Table 7.5 Early Flandrian Faunas from Thatcham and Star Carr.

	Thatcham	Star Carr
MAMMALIA		
Insectivora		
Erinaceus europaeus L., hedgehog	+	+
Sorex araneus L., common shrew	+	–
Talpa europaea L., mole	+	–
Primates		
Homo sapiens L., man (humerus)	+	–
Homo sapiens L., man (artefacts)	+	+
Lagomorpha		
Lepus sp.	–	+
Oryctolagus cuniculus (L.), rabbit	+	–
Rodentia		
Castor fiber L., beaver	+	+
Arvicola terrestris L., water vole	+	–
Carnivora		
Canis lupus L., wolf	+	+
Canis (domestic), dog	+	+
Vulpes vulpes (L.), red fox	+	+
Martes martes (L.), pine marten	+	+
Meles meles (L.), badger	+	+
Felis sylvestris Schreber, wild cat	+	+
Perissodactyla		
Equus ferus Boddaert, horse	+	–
Artiodactyla		
Sus scrofa L., wild boar	+	+
Cervus elaphus L., red deer	+	+
Alces alces L., elk	+	+
Capreolus capreolus (L.) roe deer	+	+
Bos primigenius Bojanus, (extinct) aurochs	+	+
AVES		
Graviiformes		
Gavia stellata (*Pontoppidan*), red-throated diver	–	+
Podicipediformes		
Podiceps cristatus L., great crested grebe	–	+
Podiceps ruficollis Pallas, little grebe	–	+
Ciconiiformes		
cf. *Ciconia ciconia* L., white stork	–	+
Anseriformes		
Anas platyrhynchos (L.), mallard	+	–
Anas sp. (small species), a duck	+	–
Bucephala clangula (L.), golden eye duck	+	–
Mergus serrator L., red-breasted merganser	–	+
Falconiformes		
Buteo buteo L., buzzard	–	+
Ralliformes		
Grus grus L., common crane	+	+
Charadriformes		
Vanellus vanellus L., lapwing	–	+
Passeriformes		
Turdus sp., blackbird or thrush, etc.	+	–

fish remains at Star Carr, as indicating that by zone IV (Fl Ia) fishes had not yet penetrated the Vale of Pickering via the River Derwent.

'Surface MX' at Nazeing, Essex, in the floodplain deposits of the River Lea, yielded material of common shrew *Sorex araneus*, pika *Ochotona pusilla*, bank vole *Clethrionomys glareolus*, water vole *Arvicola terrestris*, northern vole *Microtus oeconomus* and wood mouse *Apodemus sylvaticus* (Allison et al. 1952). The pollen spectra from immediately above this horizon indicate pine-birch woodland and a zone V (Fl Ib) age. The fauna is generally consistent with a woodland environment, but the occurrence of *Ochotona pusilla* – a survival from the Late Devensian – is interesting as this species now occurs only in the Palaearctic steppe (Ch. 5).

Bones of wild boar *Sus scrofa* and red deer *Cervus elaphus* are recorded from sands overlying peat and beneath estuarine clays at Belfast Lough; all apparently dating from the early Flandrian (Savage 1964, 1966). These finds suggest that both species are native to Ireland.

Vertebrate material dating from later in the Flandrian is available from such deposits as the peats of the East Anglian Fenland and from archaeological sites. Many finds are in need of critical reassessment, with regard to both identification and stratigraphy. Only the more interesting records will be considered here.

The peats of the Fen margins north of Cambridge (Godwin 1978) date from the second half of the Flandrian, i.e. subzone VIIa (Fl IId, about 7 000 years B.P.) and later. Most of the bones collected from this area (villages of Burwell, Swaffham and Reach) during the last century are probably of zone VIII age (Fl IId, early Fl III). Mammals recorded include wolf *Canis lupus*, brown bear *Ursus arctos*, otter *Lutra lutra*, beaver *Castor fiber*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus* and aurochs *Bos primigenius*. Birds include bittern *Botaurus stellaris*, mute swan *Cygnus cygnus*, whooper swan *Cygnus olor*, white-tailed eagle *Haliaetus albicilla*, common crane *Grus grus* and razorbill *Alca torda* (Northcote 1980b).

The record of elk *Alces alces*, based on droppings from peat at Ugg Mere, Cambridgeshire, and radiocarbon dated to about 3 260 years B.P. (Godwin, 1975), is now known to be incorrect. Re-examination of the material by A. Lister has shown that the droppings are too small for *A. alces*. There are no other records of this animal from later than the early Flandrian.

Vertebrae of a pelican *Pelecanus* sp. were recovered from peat near King's Lynn, Norfolk, radiocarbon dated to 3 915 ± 120 years B.P. (Forbes *et al.* 1958). Dalmatian pelican *Pelecanus crispus* is recorded from several localities in the Cambridgeshire Fens, and also from the Iron Age Lake village at Glastonbury, Somerset (Northcote 1980b).

The sole record of European pond tortoise *Emys orbicularis*, from the Flandrian of the British Isles, is based on remains of three individuals from mere peats at East Wretham, near Thetford, Norfolk (Stuart 1979). Pollen analysis of a peat sample preserved with the finds indicate a subzone VIIa (Fl IId) age.

Northern vole, not recorded from later than the early Flandrian on the mainland, occurs in Bronze or Iron Age deposits at Nornour, Isles of Scilly (Pernetta & Handford 1970).

Written sources provide most of the evidence for survival into historical times of many species which subsequently became extinct in Britain (see Table 7.6).

Flandrian faunal history

The history of the wild vertebrate fauna during the Flandrian (Fig. 7.16) is complicated by factors, not important in earlier interglacials:

(a) isolation of Britain from the Continent early in the Flandrian – preventing further immigration of terrestrial and freshwater vertebrates;

(b) extinctions, mainly of large mammals due to human activities; and

(c) the introduction by man of alien vertebrates to Britain (Ch. 10).

