletons lying, one almost immediately above the other, in organic sediments. The lower (*Palaeoloxodon antiquus*) lay in sediments of zone Ip II*b* age whereas the upper (*Mammuthus primigenius*) lay in zone Ip III deposits (West 1969). They are now displayed as excavated in the British Museum, Natural

History. Remains of other large mammals and further elephant material were also recovered. In addition to the material preserved, A. J. Sutcliffe (private communication) identified an antler of *Cervus elaphus in situ* in the 'brickearth'. Small-vertebrate remains were obtained by J. Hooker who wet-sieved a large quantity of sediment matrix from the *P. antiquus* skeleton.

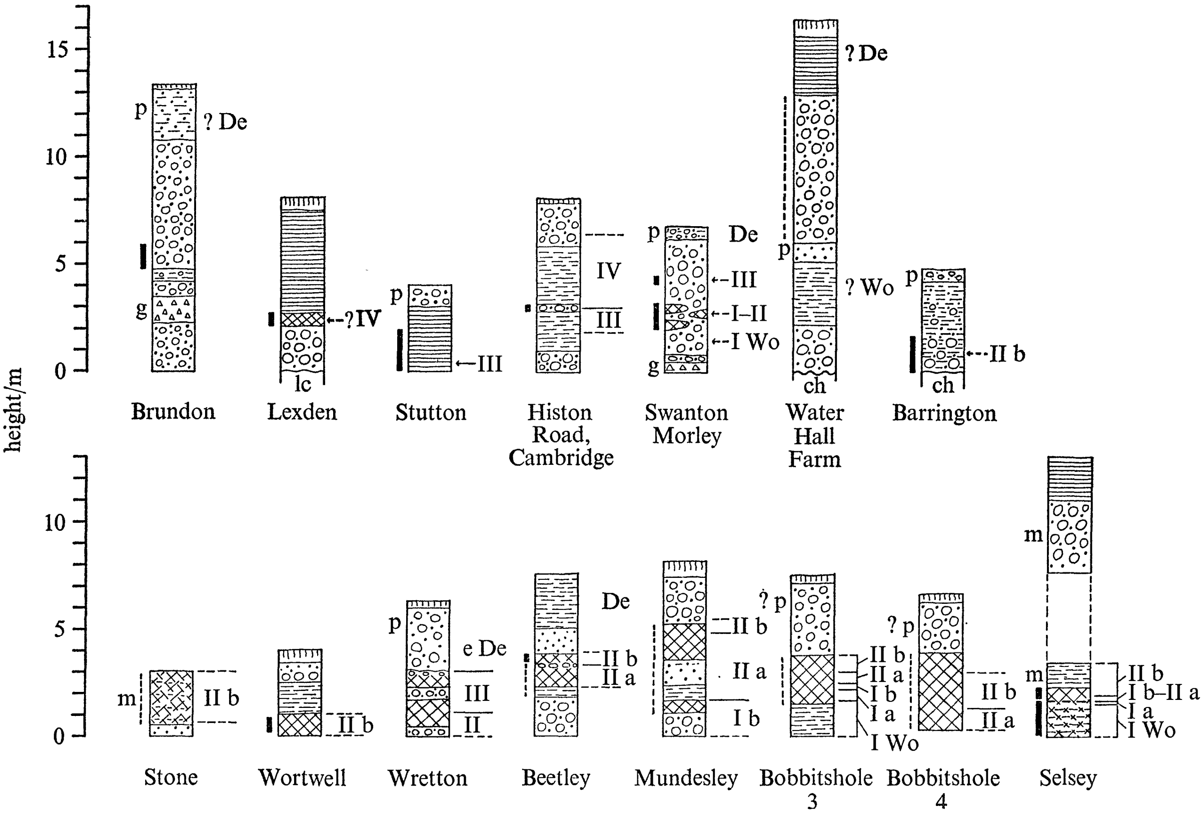

Figure 3. Representative sections at other sites. After Moir & Hopwood (1939) (Brundon); Shotton, Sutcliffe & West (1962) (Lexden); Sparks & West (1963) (Stutton); Sparks & West (1960) (Histon Road); Phillips (1972) (Swanton Morley, Beerley, Mundesley); G. Jarvis, private communication (Water Hall Farm); Fisher (1879) (Barrington); West & Sparks (1960) (Stone, Selsey); Sparks & West (1970) (Wretton); West (1957) (Bobbitshole). See figure 2 for key to stratigraphic symbols.

(*c*) *Other sites*

Representative sections at sites other than those in the Thames Valley are given in figure 3. The sections at Wretton, Norfolk in terrace deposits of the River Wissey (Sparks & West 1970) and Water Hall Farm, Hertfordshire in terrace deposits of the River Lea (G. Jarvis, private communication) are given so that the stratigraphy can be compared with the other sites. The Water Hall Farm fauna (G. Jarvis, private communication) includes *Palaeoloxodon antiquus* and *Hippopotamus amphibius* which suggests that a zone Ip II–III horizon is present within the sequence. Teeth of *Mammuthus primigenius* appear to have come from the upper part of the gravels and may date from the second half of the interglacial. The underlying, marl which has yielded small-vertebrate remains including teeth of *Microtus oeconomus* (Sutcliffe & Kowalski 1976) is penetrated by an ice-wedge pseudomorph and is therefore probably of Wolstonian age.

(i) *Brundon, Suffolk* (TL 863417)

Mammalian fossils were recovered from the base of terrace gravels of the River Stour (Moir & Hopwood 1939). The height relationships, Mollusca (Sparks & West 1963) and the mammal fauna (table 2) strongly suggest a correlation with Stutton, i.e. a zone Ip III–IV age.

(ii) *Lexden, Essex* (*about* TL 978253)

In the last century mammal remains were found in organic sediments underlying 'brickearth' – both terrace deposits of the River Colne. The stratigraphical position, temperate beetle fauna, vertebrate fauna and pollen, mostly *Pinus* and herb taxa, (Shotton, Sutcliffe & West 1962) taken together suggest a zone Ip IV date for the organic horizon.

(iii) *Stutton, Suffolk* (TM 149330) *and Harkstead, Suffolk* (TM 188338)

The fossiliferous sandy 'brickearths' on the north side of the River Stour estuary are mostly oxidized, but Sparks & West (1963) obtained a pollen sample from beneath the foreshore at Stutton which gave a conclusive zone Ip III age. The persistence of temperate and southern molluscs, mainly *Corbicula fluminalis* throughout the deposit, although gradually declining in relative abundance, suggests that the sequence covers zone Ip III and at least part of zone Ip IV. The vertebrate remains appear to have come mostly from the foreshore at a horizon above where the pollen sample was taken. I collected additional small-vertebrate remains by wet-sieving sediment from this horizon. The general similarities of stratigraphical position, lithology and fauna suggests that the nearby Harkstead deposits are of much the same age.

(iv) *Histon Road, Cambridge* (TL 444610)

At this site, terrace deposits of the River Cam, mainly consist of fine inorganic sediments – the unoxidized equivalent of 'brickearths' elsewhere (Sparks & West 1960). A few mammal remains were found in the gravel at the zone Ip III/IV boundary (Hollingworth, Allison & Godwin 1950).

(v) *Swanton Morley, Norfolk* (TG 018191)

Fossil vertebrates were found in lenses of organic deposits in gravels below the level of the modern River Wensum. Pollen analysis of the sediment matrix made it possible to assign these remains to zone Ip II*b* and Ip III (Phillips 1972). I wet-sieved a number of small-vertebrate remains out of zone Ip IIb sediments.

(vi) *Barrington, Cambridgeshire* (*e.g. Cardo's Pit:* TL 384493)

The marls, sands and gravels of the Barrington Beds, terrace deposits of a tributary of the River Cam have yielded a rich vertebrate fauna (Fisher 1879; Hughes 1911). Pollen obtained from the sediment matrix of some of the large mammal bones agrees with the vertebrate faunal evidence for a zone Ip IIb age (Gibbard & Stuart 1975).

(vii) *Stone, Hampshire* (SZ 458984)

The stratigraphy, palynology and molluscan fauna of the largely marine deposits were described by West & Sparks (1960). Part of a tusk of *Palaeoloxodon antiquus* is recorded from zone Ip IIb.

(viii) *Wortwell, Norfolk* (TM 275844)

Part of a *Palaeoloxodon antiquus* skeleton was discovered in zone Ip IIb organic deposits of the River Waveney (Sparks & West 1968).

(ix) *Beetley, Norfolk* (TF 987181)

At Beetley, about 5 km upstream of Swanton Morley on the River Wensum terrace sands and gravels include organic beds (Phillips 1972). Mammal remains were found by workmen in the 1960s and the exact provenance of most of the material is unknown, although the preservation indicates that they came from organic horizons which date from zones Ip IIa and Ip IIb. The sediment matrix from one of several bones from a single *Hippopotamus amphibius* individual gave an early zone Ip IIb pollen spectrum (Phillips 1972).

