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The Quaternary origins of the modern British mammal fauna

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The origins of the modern British mammal fauna as a recognizable assemblage are traceable through preceding temperate woodland phases at least as far back as the early part of the Middle Pleistocene. Earlier Quaternary mammal assemblages have more in common with those of the Pliocene than those of the Middle Pleistocene, but evidence for gaps in the British Early Pleistocene sequence precludes inferences concerning the nature of this change in faunal composition.

A major difficulty in reconstructing Quaternary faunal histories is in establishing stable correlations between the fragmentary terrestrial sequences from which the fossil record has been recovered and in assembling those sequences into chronological order. Existing reconstructions of Quaternary events in Britain are of hybrid origin, a mix of palynological biostratigraphy based on assumed monocyclic floral successions for a small number of major interglacial stages, with intervening cold stages identified by characteristic glacial or periglacial lithologies and structures. While this framework has served as a useful basis for some Quaternary disciplines, some interpretations of the mammalian evidence do not fit it well.

Attention is given here to information derived from fossil mammal assemblages which may be used to help determine the number and sequence of Middle and Late Pleistocene temperate woodland phases with faunas showing close links with that of the Flandrian. While much of this information is not new, it has been largely ignored in the construction of some of the more widely known schemes for Quaternary subdivision. At present five such episodes can be identified and characterized prior to the present interglacial, though further refinement may be possible as work on a more detailed account of key sites and their palaeontology progresses.

KEY WORDS:—Mammals – Quaternary – Britain – interglacial – biostratigraphy – faunal change.

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INTRODUCTION

While details of the sequence in which the component species of the modern native mammal fauna arrived in Britain after the last glaciation must be sought

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in the latest phases of the Devensian and the early Flandrian, the existence of this faunal assemblage can be traced far back into the Quaternary. The underlying similarity between those British Middle and Late Pleistocene assemblages which seem to have inhabited temperate woodland and the present native mammal fauna tends to be masked by the modern absence of locally or totally extinct

TABLE 1. The native Flandrian mammal fauna of mainland Britain. Those species which are best described as 'Devensian stragglers', briefly surviving into the early Flandrian, are excluded. The occurrence of fossil material representing these species in previous temperate woodland assemblages is denoted by asterisks, those in brackets being fossils of the same lineage; question marks denote uncertain assignment to the species listed. The columns numbered 1 to 5 indicate recognizable assemblage groupings, 1 corresponding to the Late Pleistocene *Hippopotamus* fauna of the 'Last Interglacial' and 5 corresponding to the early Middle Pleistocene fauna from the West Runton Freshwater Bed on the Norfolk coast. See text for details

		1	2	3	4	5
Erinaceus europaeus	Hedgehog				*	*
Sorex araneus	Common shrew	*	*	*		
Sorex minutus	Pygmy shrew	*	*	*	?	?
Neomys fodiens	Water shrew		*	*	(*)	(*)
Talpa europaea	Mole		*		*	*
Rhinolophus ferrumequinum	Greater horseshoe bat					
Rhinolophus hipposideros	Lesser horseshoe bat					
Myotis mystacinus	Whiskered bat					
Myotis brandti	Brandt's bat					
Myotis nattereri	Natterer's bat				*	
Myotis bechsteini	Bechstein's bat				*	
Myotis myotis	Mouse-eared bat					
Myotis daubentoni	Daubenton's bat					
Eptesicus serotinus	Serotine		*		*	
Nyctalus leisleri	Leisler's bat					
Nyctalus noctula	Noctule					*
Pipistrellus pipistrellus	Pipistrelle					
Barbastella barbastellus	Barbastelle				*	
Plecotus auritus	Common long-eared bat				*	
Plecotus austriacus	Grey long-eared bat					
Homo sapiens	Man			*	*	
Lepus timidus	Mountain hare	*		*	*	*
Sciurus vulgaris	Red squirrel		*		(*)	(*)
Castor fiber	Beaver		*	*	*	*
Muscardinus avellanarius	Dormouse				*	
Clethrionomys glareolus	Bank vole	*	*	*	*	*
Arvicola terrestris	Water vole	*	(*)	(*)	(*)	(*)
Microtus agrestis	Field vole	*	*	*	(*)	?
Apodemus sylvaticus	Wood mouse	*	*	*	*	*
Micromys minutus	Harvest mouse					
Canis lupus	Wolf	*	*	*	(*)	(*)
Vulpes vulpes	Red fox	*				
Ursus arctos	Brown bear	*	*			
Martes martes	Pine marten			*	*	*
Mustela nivalis	Weasel				*	*
Mustela erminea	Stoat	*			*	
Mustela putorius	Polecat	?				?
Meles meles	Badger	*			*	
Lutra lutra	Otter		*	*		*
Felis sylvestris	Wild cat	*		*		*
Sus scrofa	Wild boar	*	*	*		*
Cervus elaphus	Red deer	*	*	*	*	*
Capreolus capreolus	Roe deer	*	*	*	*	*
Bos primigenius	Aurochs	*	*	*		