The availability of good early Flandrian faunas is particularly valuable because the faunas of pollen zone I age from earlier interglacials are almost unknown. *Ochotona pusilla, Microtus oeconomus* and perhaps *Equus ferus* as a native species were restricted to the early Flandrian, in association with regional birch and pine forests, and probably extensive open habitats. They can be regarded as survivals from the Late Devensian. On the other hand, the earliest Flandrian faunas (zone IV – Fl Ia) already include several taxa nowadays associated with the regional temperate forest biotope, and not extending further north than southern Fennoscandia: mammals – *Erinaceus europaeus, Talpa europaea, Meles meles, Sus scrofa* and *Cervus elaphus*;

and birds – *Podiceps cristatus, Podiceps ruficollis* and *Ciconia ciconia*. This phenomenon may reflect a rapid amelioration of climate early in the Flandrian.

The record of *Oryctolagus cuniculus* from the very early Flandrian is remarkable in that this species is generally thought to have been restricted to parts of Iberia during the postglacial until its fortunes were dramatically reversed by man from Roman times onwards, when it was introduced to northern Europe. Confirmation of the Thatcham record would be desirable. It is, however, possible that the rabbit became extinct in Britain at some time after the early Flandrian and was re-introduced in Norman or Plantagenet times.

The single record of *Emys orbicularis* (three individuals) of zone VIIa (Fl IId) age, at the climatic optimum of the Flandrian, is particularly significant as there are no less than six records from the previous and generally warmer Ipswichian interglacial, and numerous Flandrian finds from Denmark and southern Sweden. The abundance of Scandinavian records is very probably related to the prevalence of warmer summers further east.

The extinction of a number of wild mammals and birds within the last 2 000 years or so is clearly related to hunting coupled with destruction of the forests and later draining of the wetlands by man. The subject is discussed in Chapter 10.

Comparison with Continental faunas

It is especially interesting to compare the Flandrian vertebrate faunal succession in Denmark and adjacent areas, as reviewed by Degerbøl (1964), with that seen in England. Important differences include the records of horse *Equus ferus* from Swedish deposits pollen-dated to zone V (Fl Ib), and the survival of elk *Alces alces* in Denmark until at least zone VIIb (early Fl III). The European pond tortoise *Emys orbicularis* is represented by numerous fossils from Denmark and southern Sweden, covering pollen zones V (Fl Ib) to VIIb (early Fl III). (Degerbøl & Krog 1951; Stuart 1979). This disparity between the numbers and stratigraphical ranges of Scandinavian and English finds reflects the warmer summers in the east, while the species was probably near the limits of its range in Britain with its cooler and more cloudy maritime climate (Ch. 3).

The modern fauna

The present-day native vertebrate fauna of the British Isles comprises about 200 breeding birds, 41 non-marine mammals (including 5 species extinct within the last 2 500 years) and 11 breeding bats, 19 primary freshwater fishes, 6 reptiles and 6 amphibians (Table 7.6).

Table 7.7 demonstrates the way in which the present-day vertebrate faunas of Britain and Ireland become progressively impoverished according to their remoteness from Continental Europe. For example, voles and snakes are native to Britain but not Ireland, and green lizard *Lacerta viridis* and garden dormouse *Eliomys quercinus* are absent from the British Isles, but are found on the adjacent part of the Continent. This phenomenon is in part due to climatic factors and a reduced variety of habitats in Ireland, but for terrestrial and freshwater species it is largely related to the timing of Flandrian land/sea level changes. These changes may have isolated Ireland from Britain (formerly connected via southwest Scotland) as early as about 9 500 years B.P., and then Britain from the Continent (formerly connected via the southern North Sea and Straits of Dover) perhaps a thousand years later (Ch. 2).

Vertebrate species occurring on the adjacent Continent at the present day, but absent from the British Isles, are almost entirely those with southern, or sometimes eastern, distributions in Europe. Presumably they were not able to advance sufficiently far north, in response to the Flandrian climatic amelioration, before Britain became isolated by the rise in sea level. It is possible, however, that a few such species did manage to reach Britain, but subsequently became extinct due to climatic or other changes, as did *Emys orbicularis*.

Significantly, the fall in species from France to Britain to Ireland is least marked in the aerial birds and bats, whose distribution is likely to be little affected by sea barriers. As far as the birds are concerned there are actually more breeding species in Britain than in the rather small area of the Continent used for comparison, which has a less varied range of habitats. Similarly, the more restricted availability of habitats, and, to a lesser extent, climatic conditions account for the rather lower numbers of breeding birds and bats in Ireland compared with Britain.

The restricted distributions within the British Isles of many native vertebrate species can be attributed wholly or partly to human interference (Ch. 10), which complicates the interpretation of natural distribution patterns determined by climatic and geographical factors. Species of mammals confined in the British Isles to offshore islands appear to have been introduced by man from the Continent (see Ch. 10).

Wheeler (1977) considers that all the primary freshwater fishes (pike *Esox lucius*; Cyprinidae (e.g. roach *Rutilus rutilus*, tench *Tinca tinca*); loaches *Cobitis taenia* and *Noemacheilus barbatulus*; burbot *Lota lota*; perch *Perca fluviatilis*, ruffe *Gymnocephalus cernua*; and miller's thumb *Cottus gobio*) now found in the British Isles, are only indigenous to the river catchments bordering the eastern English Channel and southern North Sea. The fishes are thought to have entered these rivers when they were formerly joined in the extensive land area con-

Table 7.6. Present day native British fauna of terrestrial vertebrates (*, also occurs in Ireland; †, extinct).