(x) *Mundesley, Norfolk* (TG 315366)

In the 19th century a few vertebrate remains were obtained from the cliff section in deposits filling a channel cut into the Anglian till and Cromer Forest Bed Series (Newton 1879). Phillips (1972, 1974) sampled the deposits by coring and was able to demonstrate that they covered zones Ip Ib to early Ip IIb.

(xi) *Bobbitshole, Ipswich, Suffolk* (TM 148414)

This is the type site for the Ipswichian interglacial (West 1957; Mitchell *et al.* 1973). The few small-vertebrate remains available appear from their preservation to have come from the lacustrine organic deposits which cover the entire first half of the stage.

(xii) *Selsey, Sussex* (SZ 863923)

At Selsey freshwater silts and detritus muds are overlain by marine deposits (West & Sparks 1960). The vertebrate remains were collected from two distinct horizons; Bed 1 (zones l Wo to Ip Ia) and Bed 2 (zone Ip Ib to early Ip IIb).

3. CLIMATE

A rapid rise in temperature at the beginning of the interglacial is indicated by the early immigration of thermophilous trees, and records of thermophilous water plants as early as zone Ip Ia (Phillips 1974).

Zone Ip IIb records of many animals and plants occurring in England well north of their present distributions indicate that summer temperatures were about 2–3 °C warmer than now. This would imply mean July temperatures of about 19–20 °C for southeast England (Phillips 1974; Coope 1974). Taxa recorded include: thermophilous water plants, e.g. *Trapa natans*, Mediterranean shrubs, e.g. *Pyracantha coccinea*, *Acer monspessulanum* (Phillips 1974); southern molluscs, e.g. *Corbicula fluminalis*, *Belgrandia marginata* (Sparks 1964); and southern beetles, e.g. *Onthophagus opacicollis* (Coope 1974). Phillips concluded that the climate was of mediterranean rather than continental character because the occurrence of *Hedera* and *Ilex* indicates that the winters were mild. Coope reached a similar conclusion on the basis of the zone Ip IIa/b beetle fauna from Bobbitshole.

Subsequent to zone Ip IIb the changes in forest composition, especially the success of

Carpinus in zone Ip III, may indicate increasing continentality (Phillips 1974). The persistence of *Corbicula fluminalis* and other southern Mollusca (Sparks 1964) suggests that summer temperatures remained high until the beginning of the Devensian glacial stage.

4. Vegetational history

The vegetational history of the Ipswichian has been pieced together from a number of sites, since no pollen-bearing sediments covering the entire interglacial have so far been discovered (West 1972*a*; Phillips 1974). There are however several diagrams which cover all or much of the correlative Eemian interglacial on the Continent (see Phillips 1974 for references).

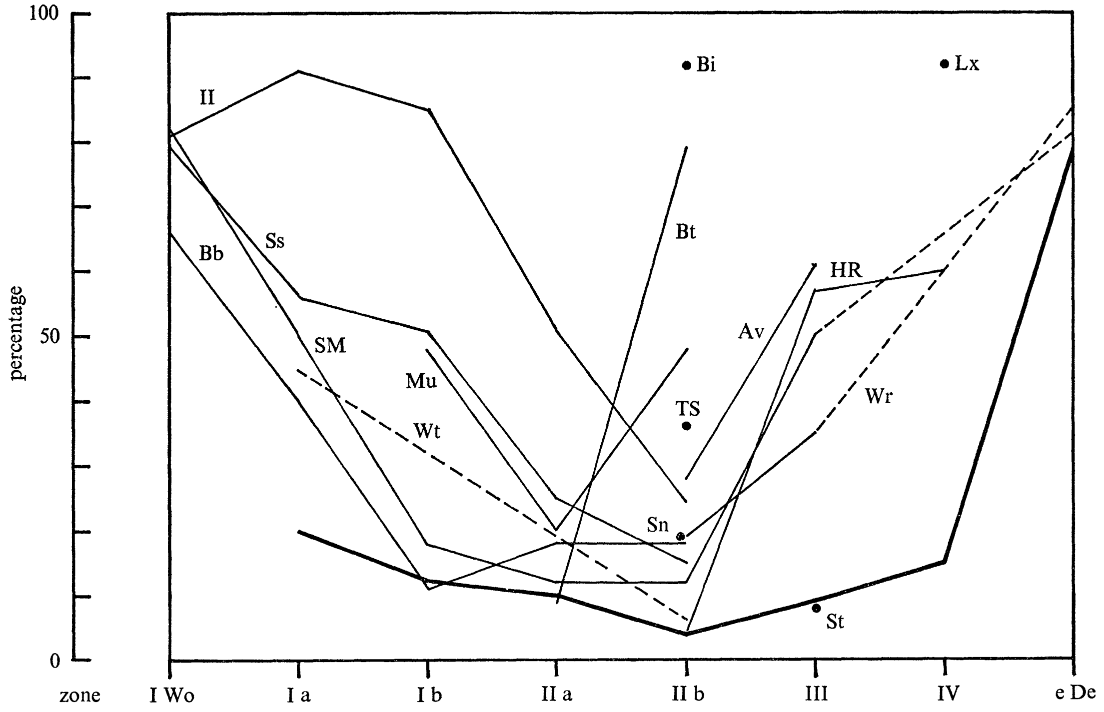

Figure 4. Generalized schematic herb pollen curves (herb pollen as percentage total land pollen) by pollen assemblage zones for English Ipswichian sites and an Eemian (= Ipswichian) site at Hollerup, Denmark. From data in Andersen (1965) (Hollerup), Franks (1960); Gibbard & Stuart (1975), Hollingworth, Allison & Godwin (1950), Phillips (1972), Shotton, Sutcliffe & West (1962), Sparks & West (1960, 1963, 1968, 1970; West (1957, 1969), West, Lambert & Sparks (1964); West & Sparks (1960, 1964), West (1974). Av, Aveley; Bb, Bobbitshole; Bi, Barrington; Bt, Beetley; HR, Histon Road; Il, Ilford; Lx, Lexden; Mu, Mundesley; SM, Swanton Morley; Sn, Stone; Ss, Selsey; St, Stutton; TS, Trafalgar Square; Wr, Wretton; Wt, Wortwell. The Hollerup curve, shown by a heavy black line, is included for comparison, as it is considered to more closely reflect regional vegetational charges.

The broad regional vegetational sequence recorded in the English diagrams is given in table 1.

The Continental diagrams, which record similar sequences and can be zoned in the same way, are mostly from lacustrine deposits and, since lakes collect the pollen rain from a wide area, tend to reflect regional vegetation cover. In contrast most of the English Ipswichian diagrams are from fluviatile sediments which incorporate a much greater proportion of pollen of local origin, from plants growing near the river.

The pollen diagram from about 8 m of lacustrine sediment at Hollerup Denmark (Andersen 1965) shows a decline in herb pollen percentages until early in zone IIb (figure 4) when closed mixed oak forest became predominant. The herb pollen percentages increase gradually through zone III suggesting that the mixed oak forest was becoming more open. This trend continues in zone IV and Ericales pollen appears in quantity indicating areas of heath vegetation in the rather open boreal forest. In the succeeding Weichselian (Devensian) glacial stage the