TABLE 2. Key elements of the Middle and Late Pleistocene and Flandrian mammal faunas arranged to show their use in deriving biostratigraphically significant groupings of temperate woodland assemblages. The groups 1 to 5 (youngest to oldest) are described in the text. Asterisks denote occurrences; F = Flandrian

		F	1	2	3	4	5
Mimomys savini	A water vole						*
Sorex savini	A giant shrew					*	*
Pliomys episcopalis	An extinct vole					*	*
Dicerorhinus etruscus	Etruscan rhinoceros					*	*
Trogontherium cuvieri	An extinct beaver				*	*	*
Pitymys subterraneus	Pine vole				*	*	*
Ursus spp. "spelaeoid"	Cave bears				*	*	*
Macaca sylvanus	Macaque			*	*		*
Castor fiber	Beaver	*		*	*	*	*
Apodemus sylvaticus	Wood mouse	*	*	*	*	*	*
Clethrionomys glareolus	Bank vole	*	*	*	*	*	*
Equus ferus	Horse			*	*	*	*
**Arvicola cantiana*	A water vole		*	*	*	*	
Dicerorhinus kirchbergensis	Merck's rhinoceros			*	*		
Dicerorhinus hemitoechus	Narrow-nosed rhinoceros		*	*	*		
Bos primigenius	Aurochs	*	*	*	*		
Crocidura spp.	White-toothed shrew			*			
Ursus arctos	Brown bear	*	*	*			
Hippopotamus amphibius	Hippopotamus		*				
**Arvicola terrestris*	Water vole	*	*				

*The water vole represented in Group 1 is a transitional morphotype; some individuals have the molar characteristics of *Arvicola cantiana*, some have the characteristics of *Arvicola terrestris*, and others are true intermediates.

Pleistocene megafauna, species that for one reason or another were absolutely excluded from recolonizing Britain after the last major cold stage. Once Middle and Late Pleistocene temperate woodland assemblages are stripped of these species, the remaining core of mainly small to medium-sized mammals is remarkably familiar (Table 1), though there are a number of small but consistent differences between assemblages. When combined with observations on progressive changes in the associated megafauna a number of readily definable faunal groups appear which are taken here as having biostratigraphic significance (Table 2).

It is the intention of this paper to put forward a framework in which to present the observable sequential changes in the composition of Quaternary interglacial mammal faunas so that they may be compared with that of the Flandrian. The framework proposed is at variance with models derived from different disciplines, notably that put forward by Mitchell *et al.* (1973) and followed by Stuart (1974, 1976, 1982) in his reconstruction of Quaternary vertebrate history.

EARLY PLEISTOCENE FAUNAS

Early Pleistocene mammal faunas are uncommon in Britain. Mammals from the Cromer Forest Bed Formation of East Anglia have been found to represent several quite distinct assemblages covering a wide span of Quaternary time (Azzaroli, 1953). A division can be made into a small number of Early Pleistocene faunas mainly attributable to the Pastonian and Pre-Pastonian stages, and a greater number of mainly Middle Pleistocene faunas from the

Beestonian, Cromerian and later stages, with a major stratigraphic hiatus between these two groups.

The Pastonian and Pre-Pastonian faunas from Sidestrand, Norfolk, recently reported by Harrison, Bates & Clayden (1988), provide good examples of their kind. The assemblages are dominated by extinct voles of the genus *Mimomys, M. pliocaenicus, M. reidi,* and *M. blanci* being the most common. Such faunas have virtually nothing in common with our present group of native mammals and are certainly very different from those of the early Middle Pleistocene, but until we can obtain an accurate estimate for the length of time represented by the hiatus in our fossil record, it cannot be said whether the differences seen are more likely to be due to one or more phases of major faunal replacement or to gradual changes in assemblage composition over a longer period.

MIDDLE AND LATE PLEISTOCENE FAUNAS

By the early Middle Pleistocene, British temperate woodland faunas already show close links with that of the Flandrian, but tracing the process of faunal transition through time is not straightforward. Our varied concepts of the number and relative order of events and biotic changes that have taken place in Britain during the last 500 000 years are arrived at by piecing together information recovered from a large number of isolated terrestrial sequences. Stratigraphic superposition is the exception rather than the rule in the Middle and Late Pleistocene geological record. Given the relatively short period of time involved, the kinds of evolutionary change which aid us greatly in ordering much of the geological succession are not often found in the Quaternary biological record, although mammals do provide a few examples where morphological change through time can help in discriminating otherwise similar fossil assemblages.