AMPHIBIA (Smith 1969)
Triturus cristatus (Laurenti), warty newt
**Triturus vulgaris* (L.), smooth newt
Triturus helveticus (Razoumoski), palmate newt
Bufo bufo (L.), common toad
**Bufo calamita* Laurenti, natterjack
**Rana temporaria* L., common frog

REPTILIA (Smith 1969)
Anguis fragilis L., slow-worm
Lacerta agilis L., sand lizard
**Lacerta vivipara* Jacquin, viviparous lizard
Natrix matrix (L.), grass snake
Coronella austriaca Laurenti, smooth snake
Vipera berus (L.), adder

MAMMALIA (modified from Corbet & Southern 1977)
(Includes species extinct within last 2 500 years, shown by †)

Insectivora
Sorex araneus L., common shrew
**Sorex minutus* L., pigmy shrew
Neomys fodiens (Pennant), water shrew
**Erinaceus europaeus* L., hedgehog? Introduced in Ireland
Talpa europaea L., mole

Lagomorpha
Lepus capensis L., brown hare. Introduced recently in Ireland.
**Lepus timidus* L., mountain hare

Rodentia
**Sciurus vulgaris* L., red squirrel ?Introduced in Ireland
†*Castor fiber* L., beaver. Extinct twelfth century or later
Muscardinus avellanarius (L.), dormouse
Clethrionomys glareolus (Schreber), bank vole. Introduced in Ireland (probably very recently)
Arvicola terrestris L., water vole
Microtus agrestis (L.), field vole
Micromys minutus (Pallas), harvest mouse
**Apodemus sylvaticus* (L.), wood mouse Introduced in Ireland
Apodemus flavicollis (Melchior), yellow-necked mouse

Carnivora
†**Canis lupus* L., wolf. Extinct eighteenth century
**Vulpes vulpes* (L.), red fox
† *Ursus arctos* L., brown bear. Extinct about tenth century
**Martes martes* (L.), pine marten
**Mustela erminea* L., stoat
Mustela nivalis L., weasel
Mustela putorius L., polecat
**Meles meles* (L.), badger
**Lutra lutra* (L.), otter
Felis sylvestris Schreber, wild cat

Artiodactyla
†**Sus scrofa* L., wild boar. Extinct probably seventeeth century
**Cervus elaphus* L., red deer
Capreolus capreolus (L.), roe deer
†*Bos primigenius* Bojanus, aurochs. Extinct by 2 500 years B.P.?

Table 7.7. Numbers of non-marine vertebrate species native to Ireland, England and the adjacent areas of Continental Europe. (Data from Muus & Dahlstrøm 1971; Wheeler 1977; Arnold & Burton 1978; Heinzel *et al.* 1972; Sharrock 1976; Brink 1967)

	Ireland	England	Belgium and north-east France
Fish (primary freshwater species)	0	19	24
Amphibians	3	6	16
Reptiles	1	6	8
Birds (breeding species)[1]	138	182	170+
Mammals (except bats)[2]	14	30	37
Bats (breeding species)	6	11	13

1. British Isles 201, Scotland 181
2. Includes species occurring within last 3000 years (see Table 7.6) and man.

necting England with the Continent in the early Flandrian. The occurrence of many of these primary freshwater species in other parts of the British Isles, is attributed to introduction by man, and the only native fishes in these areas, including Ireland, are the secondary freshwater species which are tolerant of saltwater and penetrated the rivers via the sea. Fossil evidence is needed to confirm or refute this hypothesis.

Two secondary freshwater fishes, the arctic charr *Salvelinus alpinus* and whitefishes *Coregonus* spp., are restricted to isolated occurrences in cold upland lakes in Scotland, Cumbria, North Wales, and lowland lakes in Ireland. They also occur in the Alps and elsewhere. The main present-day distributions of these fishes are, however, in arctic and northern seas, ascending rivers to spawn. The non-migratory freshwater populations are probably the descendants of Late Devensian fishes which became isolated when the main distributions shifted northward with the improved climate of the early Flandrian. A find of salmonid bones and scales, probably attributable to *Salvelinus*, from Esthwaite Water, Cumbria, in a deposit dating from the end of the Late Devensian, lends some support to this interpretation (Freshwater Biological Association 1960; Wheeler 1977).

Similar relict distributions, paralleling those of certain plants, e.g. dwarf-birch *Betula nana*, are shown by the mountain hare *Lepus timidus* and ptarmigan *Lagopus mutus*. *Lepus timidus*, recorded from southern England in the Devensian, is now indigenous only to the Scottish Highlands and Ireland, although introduced to other upland areas. In lowland Britain it is replaced by brown hare *Lepus capensis*, which however is not indigenous to Ireland. *Lagopus mutus*, also recorded from Devensian deposits in England, is now restricted to the Scottish Highlands (Sharrock 1976).

The overall distributions of many birds within the British Isles are clearly much influenced by biogeographical factors. Many species are more or less coastal, or favour upland or lowland areas, while others breed only in, for example, southern England or conversely only in Scotland, stressing the importance of climatic controls. The difficulties of disentangling such effects, from those produced by man, however, must again be pointed out (Ch. 10).

Amphibians and reptiles with distributions which, at least in part, reflect climatic factors, include natterjack *Bufo calamita* (restricted to sandy coastal and heath areas in England and south-west Ireland), sand lizard *Lacerta agilis* (restricted to sandy coastal and heath areas in England and Wales), smooth snake *Coronella austriaca* (distribution as in *L. agilis*, but restricted to southern England) and grass snake *Natrix natrix* (absent from Scotland except the Midland Valley) (Arnold 1973). Yalden (1980) has suggested that the disjunct ranges of *B. calamita, L. agilis* and *C. austriaca* result from initial early Flandrian colonization of large areas of lowland Britain, followed by a drastic reduction of range to coastal areas as forest replaced open herb vegetation. Climatic deterioration restricted their spread from these refugia when the forests were subsequently cleared by man. Of the mammals, dormouse *Muscardinus avellanarius* and harvest mouse *Micromys minutus* are probably indigenous only to England and Wales, because of climatic limitations.

8 Middle and Upper Pleistocene cold-stage faunas

General

The cold stages are characterized by climates predominantly much colder than those of the present day, but each covers complex sequences of climatic fluctuations. As currently recognized, each cold stage lasted several times longer than any interglacial. Radiocarbon dates on Devensian material show that the duration of this cold stage is at least 60 000 years, perhaps as much as 90 000 or 100 000 years (see Ch. 2).