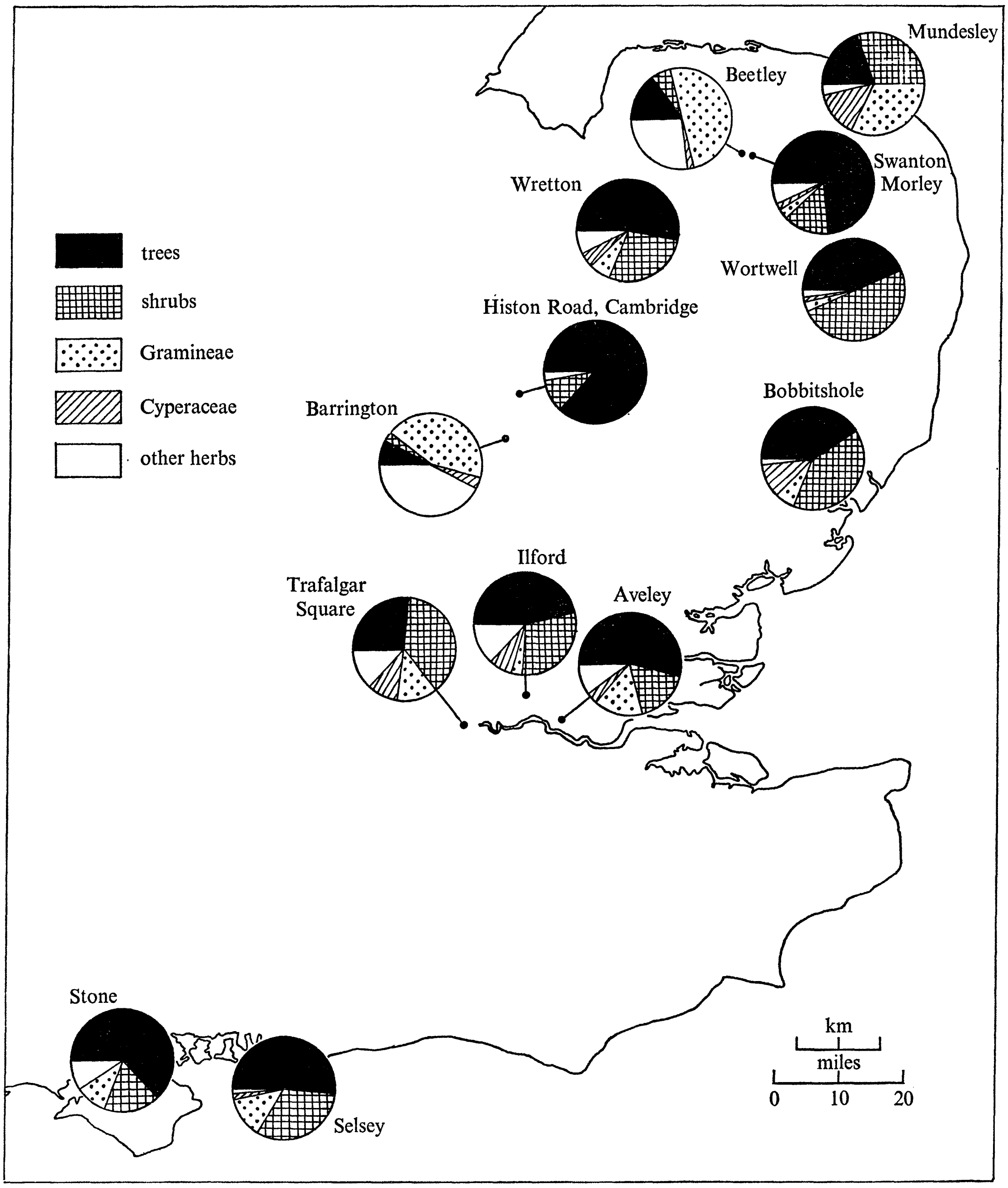

Figure 5. Pie diagrams showing representative land pollen percentages at zone Ip IIb sites. From data in Franks (1960), Gibbard & Stuart (1975), Hollingworth, Allison & Godwin (1950), Phillips (1972), Sparks & West (1968, 1970); West (1970), West, Lambert & Sparks (1964); West & Sparks (1960).

herb pollen percentage increases sharply as herb-dominated open tundra-like vegetation became widespread. The herb pollen curves for British sites show a similar overall trend to the Hollerup curve indicating a similar regional vegetational succession, and the generally much higher levels of herb pollen (figure 4) are probably the result of local pollen rain from herb-dominated vegetation in river valleys.

There is considerable variability in the pollen spectra between sites (figures 4 and 5). This variability is most marked in zone Ip IIb where the ratio of tree and shrub pollen to herb pollen is very different at sites within the same river valleys only a few kilometres apart, namely Beetley and Swanton Morley on the River Wensum, and Histon Road and Barrington on the River Cam (figure 5). This suggests that vegetational conditions could change rapidly within short distances within river valleys although the Histon Road and Barrington horizons are probably not exactly contemporareous. At Barrington herb pollen levels exceed 90 % of total land pollen (Gibbard & Stuart 1975). This herb pollen comprises mainly grasses together with Compositae, *Plantago lanceolata* and other taxa indicative of trampled and grazed grassland communities. The inorganic nature of the sediment at this site may result from soil washed in from areas of bare ground.

In zones Ip III and IV the pollen spectra suggest that the forest became progressively more open regionally. The occurrence of grassland snails *Vallonia* and *Pupilla* and the absence of woodland taxa at Histon Road (Sparks & West 1960), Stutton (Sparks & West 1963), Brundon (Kennard in Moir & Hopwood 1939) and Crayford (Kennard 1944) indicates open unwooded vegetational conditions near the depositional sites.

(*a*) *Effects of mammals on the vegetation*

The influence of mammals, in particular *Hippotamus amphibius*, on interglacial vegetation has been discussed by Turner (1975). In Africa at the present day *H. amphibius* open out short trampled grassland communities with patches of bare ground in belts over 1 km wide on either side of a river (Lock 1972). As pointed out by Turner (1975) these animals feed largely on grasses and defaecate in the water, which might lead to over-representation of Gramineae pollen in fluviatile sediments when these animals are present. This could partly account for the high levels of Gramineae recorded at Beetley and Barrington in zone Ip IIb although Phillips (1972, 1974) obtained an early zone Ip IIb pollen spectrum from the matrix of a *H. amphibius* bone from Beetley where the herb pollen was only about 28 %. Moreover the vertebrate fauna from Barrington is consistent with the picture of extensive deforestation of the river flood plain (see § 7 (*d*)).

Modern African elephants *Loxodonta africana* (Blumenbach) can cause damage by uprooting entire trees and eating bark. In areas where the elephant population is unnaturally high this has resulted in destruction of forest on an alarming scale (Laws, Parker & Johnstone 1970). It is probable that the interglacial elephants, especially *Palaeloxodon antiquus* could have been equally destructive to trees. *Castor fiber* appears to have been present throughout much of the Ipswichian (table 2). It lives in colonies and fells deciduous trees both for the bark, which is eaten, and to build dams (Corbet 1966). Areas of waterside meadows are thereby created, although it is clear that if the habitat is extensively deforested it can no longer support beavers.

Many other herbivores from voles to deer and large bovids can promote deforestation by ring-barking trees and eating tree seeds and seedlings. The nature of the herbaceous vegetation may be in turn greatly affected by the grazing and trampling activities of large herbivores.

Very local-herb-dominated communities could have been initiated as a result of rivers constantly shifting their courses within their valleys, aggradation and flooding – all of which could have inhibited tree growth. It is likely however that the activities of herbivorous mammals were important factors in the maintenance and extension of these deforested areas along river valleys.

5. Archaeology

Finds of artefacts including flakes, cores and handaxes, many of Levallois type, testify to the presence of man in England during the Ipswichian interglacial (table 2) (Moir & Hopwood 1939; Kennard 1944; Roe 1968). The lack of association of artefacts with *Hippopotamus amphibius* remains suggests the possibility that man was absent from zone Ip IIb, although the artefacts from Selsey could well be of this age.

During the Last Interglacial European man appears to have practised a hunting and food-gathering economy (Clark 1967). The uses of tools found in England probably included cutting up carcasses and dressing skins and the finds of flint flakes in direct association with the *Palaeoloxodon antiquus* skeleton at Selsey (A. J. Sutcliffe, private communication) and with a mandible of *Coelodonta antiquitatis* at Crayford (Kennard 1944) suggests that large mammals were successfully hunted.

6. Vertebrate taphonomy

There is unfortunately little data available with regard to the vertebrate taphonomy of most of the sites. Most of the remains appear to have been disarticulated prior to being incorporated in the sediments and much of this material was probably washed in as rivers eroded into their banks, as appears to have occurred at West Runton in the Cromerian (Stuart 1975). Some of the large-mammal bones from Barrington have clearly been chewed, probably by spotted hyaena, *Crocuta crocuta*. This indicated that the remains lay on the surface of the ground before being washed into the river.

The associated elephant skeletons from Aveley probably represent animals which fell down the steep London clay river bank and perhaps were drowned or became mired in the muddy channel sediments. The sediment below the upper (*Mammuthus primigenius*) skeleton was much disturbed, evidently resulting from trampling by the elephant (A. J. Sutcliffe, private communication). The skeletons of *Hippotamus amphibius* from Beetley, Swanton Morley and Barrington probably represent animals that died in the river. Complete or partial skeletons of large mammals have also been recovered from: Selsey (*Dicerorhinus hemitoechus*, *Palaeoloxodon antiquus*), Wortwell (*P. antiquus*), Stutton (*M. primigenius*) and Ilford (*D. hemitoechus*, *M. primigenius*). It is likely in some cases that carcasses were transported downstream by rivers.

Some of the large-mammal remains from the sites from which artefacts were obtained, namely Selsey, Stutton, Brundon, Ilford, Crayford, may represent animals killed by man.

The occurrence of entire articulated skeletons of *Spermophilus undulatus* at Crayford suggests that these susliks were drowned in their burrows by river floodwater.

Table 2. Fossil records of English Ipswichian/Last interglacial mammals and *Emys orbicularis*

(Museum collections: BMNH, British Museum (Natural History) London; NCM, Norwich Castle Museum; IGS, Institute of Geological Sciences London; IM, Ipswich Museum; SMG, Sedgwick Museum of Geology Cambridge.)