Assemblage composition has long dominated the approach to all branches of Quaternary biostratigraphy. For example, pollen assemblage biostratigraphy has underpinned much of the work that has taken place on the Middle and Late Pleistocene during the last 25 years (Mitchell *et al.*, 1973) and has been used as the basis for detailed reconstructions of Quaternary vertebrate history by Stuart (1974, 1976, 1982). Stuart's model is entirely consistent with the proposed floral history of the Quaternary with its three Middle and late Pleistocene interglacial stages—Cromerian, Hoxnian and Ipswichian—but produces the need for quite sudden faunal changes during the course of some of the florally defined interglacial periods. For example, Stuart & West (1976) have proposed, on the basis of palynological data, that the evolutionary transition between two morphological 'species' in the water vole lineage, *Mimomys savini* and *Arvicola cantiana,* must have been accomplished within the latter part of the Cromerian interglacial stage as a sudden replacement of one form by the other, an interpretation questioned by Bishop (1982) who put forward evidence for assemblages containing *A. cantiana* being regarded as post-Cromerian (and see von Koenigswald, 1973). Sutcliffe & Kowalski (1976) have also argued that too many quite distinct mammal faunas have been assigned to the Ipswichian interglacial stage on the basis of associated pollen spectra, citing the differences between assemblages from Aveley, Essex and the Trafalgar Square area of London as a major example. The crux of these criticisms is that floral evidence alone does not always permit discrimination between temperate episodes which

appear to be distinct on other criteria, and that differences must rank higher than similarities when it comes to this kind of decision.

Taking the biostratigraphic information derivable from British Middle and Late Pleistocene mammal assemblages *in its own right*, it is possible to construct a different faunal history for the same period. Indirect support for the view that there may be more distinct temperate stages hidden in the British record comes from the greatly extended number of major Quaternary climatic fluctuations recognized in the marine oxygen isotope record (Shackleton & Opdyke, 1973). The assemblage groupings proposed here are independent of any predetermined position for them in existing Quaternary chronologies. The group numbers have no significance other than for reference, nor is it implied that further subdivision or combination is impossible. The groups include only those assemblages for which there is reasonable mammalian evidence for contemporary temperate woodland. In this respect the co-abundance of *Clethrionomys glareolus* and *Apodemus sylvaticus* is taken as a good independent guide (Currant, 1986), although in some assemblages associations of other woodland indicators such as *Dama dama* and *Sus scrofa* have to be relied on in the absence of reliable information on either associated small mammals or other environmentally diagnostic biota. A summary of the characteristic features of the various assemblage groupings is given in Table 2.

Group 5 assemblages

Group 5 is represented by material recovered from the West Runton Freshwater Bed exposed in the cliff section at West Runton, Norfolk. This is the type locality of the Cromerian interglacial. An updated list of the vertebrate fauna has recently been given by Stuart (1988). The commonest mammal found here is a water vole, *Mimomys savini*, believed to have given rise to the later form *Arvicola cantiana* by an increase in the crown height of its molar teeth to the point where roots were no longer developed, a not uncommon phenomenon in the microtine rodents (Hinton, 1926).

Group 4 assemblages

Group 4 is represented by mammals found in a fluviatile channel at Ostend, near Bacton, Norfolk (Stuart & West, 1976); from the 'Pink Breccia' in cave deposits at Westbury-sub-Mendip, Somerset (Andrews, in press); and from Unit 4c in ancient shoreline deposits at Boxgrove, West Sussex (Currant & Parfitt, unpublished). These temperate woodland faunas all contain water voles of the *Arvicola cantiana* evolutionary grade. It is considered unlikely that the change from *Mimomys savini* to *A. cantiana* could have been accomplished suddenly during the climatic optimum of a single interglacial stage without there being at least some evidence of transitional morphologies. Group 5 and 4 assemblages are otherwise of broadly similar composition. As can be seen from Table 1, many of our Flandrian native species are represented in these early Middle Pleistocene interglacial assemblages.