Each cold stage covers a period in which climatic and vegetational conditions varied widely. For much of the time, however, the vegetation was herb-dominated mainly with grasses and sedges, but there were also milder periods which permitted the growth of tree birch and conifers, and, on the other hand, intensely cold phases with very little fauna or flora ('polar desert') may also have occurred. Some beetle faunas of Devensian age indicate that there were short periods of warm climate which were not accompanied by the establishment of woodland, although perhaps they resulted in a richer herb growth.

During the Devensian the main phase of glaciation appears to have been late in the stage, between about 18 000 and 15 000 radiocarbon years B.P. The relative timings of glaciations within earlier cold stages can only be estimated very roughly (see Ch. 2). There are considerable difficulties in dating fossiliferous deposits to or within particular cold stages older than the Devensian, because such deposits are well beyond the range of radiocarbon dating and, unlike interglacials, also lack a continuous pollen or other biostratigraphical record.

The vertebrate faunas of the Middle and Upper Devensian can be dated by radiocarbon and usually related to fossil floras and beetle faunas. Again, however, there exists no continuous biostratigraphical record for much of the stage, and all too often one is relying solely on the accuracy of radiocarbon dates.

Early Devensian deposits are beyond the range of radiocarbon dating, or near the limits of the method, but fortunately there exists a fairly continuous pollen record for some of this period, and the woodland interstadials can probably be distinguished on their pollen spectra (Ch. 2). A further difficulty with cold-stage vertebrate faunas is that at most open sites the fossils, which often occur in very large numbers, are generally not found in the datable organic horizons but in the sands and gravels above and below.

For the reasons given above it is not possible to reconstruct the history of the vertebrate fauna through the Beestonian, Anglian or Wolstonian stages even in outline. The changes in the mammal faunas during the Devensian, however, can be followed in some detail.

The typical vertebrate faunas of the cold stages, excluding periods with woodland interstadials on the one hand and polar desert on the other, comprise: (a) extinct taxa; (b) taxa now confined to arctic or rarely alpine regions; (c) taxa nowadays characteristic of steppe; and (d) animals now confined to regions further south.

These associations are remarkably similar for the Anglian, Wolstonian and Devensian stages and reflect climatic and vegetational conditions not represented anywhere in the world at the present day.

There is a rather marked reduction in species diversity in cold-stage faunas in comparison with those of interglacial age. On the other hand, the abundance of bones, especially of *Bison priscus*, recovered from many deposits of Devensian age indicates that during certain phases within cold stages the vertebrate biomass may have considerably exceeded that of any time within an interglacial period.

Table 8.1. Mammal faunas from pre-Devensian cold stages. Be, Beeston; Ang, Anglian; Wo, Wolstonian

Stage/substage	West Runton Be	Beeston Be	Mundesley e-Ang	Wallingford ?Ang	Homersfield ?Ang	Hoxne l-Ang	Baginton-Lillington Gravels e-Wo	Broome Heath Wo	Bakers Hole Wo	Water Hall Farm l-Wo
PRIMATES										
Homo sapiens L., man	–	–	–	?	–	–	–	–	+	–
RODENTIA										
Spermophilus sp., suslik	–	–	+	–	–	–	–	–	–	–
Lemmus lemmus (L.), Norway lemming	–	–	–	+	–	–	–	–	–	–
Arvicola cantiana (Hinton), extinct water vole	–	–	–	+	–	–	–	–	–	–
Microtus oeconomus (Pallas), northern vole	–	–	–	–	–	–	–	–	–	+
Microtus gregalis (Pallas), tundra vole	–	–	–	+	–	–	–	–	–	?
CARNIVORA										
Crocuta crocuta Erxleben, spotted hyaena	–	–	–	–	–	–	+	–	–	–
PROBOSCIDEA										
cf. *Mammuthus trogontherii Pohlig*, extinct elephant	–	+	–	–	–	–	–	–	–	–
Mammuthus primigenius Blumenbach, mammoth	–	–	–	–	+	–	+	+	+	–
PERISSODACTYLA										
Equus ferus Boddaert, horse	–	–	–	+	+	–	+	–	+	–
Coelodonta antiquitatis Blumenbach, woolly rhino	–	–	–	–	+	–	+	–	+	–
ARTIODACTYLA										
Megaceros giganteus Blumenbach, giant deer	–	–	–	–	+	–	–	–	–	–
Cervus elaphus L., red deer	–	–	–	–	–	+	–	–	–	–
Rangifer tarandus L., reindeer	–	–	–	+	+	–	+	–	–	–
Indet. deer	+	–	–	–	–	–	–	–	–	–
Bison sp. or *Bos* sp., bison or aurochs	+	–	–	–	+	–	+	+	–	–

Pre-Devensian Cold Stages (Fig. 8.1, Table 8.1)

The very few available 'cold' faunas for which a pre-Devensian age can be demonstrated are very similar to typical faunas of Devensian age. The implication is that the former are perhaps fairly common, but in general are assumed to be of Devensian age in the absence of clear stratigraphical evidence.

The paucity of faunas and the impossibility of dating deposits precisely within the stage, precludes any attempt at present to reconstruct faunal histories for the Beestonian, Anglian and Wolstonian cold stages.

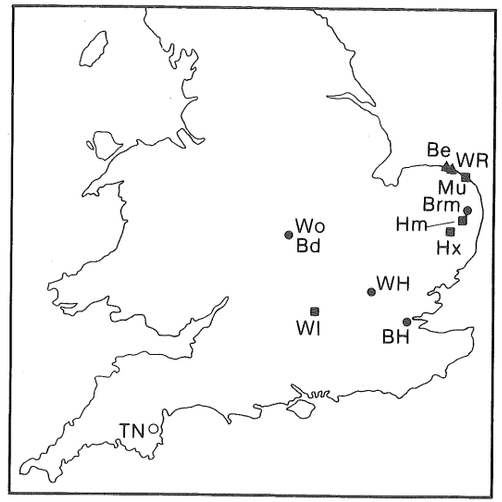


Fig. 8.1. Location map of Beestonian, Anglian and Wolstonian vertebrate sites. ▲, Beestonian; ■, Anglian; ●, Wolstonian; (cave sites shown by open symbols). Bd, Brandon; Be, Beeston; BH, Baker's Hole, Northfleet; Brm, Broome Heath; Hm Homersfield; Hx, Hoxne; Mu, Mundesley; TN, Tornewton Cave; WH, Water Hall Farm; Wl, Wallingford; Wo, Wolston, WR, West Runton.