Selsey	(BMNH)	Swanton Morley	(NCM)
Mundesley	(NCM)	Aveley	(BMNH)
Bobbitshole	(IM)	Histon Road, Cambridge	(IGS)
Beetley	(NCM)	Stutton	(IM)
Barrington	(SMG, BMNH, IGS)	Harkstead	(IM)
Trafalgar Square, London	(BMNH)	Brundon	(IM, BMNH)
		Ilford	(BMNH, IGS)
Stone	(BMNH)	Lexden	(BMNH)
Wortwell	(NCM)	Crayford and Erith	(BMNH, IGS)

pollen zone ...	1 Wo–Ia	Ib–early IIb		1 Wo–IIb	IIa–IIb	IIb							III		III–IV		probably III–IV			? IV		
site ...	Selsey	Selsey	Mundesley	Bobbitshole	Beetley	Beetley	Barrington	Trafalgar Square	Stone	Wortwell	Swanton Morley	Aveley	Swanton Morley	Aveley	Histon Road	Stutton	Harkstead	Brundon	Ilford	Lexden	Crayford	
MAMMALIA																						
Insectivora																						
1. *Sorex araneus* L., common shrew	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	1
2. *Neomys fodiens* (Pennant), water shrew	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	2
3. *Crocidura* cf. *suaveolens* (Pallas), lesser white-toothed shrew	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	3
Primates																						
4. *Homo sapiens* L., man (artifacts)	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	–	+	4
Rodentia																						
5. *Spermophilus* (= *Citellus*) *undulatus* (Pallas), longtailed Siberian suslik.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	5
6. *Castor fiber* L., beaver	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–	6
7. *Dicrostonyx torquatus* (Pallas), arctic lemming	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	7
8. *Lemmus lemmus* (L.), Norway lemming	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	8
9. *Clethrionomys glareolus* (Schreber), bank vole	–	–	–	+	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	9
10. *Arvicola cantiana* (Hinton), a water vole	–	–	–	+	–	–	+	–	–	–	+	+	–	+	–	+	+	–	+	–	–	10
11. *Microtus agrestis* (L.), field vole	–	–	–	(+)	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	11
12. *Microtus oeconomus* (Pallas), northern vole	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	12

13. *Microtus* sp., a vole	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	13
14. cf. *Microtus* sp., a vole	−	−	−	−	−	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	14
15. *Apodemus* (sylvaticus group), wood mouse	−	−	−	+	−	−	−	−	−	−	+	−	−	−	−	+	−	−	−	−	−	15
Carnivora																						
16. *Canis lupus* L., wolf	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	+	16
17. *Ursus arctos* L., brown bear	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	+	+	−	+	17
18. *Meles meles* (L.), badger	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	18
19. *Crocuta crocuta* Erxleben, spotted hyaena	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	19
20. *Panthera leo* (L.), lion	−	−	−	−	−	−	+	+	−	−	−	−	−	−	−	+	−	+	+	−	+	20
Proboscidea																						
21. *Palaeoloxodon antiquus* Falconer & Cautley, straight-tusked elephant	−	+	+	−	+	−	+	+	+	+	+	+	−	−	−	+	+	+	+	−	−	21
22. *Mammuthus primigenius* Blumenbach, mammoth	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+	+	22
Perissodactyla																						
23. *Equus caballus* L., horse	+	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	−	+	+	−	+	23
24. *Dicerorhinus hemitoechus* (Falconer), a rhinoceros	−	+	−	−	−	−	+	(+)	−	−	−	−	−	−	−	−	−	+	+	+	+	24
25. *Coelodonta antiquitatis* Blumenbach, woolly rhinoceros	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	25
Artiodactyla																						
26. *Hippotamus amphibius* L., hippopotamus	−	−	−	−	−	+	+	+	−	−	−	−	+	−	−	−	−	−	−	−	−	26
27. *Megaloceros giganteus* (Blumenbach), giant deer	−	−	−	−	+	−	+		−	−	−	−	−	−	−	+	−	+	+	−	+	27
28. *Dama dama* (L.), fallow deer	−	−	−	−	−	−	+	+	−	−	+	−	−	−	−	−	−	−	−	−	−	28
29. *Cervus elaphus* L., red deer	−	−	−	−	+	−	+	+	−	−	−	−	−	+	+	+	+	+	+	−	+	29
30. *Bos primigenius* Bojanus, aurochs	−	−	−	−	−	−	+	+	−	−	−	−	+	−	−	−	−	(+)	+	−	+	30
31. *Bison priscus* Bojanus, a bison	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	+	+	−	+	31
32. *Bos* sp. or *Bison* sp., aurochs or bison	−	−	−	−	+	−	−	−	−	−	−	+	−	+	+	+	+	−	−	−	−	32
33. *Ovibos moschatus* (Zimmerman), musk ox	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	33
REPTILIA																						
34. *Emys orbicularis* L., pond tortoise	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	34

7. Faunal history and palaeoecology

(*a*) *Introduction*

The fossil records of Ipswichian mammals and *Emys orbicularis* in relation to pollen assemblage zones are given in table 2.

Throughout much of the preceeding (Wolstonian) and succeeding (Devensian) glacial stages treeless tundra-like vegetation south of the ice sheets supported a rich fauna including mammals nowadays: (*a*) extinct (*Mammuthus primigenius*, *Coelodonta antiquitatis*); (*b*) living in steppe (*Equus caballus*); or (*c*) living in tundra (*Dicrostonyx torquatus*, *Lemmus lemmus*, *Rangifer tarandus*) (Stuart 1974). Climatic amelioration and the northwards spread of forests early in the Ipswichian were accompanied by immigration of temperate vertebrates to England. Deterioration in climate and retrogressive changes in the vegetation cover towards the end of the stage were similarly reflected in the sequence of faunas which merged gradually into those of the Devensian.

(*b*) *Late Wolstonian to zone Ip Ia*

Only *Equus caballus* is recorded from the late Wolstonian or perhaps the earliest Ipswichian, in association with regional open grassland vegetation.

(*c*) *Zones Ip I to Ip II*

Although faunal remains are known from the early part of the Ipswichian, during which the regional vegetation changed from boreal to mixed oak forest, unfortunately none of the material can be related very precisely to the pollen assemblage zones. All that can be said is that *Emys orbicularis*, *Castor fiber*, *Palaeoloxodon antiquus* and *Dicerorhinus hemitoechus*, all temperate interglacial animals, were probably present by zone Ip IIa if not earlier.

(*d*) *Zone Ip IIb*

The regionally predominant mixed oak forest of zone Ip IIb was accompanied by many animals more-or-less characteristic of temperate forest habitats at the present day, e.g. *Clethrionomys glareolus*, *Apodemus* (sylvaticus group), *Meles meles* and *Dama dama*. The only elephant present at this time, the extinct *Palaeoloxodon antiquus* was judging from its dentition probably primarily a forest animal (see §7(*e*)).

The common occurrence of locally deforested areas in the river valleys is also reflected in the mammal faunas from several zone Ip IIb sites, notably Barrington (Gibbard & Stuart 1975), where the very high levels of herb pollen suggest that the broad river valley was mostly covered by herbaceous vegetation (see §4). The fauna includes *Microtus agrestis*, a vole nowadays characteristic of ungrazed grassland (Corbet 1966) and the carnivores *Panther leo* and *Crocuta crocuta* which are typical of African savanna areas at the present day, avoiding dense forest (Dorst & Dandelot 1970). The extinct rhinoceros *Dicerorhinus hermitoechus* appears to have been adapted to feeding primarily on low growing grasses and other herbs. Zeuner (1932) considered that the backward sloping occiput and orientation of the occipital condyles in both this species and the cold stage woolly rhinoceros *Coelodonta antiquitatis*, by analogy with living rhinoceroses, indicated that they carried their heads low feeding on low-growing herbs. The skulls of *D. hemitoechus* from Barrington and Ilford resemble that of the living African white rhinoceros *Ceratotherium simum* (Burchell) which generally carries its head low and feeds almost exclusively on low-growing grasses (Dorst & Dandelot 1970). The extreme hypsodonty of the cheek teeth in *C. simum* may be related to diet since grasses have a high silica content resulting in rapid dental attrition. The less hypsodont teeth of both *D. hemitoechus* and *C. antiquitatis* suggests that their diets included a greater proportion of less abrasive low-growing herbs.

Adult stags of *Megaloceros giganteus* carried enormous antlers, with total spans exceeding 3 m, which would have precluded living in forest for much of the year. Where this extinct deer is better known, almost at the end of the Midlandian (Devensian) in Ireland it is associated with regionally open park-tundra vegetation (Mitchell & Parkes 1949). *Hippopotamus amphibius* nowadays is found in African rivers and lakes, bordered by short grassland communities, the development of which are largely influenced by the activities of this animal (see § 4 (*a*)). It feeds both on grasses and aquatic plants (Dorst & Dandelot 1970).

It is probable that the wide variety of plant communities together with availability of water in the river valleys supported a richer and more dense mammal population than the unbroken regional forest.

Many cave sites in England and Wales have yielded faunas suggesting an approximate correlation with zone Ip II. For example the faunas from two carefully excavated cave sites; Joint Mitnor Cave and Tornewton Cave (Hyaena stratum), both in Devon, include *C. crocuta*, *P. leo*, *P. antiquus*, *D. hemitoechus*, *H. amphibius* and *D. dama* (Sutcliffe 1960; Sutcliffe & Zeuner 1962). A few taxa occur that have not been recorded from pollen-dated open sites, namely: *Lepus* sp. (a hare), *Vulpes vulpes* (L.) (red fox), *Felis sylvestris* Schreber (wild cat) and *Sus scrofa* L. (wild boar). The two latter animals are generally associated with temperate forest at the present day (Corbet 1966).