Group 3 assemblages

Group 3 faunas differ from the earlier assemblages in several important characters. The small mammals show a decrease in diversity with the loss of the

giant shrew *Sorex savini* and the vole *Pliomys episcopalis*. There is also a major change in the composition of the rhinoceros fauna, *Dicerorhinus etruscus* being replaced by *Dicerorhinus kirchbergensis* and *Dicerorhinus hemitoechus*. The aurochs, *Bos primigenius*, makes its first appearance in this group as an important element of subsequent British warm stage faunas. Groups 5 to 3 are unified by the occurrence of the pine vole *Pitymys subterraneus* (=*P. arvaloides*), the extinct beaver *Trogontherium cuvieri* and bears which show various stages of development of the cave bear lineage (*Ursus savini*—*U. deningeri*—*U. spelaeus*). Group 3 assemblages can be identified at several sites including Swanscombe, Kent (Sutcliffe, 1964) and Clacton, Essex (Singer *et al.*, 1973). They probably correspond to the Hoxnian interglacial of the floral sequence; *Trogontherium cuvieri* is one of the few mammals recorded from the warmer part of the type sequence at Hoxne, Suffolk (Stuart, 1982).

Group 2 assemblages

While differing from earlier groups in the characters already mentioned Group 2 assemblages can be distinguished from all previous and subsequent stages by the occurrence of one or more species of white-toothed shrew, *Crocidura* spp. (Currant, 1986). They share with earlier temperate woodland faunas such species as the macaque. *Macaca sylvanus*, and horse, *Equus ferus*, but the bears are now represented by *Ursus arctos*, the brown bear. The classic area for this faunal grouping is the old '*Cyrena*' brickfields of Grays Thurrock, Essex, part of the 'Middle Terrace' complex of the Lower Thames (see Zeuner, 1945). Similar assemblages are known from the lower part of the sequence at Aveley, Essex (Stuart, 1976); from the Cudmore Grove channel, East Mersea, Essex (Bridgland *et al.*, 1989); and from Itteringham in Norfolk (personal observation). Deposits yielding faunas belonging to this group have produced pollen spectra variously assigned to the Ipswichian and Hoxnian interglacial stages.

Group 1 assemblages

Group 1 is represented by the '*Hippopotamus* fauna' as found at many sites throughout England and Wales, most notably Barrington, Cambridgeshire (Gibbard & Stuart, 1975); Trafalgar Square, London (Franks, 1960; Sutcliffe & Kowalski, 1976); Victoria Cave, North Yorkshire (Gascoyne, Currant & Lord, 1981) and Joint Mitnor Cave, Devon (Sutcliffe, 1960). These assemblages have also been assigned to the Ipswichian interglacial stage on the basis of associated pollen samples. Uranium series age determinations on stalagmite enclosing characteristic elements of this fauna at Victoria Cave indicate an age of around 120 000 years BP. Only one rhinoceros is found in these faunas, *Dicerorhinus hemitoechus*. Horse, *Equus ferus*, macaque, *Macaca sylvanus* and beaver, *Castor fiber*, are absent from Group 1 assemblages, although beaver makes a reappearance in the Flandrian. As beaver was one of the few mammals found at the Ipswichian type site at Bobbitshole, Ipswich, Suffolk (Stuart, 1976) it is possible that the true Ipswichian floral assemblage belongs with the Group 2 mammal assemblage. While this is a fairly drastic modification of existing correlations, it could be a major step towards resolving the long standing dispute over supposed 'Ipswichian' faunas. At Cudmore Grove, East Mersea, Essex, closely adjacent

channel sequences at similar heights contain quite distinct Group 2 and Group 1 assemblages, countering the argument that the differences between these faunas might be due to regional or ecological factors (Bridgland *et al.*, 1989).

DISCUSSION

The proposed faunal groupings necessarily involve two major modifications to previous models: acceptance of there having been a major temperate woodland episode between the Cromerian and Hoxnian interglacials of the floral sequence and a change in the relative position of the Ipswichian interglacial as originally defined so that it is no longer synonymous with the 'Last Interglacial'. This account is a first attempt to summarize the mammalian evidence into an alternative scheme viewed from the perspective of the progressive development and refinement of a distinctive British temperate woodland fauna. The groupings have the advantage of assuming no great changes in faunal composition in the course of any particular period of climatic optimum.

Excluded from the present discussion are a number of assemblages which may well represent interglacial environments other than temperate woodland, most notably the open grassland faunas found at such sites as Ilford, Essex, which appear to post-date Group 2 but pre-date Group 1 and are characterized by a distinctive form of the mammoth, *Mammuthus primigenius*, with small teeth (Leith Adams, 1877–81). This kind of mammoth is found in deposits overlying a Group 2 assemblage at Aveley, Essex, while it has been found in deposits underlying a Group 1 assemblage at Marsworth, Buckinghamshire (Green *et al.*, 1984). Such faunas appear to have only relatively minor affinites with that of the Flandrian, but the small mammals which would figure strongly in a proper comparison are currently very poorly known.

These observations are based on parts of a more detailed analysis of the biostratigraphy of Quaternary faunas currently in preparation by the author.

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