Beestonian Stage

At present only four fossil mammal specimens can be confidently assigned to the Beestonian Cold Stage. A mandible of an elephant apparently intermediate between *Archidiskodon meridionalis* and *Mammuthus trogontherii*, was found *in situ* in the cliff at Beeston, Norfolk, in marine beach sands and gravels (Bed O), assigned to the Beestonian Stage, and resting on an eroded surface of Pastonian marine silts (West 1980a). Pollen spectra from Bed O consist mainly of grasses, birch and pine, but with some pollen of thermophilous trees probably reworked from the Pastonian. A cool climate and grassy vegetation with stands of birch and pine can be tentatively inferred.

At West Runton, Norfolk, the topmost bed of the pre-West Runton Freshwater Bed (Cromerian) succession (Bed i) consists of sands and silts with marine shells assigned to the Beestonian Stage (West 1980a). *Bison* and a deer are recorded from this bed.

Anglian Stage

A crushed skeleton of a suslik *Spermophilus* sp. was found in freshwater silts ('Arctic Bed') immediately beneath the till in the cliff at Mundesley, Norfolk (Newton 1882b). These silts are now referred to the Early Anglian Cold Stage, and the pollen spectra indicate open grassland and a cold climate (West 1980a). Unfortunately, this constitutes the only known fossil mammal definitely dated to the beginning of this stage. The association of *Spermophilus* with unwooded vegetational conditions is consistent with the ecology of this genus at the present day.

The Wallingford Fan Gravels occur, as remnants of a formerly more extensive sheet, near Benson, Oxfordshire. The deposits, about 6 m thick, mainly comprise chalky flint gravels, thought to have been soliflucted (coombe deposits), and angular flint gravels and sands with seams of sands, calcareous silts and clays, largely deposited under fluviatile conditions (Horton & Whittow, in Shephard-Thorn & Wymer 1977). The stratification has been contorted by cryoturbation, and ice-wedge casts also testify to permafrost conditions during the deposition of these beds. The Wallingford Fan Gravels appear to grade to the level of the Winter Hill or Black Park Terrace of the River Thames, which suggests an Anglian age, but this is by no means certain.

In Hall's Pit near Benson, Dr A. Horton found in the calcareous silt unit (unit ii) non-marine Mollusca and rare vertebrate remains including frog *Rana* sp. and/or toad *Bufo* sp., Norway lemming *Lemmus lemmus*, extinct water vole *Arvicola cantiana*, tundra vole *Microtus gregalis*, horse *Equus ferus*, and reindeer *Rangifer tarandus*.

A single well-dated record of red deer *Cervus elaphus* from the Late Anglian is known from Hoxne, Suffolk. Three foot bones were found resting on the surface of the Anglian till in lacustrine clay mud and marl (Bed F) containing pollen indicative of the Anglian late-glacial (Spencer, in West 1956). The pollen points to open herb-dominated vegetational conditions with sea buckthorn *Hippophaë* scrub. This gives a clear association of *C. elaphus* with unwooded vegetational conditions (Ch. 5).

In the valley of the River Waveney, which is the boundary between Norfolk and Suffolk, two distinct terraces occur above pollen-dated Ipswichian deposits, at Wortwell, Norfolk (see Ch. 2) which are at approximately the level of the modern flood-

plain (Sparks & West 1968). The higher, and therefore presumably older, Homersfield Terrace surface is at approximately 8 m above the floodplain. In the early 1950s mammalian remains were collected from sands and gravels of this terrace at Homersfield, Suffolk, by Prof. B. Funnell, and the fauna comprises mammoth *Mammuthus primigenius*, woolly rhino *Coelodonta antiquitatis*, horse *Equus ferus*, reindeer *Rangifer tarandus*, giant deer *Megaceros giganteus* and a large bovid *Bison* or *Bos*, and is thus a typical cold-stage fauna, identical to faunas of Wolstonian or Devensian age. Recent work by Coxon (1979) has shown that at nearby Flixton, the Homersfield Terrace deposits are intimately associated with chalky till. This and the height relationships to the type Hoxnian interglacial lake deposits at Hoxne, also in the Waveney Valley area, suggest an Anglian age for this terrace. Previously the terrace had been tentatively ascribed to the Wolstonian Stage by Sparks and West.

Wolstonian Stage

The surface of the Broome Terrace of the River Waveney lies about 3 m above the floodplain. Teeth of mammoth *Mammuthus primigenius*, and bones of a bovid *Bison* sp. or *Bos* sp., have been found in the sands and gravels of this terrace at Broome Heath, and organic deposits at this site have yielded a full-glacial flora of plant macrofossils. The discovery of reworked Hoxnian plant remains at this site by Coxon here confirms the Wolstonian age previously suggested by Sparks and West (1968).

Large-mammal remains have been collected from pits in the fluviatile Baginton-Lillington Gravel in the vicinity of Wolston, Warwickshire (Shotton 1953, 1968). These deposits are the lowest member of the type sequence of the Wolstonian, and most probably date from the very early part of this stage. The fauna is given as: spotted hyaena *Crocuta crocuta*, mammoth *Mammuthus primigenius*, straight-tusked elephant *Palaeoloxodon antiquus*, woolly rhino *Coelodonta antiquitatis*, horse *Equus ferus*, reindeer *Rangifer tarandus* and bison *Bison* sp. or aurochs *Bos* sp. The record of *P. antiquus*, if correct, is unexpected in a cold-stage fauna.