(*e*) *Zones Ip III to Ip IV*

The rather marked changes in the mammal fauna from zone Ip IIb to zone Ip III appear to be correlated with regional, rather than local, vegetational changes from closed mixed oak forest to more open temperate forest with much *Carpinus* (hornbeam). *Mammuthus primigenius* is first recorded from the beginning of zone Ip III at Aveley and both this species and the typical interglacial elephant *Palaeoloxodon antiquus* were present in England during zone Ip III and part of zone Ip IV. Where they occur together remains of *M. primigenius* are considerably more abundant than those of *P. antiquus* (see § 8 (*g*)), possibly because the former frequented the areas of herbaceous vegetation near the rivers, whereas the latter preferred the forest. The molars of *M. primigenius* with numerous close-packed lamellae are better-suited to grazing than those of *P. antiquus* which was probably more of a browser. *Equus caballus* is also recorded from zone Ip III at Aveley, having been absent since the beginning of the stage, and was from then onwards a prominent member of the fauna. At the present day it is or was until recently a gregarious grazing animal, generally characteristic of areas of temperate grassland. The fauna as a whole still contained many forest elements, although *Dama dama* is not recorded after zone Ip IIb. *H. amphibius* was present in the early part of zone Ip III at Swanton Morley but is otherwise not recorded after zone Ip IIb. Animals which appear to have lived in locally deforested areas of river valleys in zone Ip IIb, i.e. *Panthera leo*, *Dicerorhinus hemitoechus* and *Megaloceros giganteus*, continued to live in the generally more open forests of zones Ip III and Ip IV. *Crocuta crocuta* is however not recorded, but this may be of little significance since its remains are rarely met with in open sites of zone Ip II age.

(*f*) *Zone ? Ip IV*

At Lexden *Dicerorhinus hemitoechus* and *Mammuthus primigenius* are recorded in association with pollen spectra indicating predominantly herb-dominated vegetation with boreal forest also present, perhaps further away from the river.

West & Sparks (1960) obtained pollen spectra from St Côme de Fresné on the Normandy Coast, characteristic of zone Ip IV, although the possibility of an early Devensian (Chelford interstadial) age could not be entirely excluded. The regional vegetation cover appears to have been boreal forest with extensive local herb-dominated vegetation (about 75% herb pollen). The fauna, identified by Guillaume, includes *Canis lupus*, *M. primigenius*, *Equus caballus*, *Coelodonta antiquitatis*, *Bos* sp. and *Bison priscus*.

The Crayford fauna also appears to reflect a very marked local and regional opening out of the boreal forest towards the end of the Ipswichian. The absence of *Palaeoloxodon antiquus*, persistence of *Panthera leo*, *M. primigenius*, *E. caballus* and *D. hemitoechus* and the appearance of *Spermophilus undulatus*, *Lemmus lemmus*, *Discrostonyx torquatus*, *C. antiquitatis* and *Ovibos moschatus* suggests predominantly open herb-dominated vegetation. The presence of *D. hemitoechus*, and *Bos primigenius*, and the absence of *Rangifer tarandus* however readily distinguish the fauna from those of Devensian age.

(*g*) *Climate and distribution*

The occurrence of a number of living vertebrate taxa in the Ipswichian outside their present distributions is consistent with other evidence for climatic change. It is unlikely in most cases that mammals are directly limited by climatic factors, but they are dependent on the vegetational conditions in terms of food and habitat structure.

(i) *Taxa with southern distributions*

The occurrence of *Emys orbicularis*, *Crocidura* cf. *suaveolens* and *Hippopotamus amphibius* in the Ipswichian appears to be related to the prevalence of warmer climatic conditions than at the present day. The presence of *Panthera leo* and *Crocuta crocuta* however is not climatically significant since both were also present in England during the Devensian (Last) glaciation. Their absence from Europe at the present day may have been influenced by man.

Emys orbicularis (zones ? Ip II a and Ip III-IV). At the present day the breeding range of the pond tortoise is mainly eastern European and Mediterranean. Warm dry summers are essential for the eggs to hatch. Non-breeding individuals occur as far north as northern France and Germany, limited by the 18 °C July isotherm. Fossil remains are known from deposits of probable Hoxnian age at Ingress Vale, Kent and from the Flandrian of Denmark, Sweden and England (Degerbøl & Krog 1951).

Crocidura cf. *suaveolens* (zone Ip II b). The genus *Crocidura* is distributed in southern and central Europe as far north as northern France but not reaching the Baltic coast. The northern limit of *C. suaveolens* runs from Aquitaine eastwards, although it is also present on the Scilly Isles and some of the Channel Islands to which it was probably introduced by man (Brink 1967; Corbet 1966).

Hippopotamus amphibius (zones Ip II b and early Ip III). The hippopotamus is nowadays confined to Africa. Its amphibious habits suggest that it could not live in regions where rivers are liable to freeze over in winter. Its virtual absence from much of central and eastern Europe during the Pleistocene suggests that it could not tolerate the colder winters of a more continental climate. Its presence in England during the temperate zones of the Ipswichian is consistent with the prevalence of warm summers and mild winters in the more oceanic west. With the exception of finds from the early Middle Pleistocene Cromer Forest Bed Series of the Norfolk and Suffolk coasts, the numerous records of *H. amphibius* from England and Wales probably all date from the Ipswichian. Although not recorded from further north than Stockton-on-Tees, County Durham (Sutcliffe 1959) its apparent absence from Scotland could result from the lack of Ipswichian deposits in the region rather than having any climatic significance.

(ii) *Taxa with northern or steppe distributions*

The appearance of a number of northern and steppe animals, which anticipates the Devensian fauna, at Crayford probably towards the end of the Ipswichian is especially interesting as these animals occur in association with southern Mollusca which suggest that the climate was still warm. A marked increase in the degree of continentality of the climate, i.e. warm summers and cold winters is a possibility.

Dicrostonyx torquatus (zone ? Ip IV). The arctic lemming is a characteristic holarctic tundra animal although it does not occur in Scandinavia (Ellerman & Morrison-Scott 1966).

Lemmus lemmus (zone ? Ip IV). The Norway lemming is essentially an animal of the tundra, including mountain tundra of Scandinavia. Its range extends southwards into boreal forest in lemming years' (Brink 1967; Corbet 1966). Both this and the previous species were widespread in Europe, including Britain, during the Upper Pleistocene glacial stages.

Microtus oeconomus (zone ? Ip IV). In Europe the northern vole has a patchy distribution mostly in the north and northeast ranging from tundra through boreal forest to the northern half of the deciduous forest zone (Brink 1967; Corbet 1966). At Crayford remains of this species are much more abundant than those of lemmings.

Ovibos moschatus (zone ? Ip IV). The musk ox is now restricted to the tundra of North America and Greenland (Banfield 1974), but it appears to have been widespread in Europe including Britain during the Weichselian (Devensian) glacial stage (Stuart 1974).

Spermophilus undulatus (zone ? Ip IV). Susliks occur in the desert, steppe and tundra regions, of the Holarctic in association with open vegetational conditions (Ellerman & Morrison-Scott 1966). The Crayford form appears to be referable to the living *S. undulatus* (Mayhew 1975) which is found in non-forested areas from the Tien Shan to Mongolia and eastern Siberia.

(*h*) *Possible isolation from the Continent*

Evidence from the heights of pollen-dated freshwater/marine sediment contacts and raised beach deposits in England and the Continent suggests that sea level rose well above present level in zone Ip IIb, not falling below present level until at least the end of zone Ip III (West 1972*b*). If this was so it is possible that during some part of zones Ip IIb and Ip III Britain was cut off from the Continent by sea, although according to Shotton (1962) the raised beaches cannot be traced around either side of the present-day Straits of Dover. On the other hand Destombes, Shephard-Thorn & Redding (1975) state that traces of raised beaches occur near Rye and Sandwich at about the same height (5–8 m above present-day sea level) as the raised beaches of Black Rock, Brighton and Sangatte, near Calais. These authors conclude that a narrow strait was in existence during the Last interglacial The presence of Mediterranean marine molluscs in the Eemian of the Netherlands (de Jong 1967) implies that the Channel seaway existed during part of the interglacial. This receives some support from palaeobotanical evidence

(West 1970), but does not accord very well with the appearance of *Equus caballus* and *Mammuthus primigenius* early in zone Ip III when neither animal is recorded from any of the zone Ip II b sites. It is possible however that they survived through the first half of the interglacial perhaps in Scotland, although no deposits of Ipswichian age have so far been discovered in this area. On the other hand the lack of Ipswichian records of *Pitymys* (pine voles) in Britain, although this genus is represented in both Cromerian and Hoxnian interglacial deposits (Stuart 1974), may be due to isolation from the Continent. At the present day *Pitymys* has a rather southern distribution in Europe occurring as far north as the Channel coast of France although absent from Britain (Brink 1967). This suggests that it did not advance sufficiently far northwards, in response to the Flandrian climatic amelioration, to reach Britain before the formation of the Straits of Dover probably at the beginning of zone Fl II. It is interesting however that *Crocidura* which has a similar present day distribution to *Pitymys* nevertheless did manage to reach Britain in the Ipswichian.