At Brandon, Warwickshire, fossiliferous silts occupying a channel within the Baginton-Lillington gravels yielded a very interesting fauna of freshwater fishes (Osborne & Shotton 1968). According to H. Greenwood is Osborne & Shotton (1968), the species present include pike *Esox lucius*, gudgeon *Gobio gobio*, possibly minnow *Phoxinus phoxinus*, chub *Leuciscus cephalus*, roach *Rutilus rutilus*, various other undetermined cyprinids, perch *Perca fluviatilis* and three-spined stickleback *Gasterosteus aculeatus*. The beetle fauna is stated to include some southern forms and lacks arctic stenotherms, and the pollen spectra indicate meadow birch woodland Kelly (1968). *Gobio gobio* and *L. cephalus* do not occur further north than southern Scandinavia at the present day.

The general picture is of a cool but not arctic climate, suggesting interstadial conditions within the Early Wolstonian.

At Northfleet, Kent, in a small tributary valley of the River Thames, coombe rock, frost-heaved chalk, soliflucted gravels and loess underlie freshwater silts, attributed to the Ipswichian Interglacial on the basis of temperate non-marine molluscan faunas. Further periglacial deposits occur above (Kerney & Sieveking, in Shephard-Thorn & Wymer 1977). Excavations at the Baker's Hole pit early in the present century (Smith 1911) yielded a few large-mammal remains (Table 8.1) from the earlier periglacial deposits, which appear to be of Wolstonian age – again probably from late in this stage.

Lacustrine stonewort *Chara* marls at Water Hall Farm, Hertfordshire, occur beneath sands and gravels containing *Hippopotamus amphibius* and other mammals indicative of the Ipswichian interglacial. The marls are penetrated by one or more ice-wedge casts which indicate a Wolstonian age, most probably near the end of this stage. Small vertebrates from the deposit include pike *Esox lucius*, frog *Rana* sp. and/or toad *Bufo* sp. and northern vole *Microtus oeconomus*.

In Tornewton Cave, Torbryan, Devon, a series of deposits with vertebrate fossils represents parts of the Wolstonian, Ipswichian, Devensian and Flandrian Stages (Sutcliffe & Zeuner 1962) (see Fig. 7.11). The oldest fossiliferous bed, termed the Glutton Stratum, thought to have been soliflucted into place, contains stalagmite apparently shattered by freeze-thaw processes, and has yielded arctic mammals. The immediately overlying Bear Stratum has much the same fauna but lacks evidence of periglacial conditions. The stratigraphical position of these beds, beneath the Hyaena Stratum with its characteristic Ipswichian fauna, suggests that both the Glutton and Bear Strata are of Wolstonian age; most probably dating from near the end of the stage. Unfortunately, however, there are strong suspicions that the faunal remains from the Glutton Stratum are mixed with material of interglacial age.

Mammals recorded from the Glutton and Bear Strata are bear *Ursus* sp., wolf *Canis lupus*, red fox *Vulpes vulpes*, lion *Panthera leo*, badger *Meles meles*, clawless otter *Aonyx antiqua* Blainville, glutton *Gulo gulo*, mountain hare *Lepus timidus*, horse *Equus ferus*, rhinoceros cf. *Coelodonta* sp., reindeer *Rangifer tarandus* and a small bison or aurochs (Sutcliffe & Zeuner 1962). Small vertebrates include fishes, frogs and/or toads, common hamster *Cricetus cricetus*, a small hamster assigned to the extinct *Allocricetus bursae*, steppe lemming *Lagurus lagurus*, arctic lemming *Dicrostonyx torquatus*, Norway lemming *Lemmus lemmus* and northern vole *Microtus oeconomus* (Kowalski 1967; Sutcliffe & Kowalski 1976. The status of the records of snow vole *Microtus nivalis* from this site have been discussed in Chapter 3. Birds identified from these beds by Harrison (1980) include ducks, kestrel *Falco tinnunculus*, eagle owl *Bubo bubo*, crossbill *Loxia* cf. *curvirostra*, carrion crow *Corvus corone* and raven *Corvus corax*. A fragment found in the Glutton Stratum is the sole basis for the description of the extinct patridge *Alectoris sutcliffei* Harrison. Confirmation of this record with more material would be desirable.

The Glutton and Bear Strata faunas show a mixture of steppe, boreal-arctic, and temperate components as is seen in many Devensian faunas, although the steppe contribution, including hamsters and *Lagurus lagurus*, is especially marked. The presence of the distinctly temperate *Meles meles*, and if correct of *Loxia curvirostra*, a species dependent on coniferous trees, however, either indicates interstadial conditions or may reflect contamination with interglacial material.

Comparison with Continental faunas

Some of the faunas from central Europe (e.g. Stránská Skála, Vértesszöllös, Mauer) which have been ascribed to the Elsterian (Anglian) (Kahlke 1975a), could be more convincingly correlated with the Cromerian Interglacial (Ch. 7). Faunas of probable Elsterian age listed by Kahlke, e.g. Bornhausen and Neuekrug (Harz), West Germany, include *Mammuthus trogontherii*, *Coelodonta antiquitatis*, *Rangifer tarandus* and *Bison priscus*.

At Steinheim (Murr), West Germany, the 'Main Mammoth Gravels' overlying the gravels with a Holsteinian fauna (Ch. 7) and therefore of probable Saalian age, have yielded a fauna which includes elephants referred to both *M. trogontherii* and *M. primigenius*, *C. antiquitatis*, *Megaceros giganteus* and *B. priscus* (Kahlke 1975a).

Similar faunas assigned to the 'Rissian' (Saalian, Wolstonian) Cold Stage are recorded from the cave sequences of Southern France (Lumley 1976). The southern location, however, is reflected in the occurrence of such temperate species as fallow deer *Dama dama* and aurochs *Bos primigenius* in many of these faunas and the proximity to mountainous areas by the many finds of ibex *Capra ibex* and chamois *Rupicapra rupicapra*.

Devensian stage

An outline of the stratigraphy, climate, vegetation and history of the beetle faunas of this stage is given in Chapter 2.

Sites and faunas (Fig. 8.2, Table 8.2)

The vertebrate faunas of the Devensian are far better known than those of earlier cold stages, and have been found in most areas of the British Isles. Open-site records are mostly from fluviatile deposits, but some of the best-preserved material comes from lacustrine sediments. Most assemblages from caves are also of Devensian age. Unfortunately, however, the majority of finds are neither accurately stratified nor dated.

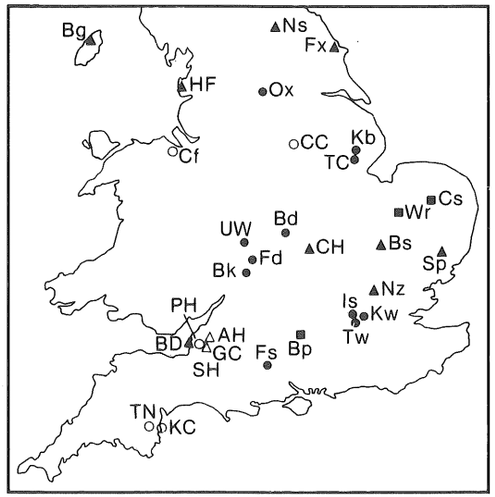
Early Devensian (pre-50 000 radiocarbon year B.P.)
Early Devensian vertebrate faunas are known so far almost entirely from only two localities, both in Norfolk (Table 8.2).

In the early 1960s excavations for a flood-relief channel along the Fenland margin at Wretton, Norfolk, revealed an extremely complex sequence of Ipswichian and Devensian deposits of the River Wissey (Sparks & West 1970; West *et al.* 1974) (Fig. 8.3). The Devensian sediments record deposition in a wide range of environments. Much of the

Table 8.2. Mammal faunas from well-stratified/dated Devensian open sites. Circled crosses indicate radiocarbon-dated records. Other Middle and Upper Devensian records are more broadly associated with the radiocarbon dates given.

	Early		Middle							Late						
Pollen zone/approx. radiocarbon date (years B.P.)	Herb substage —	Chelford	43 140	43 000	42 000	38 200	34 800	28 200	27 650	19 500	II/.11 000–12 000	III/11 561	II/11 993	III/pre-10 413	III	III/pre-9 880
	Wretton	Coston	Isleworth	Tattershall Castle	Upton Warren	Fladbury	Kirkby-on-Bain	Brandon	Beckford	Barnwell Stn	e.g. Ballybetagh	Neasham	Blackpool	Flixton	Nazeing	Sproughton
PRIMATES																
Homo sapiens L., man	–	–	–	–	–	–	–	–	–	–	–	–	⊕	+	–	+
RODENTIA																
Dicrostonyx torquatus (Pallas), arctic lemming	–	–	–	–	+	–	–	⊕	–	–	–	–	–	–	+	–
Lemmus lemmus (L.), Norway lemming	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+[1]	–
Arvicola cantiana (Hinton), extinct water vole	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Microtus oeconomus (Pallas), northern vole	–	–	⊕	–	–	–	–	–	–	–	–	–	–	–	+	–
Microtus gregalis (Pallas), tundra vole	–	–	⊕	⊕	–	–	–	–	+	–	–	–	–	–	+	–
Microtus agrestis L., field vole	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Microtus sp., a vole	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
CARNIVORA																
Canis lupus L., wolf	+	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–
Alpex lagopus (L.), arctic fox	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ursus arctos L., brown bear	+	–	⊕	+	–	–	–	–	–	–	–	–	–	–	–	–
PROBOSCIDEA																
Mammuthus primigenius Blumenbach, mammoth	+	+	+	+	+	+	+	–	+	+	–	–	–	–	–	–
PERISSODACTYLA																
Equus ferus Boddaert, horse	+	–	+	+	+	+	+	–	+	+	–	–	–	+	–	+
Coelodonta antiquitatis Blumenbach, woolly rhino	+	+	+	+	+	+	+	–	+	+	–	–	–	–	–	–
ARTIODACTYLA																
Cervus elaphus L., red deer	–	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Rangifer tarandus L., reindeer	+	+	⊕	⊕	+	–	–	–	–	+	+	–	–	–	–	+
Megaceros giganteus (Blumenbach), giant deer	–	–	+	–	–	–	+	–	–	–	+	–	–	–	–	–
Alces alces (L.), elk	–	–	–	–	–	–	–	–	–	–	–	⊕	⊕	–	–	–
Bison priscus Bojanus, extinct bison	+	+	⊕	⊕	+	–	+	–	+	–	–	–	–	–	–	–
Ovibos moschatus Zimmerman, musk ox	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–

1. Could be slightly older



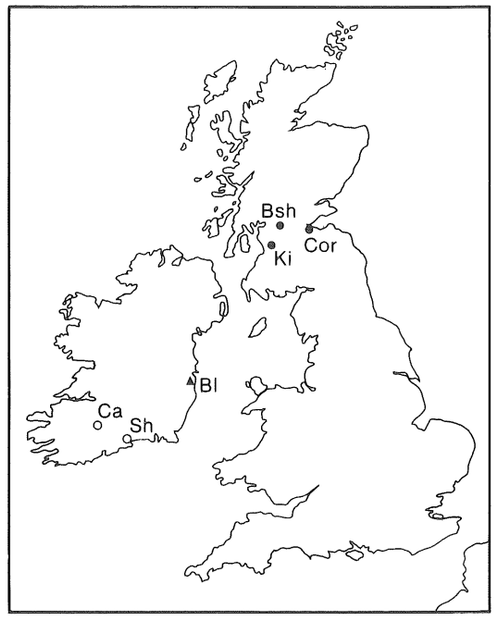


Fig. 8.2. Location map of Devensian vertebrate sites. ■, Early Devensian; ●, Middle Devensian (or uncertain); ▲, Late Devensian; (cave sites shown by open symbols). AH, Aveline's Hole; BD, Brean Down; Bd, Brandon; Bg, Ballaugh; Bk, Beckford; Bl, Ballybetagh; Bp, Brimpton; BS, Barnwell Station, Cambridge; Bsh, Bishopbriggs; Ca, Castlepook Cave; Cor, Corstophine; CC, Creswell Crags (Robin Hood's Cave, Pinhole Cave); Cf, Cefn Cave; CH, Clifford Hill; Cs, Coston; Fd, Fladbury; Fx, Flixton; Fs, Fisherton; GC, Gough's Cave; HF, High Furlong, Blackpool; Is, Isleworth; Kb, Kirkby-on-Bain; KC, Kent's Cavern Ki, Kilmaurs; Kw, Kew; Ns, Neasham; Nz, Nazeing; Ox, Oxbow; PH, Picken's Hole; Sh, Shandon Cave; SH, Sun Hole; Sp, Sproughton; TC, Tattershall Castle; TN, Tornewton Cave (Reindeer Stratum); Tw, Twickenham; UW, Upton Warren; Wr, Wretton.