8. TAXONOMY

The whereabouts of museum collections of Ipswichian material are given in table 2. The more important references to faunas of these sites are: Cotton (1847), Dawkins & Reynolds (1872–1939), Fisher (1879), Franks (1960), Gibbard & Stuart (1975), Hinton (1926), Hollingworth *et al.* (1950), Hughes (1911), Kennard (1944), Sutcliffe & Kowalski (1976), Moir & Hopwood (1939), Newton (1879), Shotton *et al.* (1962), Sparks & West (1963, 1970), Sutcliffe in West & Sparks (1960), Sutcliffe (1960, 1964), West (1969). Preliminary faunal lists for the Ipswichian were given by me (Stuart 1974).

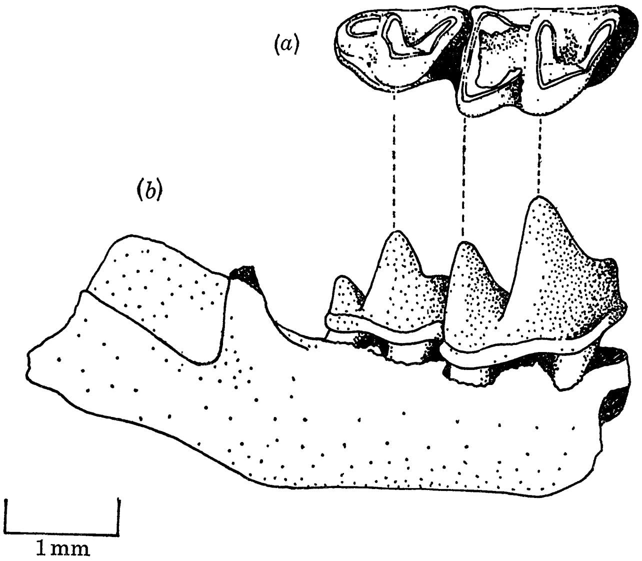

FIGURE 6. *Crocidura* cf. *suaveolens* zone Ip II *b* Aveley, fragment of right mandible. A, crown view of M_2 and M_3; B, buccal view of mandible and molars.

The older identifications have been checked and the lists from each site revised. *Bos* and *Bison* have been distinguished solely on the basis of skulls and horn cores. Certain taxa are discussed in some detail below. The record of *Meles meles* from Barrington is based on a rolled incomplete femur (Sedgwick Museum no. D31931). Other badger material from this locality is probably recent.

(*a*) Crocidura *cf.* suaveolens (*Pallas*)

A partial right mandible of a shrew from zone Ip IIb deposits at Aveley is clearly referable to the genus *Crocidura* because of the characteristically reduced talonid on M_3 (figure 6). The specimen is comparable in size to the smallest European species *C. suaveolens*. The only previous record of this genus from mainland Britain is based on mandibles, of similar size to the two larger European species *C. russula* (Hermann) and *C. leucodon* (Hermann), from deposits of possible Ipswichian age in the 'Vivian Vault' of Tornewton Cave Devon (Rzebik 1968).

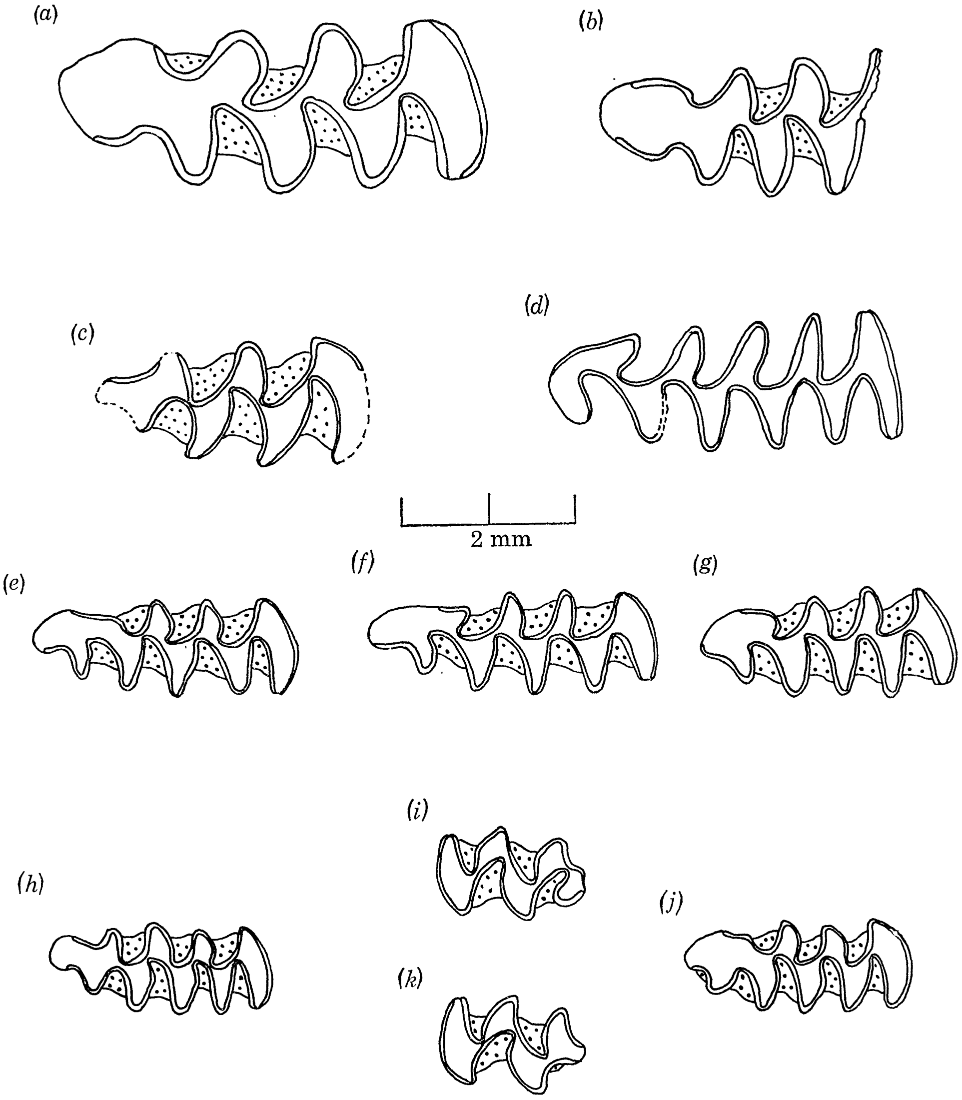

FIGURE 7. Crown patterns of molars of recent and Ipswichian voles and lemmings. (*a*) *Arvicola terrestris* M_1, recent England, *N.B.*: enamel thicker on concave sides of angles. (*b*) *A. cantiana* incomplete M_1, Stutton, *N.B.*: enamel thicker on convex sides of angles. (*c*) *Lemmus lemmus* M_1, Crayford. (*d*) *Dicrostonyx torquatus* M_1, Crayford. (*e–g*) *Microtus eoconomus* M_1's, Crayford showing variation in shape of anterior loop – most specimens approximate to (*e*). (*h*) *M. agrestis* M_1 Stutton. (*i*) *M. agrestis* M^2 Stutton. *N.B.*: extra lingual angle. (*j*) *Microtus* sp. M_1 Stutton. (*k*) *Microtus* sp. M^2 Stutton. *N.B.*: absence of extra angle.

(*b*) Microtus agrestis (*L.*)

M_1's with anterior loops of *M. arvalis/agrestis* type and comparable in size with recent *M. agrestis* occur at Bobbitshole, Barrington and Stutton (figures 7 and 8). M^2's with the extra posterior-lingual angle diagnostic of *M. agrestis* are present at Barrington and Stutton (figure 7 (*i*)).

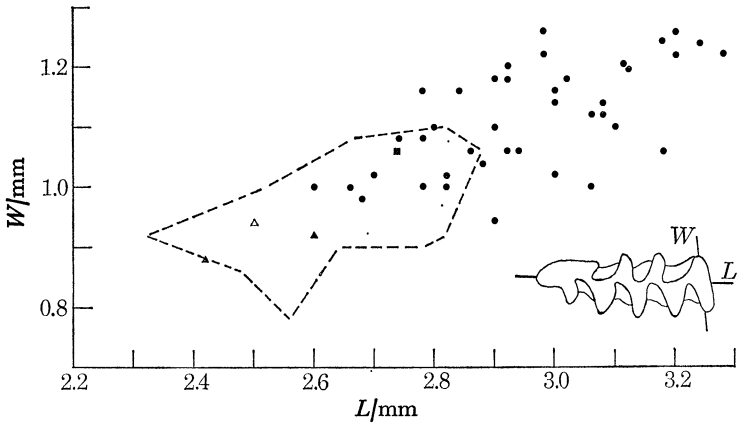

FIGURE 8. Scatter diagram of length (*L*) against width posterior loop (*W*) M_1 in recent and Ipswichian *Microtus*. Dashed line, scatter periphery of recent Norfolk *M. agrestis* (see Stuart 1975, fig. 7*a*); $N = 50$, length $\bar{x} = 2.67$, $s = 0.12$, width $\bar{x} = 0.96$, $s = 0.06$. Crayford: *M. oeconomus* $N = 40$, length $\bar{x} = 2.95$, $s = 0.17$, width $\bar{x} = 1.11$, $s = 0.09$. Stutton B: *Microtus* sp, others *M. agrestis*. ●, Crayford; ▲, Stutton A; △, Stutton B; ■, Barrington.

(*c*) Microtus oeconomus (*Pallas*)

Hinton (1926) referred the *Microtus* material from Crayford and Erith to three species on the basis of M_1 anterior loop shape. A scatter diagram of M_1 dimensions (figure 8) however suggests that only one taxon is present. The consistently large size compared with *M. agrestis* (figure 8) and the anterior loop shape of the majority of specimens (figure 7 *e*, *f*, *g*) indicate identification to *M. oeconomus*. None of the M^2's examined is of *M. agrestis* type.

(*d*) Microtus *sp.*

A single M_1 from Stutton, although having an anterior loop of *M. oeconomus* type (figure 7*j*) lies outside the range of the Crayford material (figure 8). The occurrence of an M^2 lacking the extra angle (figure 7*k*) also suggests that a species of *Microtus* in addition to *M. agrestis* was present at Stutton.

(*e*) *Arvicola cantiana* (Hinton)

Koenigswald (1973) has referred fossil *Arvicola* molars to *A. cantiana* when the enamel is thicker on the convex side of the angles and to the living *A. terrestris* when the concave side is thicker. There is considerable variation in this character in the Ipswichian material examined (all molars):

site	zone	thicker convex	not markedly differentiated	thicker concave
Ilford	probably III–IV	1	0	0
Harkstead	probably III–IV	4	2	0
Stutton	III–IV	16	7	0
Aveley	III	0	1	0
Aveley	IIb	0	2	0
Swanton Morley	IIb	0	2	0
Barrington	IIb	5	9	6
Bobbitshole	l Wo–IIb	1	2	0

It is likely that much larger samples of Ipswichian *Arvicola* would reveal interesting temporal and perhaps geographical variation in this character. In view of the prevailing type of enamel differentiation and the small size compared with modern English *A. terrestris* (figures 7 *a*, *b* and 9) the fossil material is best referred to *A. cantiana*.

(*f*) Dicerorhinus hemitoechus (*Falconer*) *and* Coelodonta antiquitatis (*Blumenbach*)

Two species of *Dicerorhinus: D. hemitoechus* and *D. kirchbergensis* have been claimed to occur at Crayford and Ilford (Kennard 1944; Sutcliffe 1960, 1964). A third species of rhinoceros

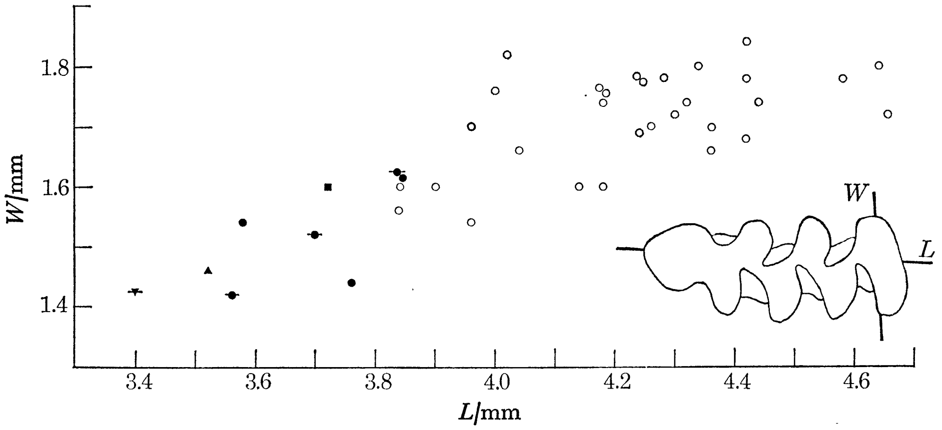

FIGURE 9. Scatter diagram of length (*L*) against width posterior loop (*W*) M_1, in recent and Ipswichian *Arvicola*. Recent Shropshire *A. terrestris*, $N = 30$, length $\bar{x} = 4.23$, $s = 0.22$, width $\bar{x} = 1.72$, $s = 0.08$. *A. cantiana* Stutton, Harkstead, N = 12 (n.b. only 6 shown in figure) length O.R. = 3.28–3.84 $\bar{x} = 3.64$, $s = 0.17$. Line through symbol indicates length estimated on incomplete material. ○, Recent; ●, Stutton, Harkstead; ▲, Ilford; ▼, Barrington; ■, Aveley (zone I p III).

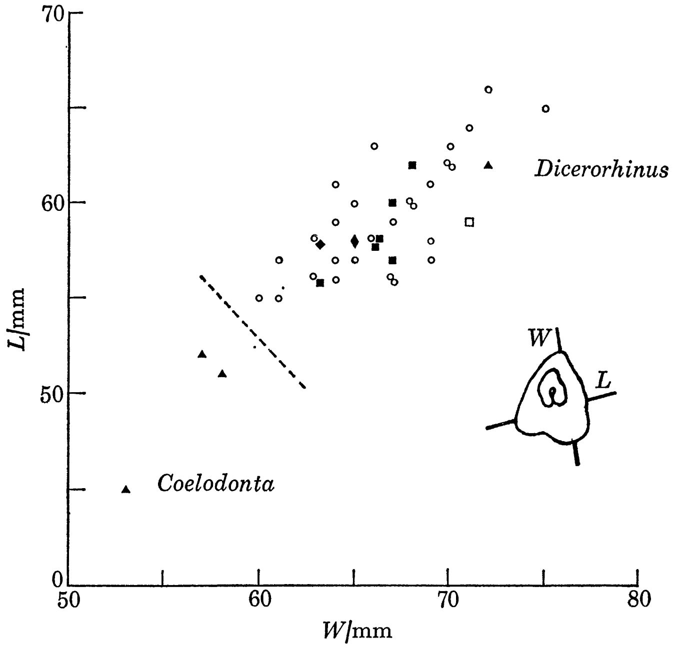

FIGURE 10. Scatter diagram of length (*L*) against ectoloph width (*W*) (both measured at crown base) M^3 of Ipswichian rhinoceroses. *Coelodonta antiquitatis* occurs only at Crayford. *Dicerorhinus hemitoechus*: Barrington, $N = 27$, length $\bar{x} = 59.3$, $s = 3.1$, width $\bar{x} = 66.5$, $s = 3.5$; Ilford, $N = 6$, length $\bar{x} = 58.3$, $s = 2.1$, width $\bar{x} = 66.2$, $s = 1.7$. ○, Barrington; □, Selsey; ■, Ilford; ◆, Brundon; ♦, Lexden; ▲, Crayford.

Coelodonta antiquitatis, present only at Crayford, is readily recognizable from the small size (figure 10) and coarsely corrugated enamel of the cheek teeth. According to Sutcliffe (1960, 1964) the cheek teeth of the two *Dicerorhinus* species can be distinguished on size (*D. kirchbergensis* is larger), degree of hypsodonty, amount of cement, smoothness of enamel and shape

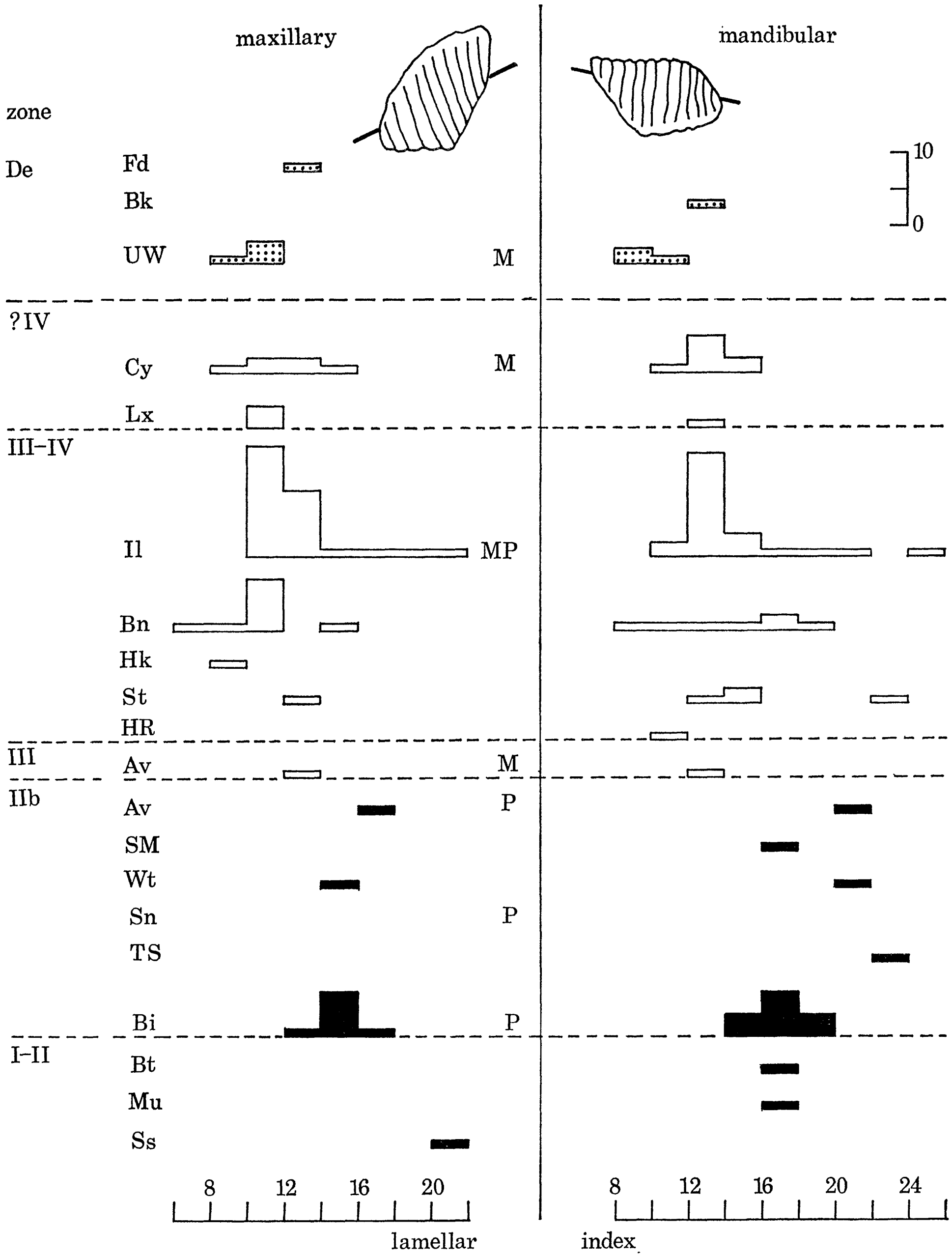

FIGURE 11. Histograms of lamellar indices (length molar in millimetres divided by number of plates) for molars of Ipswichian and Devensian elephants arranged stratigraphically. Indices for maxillary and mandibular teeth shown separately. Solid black: definite *Palaeoloxodon antiquus* from first half of Ipswichian interglacial, stipple: definite *Mammuthus primigenius* from Middle Devensian deposits. M, tusk of *Mammuthus primigenius* recorded; P, tusk of *Palaeoloxodon antiquus* recorded. Fd, Fladbury; Bk, Beckford, UW, Upton Warren (all in Worcestershire). Cy, Crayford; Lx, Lexden; Il, Ilford; Bn, Brundon; Hk, Harkstead; St, Stutton; HR, Histon Road; Av, Aveley; SM, Swanton Morley; Wt, Wortwell; Sn, Stone; TS, Trafalgar Square; Bi, Barrington; Bt, Beetley; Mu, Mundesley; Ss, Selsey.

of M^3. Critical examination of the available Ipswichian material however failed to detect any constant differences. Moreover a scatter diagram of M^3 dimensions (figure 10) suggests that only one species, here provisionally referred to *D. hemitoechus*, was present in the Ipswichian and that no significant size changes occurred during this interglacial.

(*g*) Palaeoloxodon antiquus *Falconer & Cautley and* Mammuthus primigenius *Blumenbach*)

Fossil elephant material is available from nearly all of the sites considered here, and would repay a detailed study. The data presented here are intended primarily to establish which species are present at each site.

The tusks of *M. primigenius* are strongly curved and spirally twisted and can readily be distinguished from those of *P. antiquus* which are only gently curved. Identifications of the few tusks available are incorporated in figure 11. Numerous molars are available for study but they present many problems of identification. In *P. antiquus* molars the lamellae tend to be few and widely spaced with thick enamel, whereas those of *M. primigenius* have more numerous close packed lamellae with thinner enamel, but many teeth are of intermediate type. Because of the method of successional tooth replacement peculiar to elephants it is often impossible to be certain which molar is represented in the case of fossils, especially when more than one species is present. In recent African elephant *Loxodonta africana* Blumenbach the lamellar index, i.e. the length of the tooth in millimetres divided by the number of plates, for mandibular molars increases from M_1 to M_6, although M_5 and M_6 are very close (Laws 1966). This index, which is a measure of the degree of packing of the lamellae on the molars, was calculated for samples of fossil teeth (figure 11). With the exception of the Histon Road specimen, probably an M_3, the smaller teeth were not measured and the samples probably comprise mainly 5th, 6th with some 4th molars. Maxillary and mandibular molars are plotted separately because the latter have higher indices.

In spite of the difficulties and some overlap of indices for the two taxa the general pattern is clear. *P. antiquus* is the only elephant recorded from the first half of the interglacial but from zone Ip III onwards it was accompanied by *M. primigenius*. Where both species occur together remains of *M. primigenius* are always more abundant, and at sites dating from the succeeding Devensian cold stage and probably also at Crayford, it is the only elephant present. The low lamellar index values for the Ipswichian mammoth molars show that they are referable to *M. primigenius*, rather than *Mammuthus trogontherii* (see Guenther 1969).

9. Conclusions

The climatic and vegetational changes through the Ipswichian interglacial in England were accompanied by corresponding changes in the mammal fauna. The tundra-like vegetation of the preceeding Wolstonian glacial stage, which supported a fauna including *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus caballus*, lemmings and *Rangifer tarandus*, gave way to regional mixed oak forest and a temperate fauna including *Palaeoloxodon antiquus*, *Dama dama* and *Hippopotamus amphibius* by zone Ip IIb, in response to ameliorating climatic conditions with warm summers and mild winters. The presence of local deforested areas of herbaceous vegetation in many river valleys supported such animals as *Dicerorhinus hemitoechus* and *Megaloceros giganteus*. At the beginning of zone Ip III the temperate forest appears to have become generally more open, perhaps related to increasing continentality or edaphic changes, and was accompanied by the reappearance of *M. primigenius* and *E. caballus*. If, as is suggested by other evidence, Britain was separated from the Continent at this time these two animals perhaps repopulated southeast England from refugia in the north or Scotland. Zone Ip III shows some loss of forest animals compared with the previous zone, notably *D. dama*. *H. amphibius* probably did not survive beyond the early part of zone Ip III. Towards the end of zone Ip IV, which is considered to be the most likely age of the Crayford deposits, the climate probably became rather cooler and more continental and open boreal forest appears to have become established. Extensive areas of herbaceous vegetation probably grew in many river valleys. The mammal fauna changed markedly, in the loss of the forest elephant *P. antiquus* and the appearance of a number of animals, e.g. *C. antiquitatis* and *Ovibos moschatus*, which are typical of the succeeding Devensian glacial stage. Finally further climatic deterioration at the beginning of the Devensian resulted in the return of a tundra type of vegetation accompanied by a similar fauna to that of the Wolstonian.

The presence of fairly extensive areas of herb-dominated vegetation in river valleys when the regional vegetation cover was forest, as shown by the high levels of herb pollen at many sites, although likely to have been initiated by fluviatile processes was very probably maintained and extended by the activities of herbivorous mammals.

The records of southern plants and invertebrates indicating that much of the Ipswichian the climate was warmer than now supported by the occurrence in England of *Emys orbicularis*, *Crocidura* cf. *suaveolens* and *Hippopotamus amphibius* well north of their present ranges. It is however possible that the absence of the latter animal from Europe in the postglacial is due to man. On the other hand the presence of *Spermophilus undulatus* and animals of tundra: *Dicrostonyx torquatus*, *Lemmus lemmus*, *Ovibos moschatus* at Crayford, probably dating from the end of the interglacial, is most likely to be related to generally open vegetational conditions, since remains of these animals were found in direct association with temperate and southern Mollusca.

Finds of artefacts show that man was present during the interglacial and that large mammals were hunted. More evidence is required in dating man in relation to pollen zones however, and at present the data are inadequate to determine whether he had a significant effect on the mammalian fauna.

I thank Dr C. L. Forbes (Sedgwick Museum of Geology, Cambridge), Mr R. Markham (Ipswich Museum), Mr B. McWilliams (Norwich Castle Museum), Dr A. J. Sutcliffe (British Museum, Natural History), and Mr C. Wood (Geological Survey Museum Institute of Geological Sciences), for access to collections in their care. Mr G. Jarvis kindly made available his unpublished work on Water Hall Farm. I have especially benefited from discussions on various aspects of this work with Dr P. L. Gibbard, Dr K. A. Joysey, Dr D. F. Mayhew, Dr L. Phillips, Dr A. J. Sutcliffe, Dr C. Turner and Professor R. G. West, F.R.S. The support of an N.E.R.C. Research Fellowship is gratefully acknowledged.

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