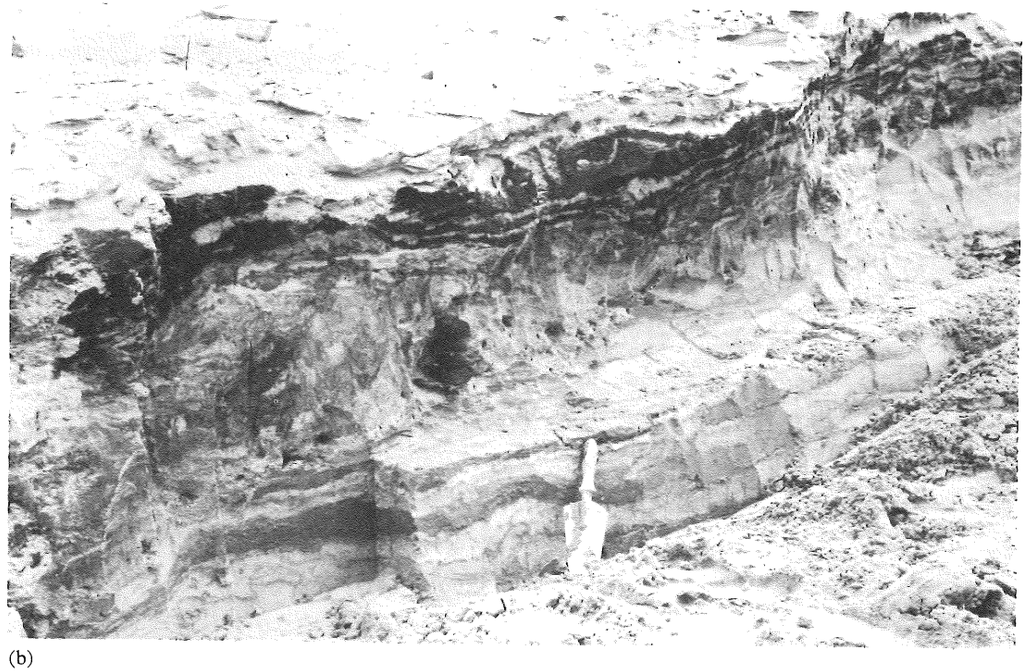
sequence comprises fluviatile sands, silts and gravels, with fine clastic and organic sediments in small enclosed basins thought to have been formed by the melting of ice mounds. Eight local pollen zones A to H, representing three herb substages and two woodland substages (interstadials) were recognized on the basis of pollen spectra. The later interstadial is thought to be equivalent to the Chelford (Cheshire) woodland substage, and the earlier designated as the Wretton woodland substage. These may correlate with the Brørup and Amersfoort interstadials respectively recognized in Denmark, North Germany and the Netherlands.

Bones of wolf *Canis lupus* have been found *in situ* in beds with pollen spectra of herb substage I type (Fig. 8.3b). The majority of the Wretton mammal material was found loose in the mounds of excavated deposits, but all or most of it probably comes from the beds of herb substage I age; a conclusion corroborated by the uniformity of the fauna. The abundant fossils, collected by Dr K. A. Joysey, are now being studied by him in collaboration with the author (Table 8.2).

The extinct bison *Bison priscus* is by far the best-represented taxon, followed by reindeer *Rangifer tarandus*. The other taxa, *Canis lupus*, arctic fox *Alopex lagopus*, bear *Ursus* sp., mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis* and horse *Equus ferus*, are mostly represented only by one or two specimens each. The picture of large herds of grazing bison and reindeer is entirely consistent with the palaeobotanical evidence for a rich herbaceous vegetation. The predominance of male shed antlers at Wretton indicates that reindeer herds were in the area mainly in the winter (see Ch. 5).

Beetle remains recovered from zones A and B of Wretton herb substage I were interpreted as suggesting open, rather marshy, grassland with sandy soils, and a cool but not arctic climate (Coope, in West *et al.* 1974). There is, however, a marked disagreement between the beetle faunas and the pollen

(a)



(b)

Fig. 8.3. Early Devensian river terrace deposits at Wretton, Norfolk. (a) general view of flood-relief channel looking eastwards towards Wretton Fen Bridge. The high banks on either side consist of excavated spoil in which many bones were found. *In situ* deposits are exposed in sections above and below water level. (b) section in south bank showing sands and silts, overlain by organic deposits yielding herb substage I pollen spectra (see text). A partial skeleton of wolf *Canis lupus* was found in the sands and silts. The scapula and another bone are visible in the photo to the left and above the trowel.

spectra for zones F and G. According to Coope, the beetles indicate a severe arctic climate, whereas the pollen shows the development of pine *Pinus* and spruce *Picea* forest. This discrepancy has yet to be resolved.

Organic deposits in sands and silts of the second terrace of the River Cam at Sidgwick Avenue, Cambridge, have been attributed to the Early Devensian (Lambert, Pearson & Sparks 1962). Plant macrofossils indicate an open unwooded landscape and a climate colder than today. A skull of *Bison priscus* was recovered from these deposits.

Organic sands and silts beneath gravels at Coston near Barnham Broom, Norfolk, have yielded macroscopic plant remains, molluscs and vertebrate remains. Preliminary pollen analyses by P. L. Gibbard indicate spruce *Picea*/pine *Pinus* forest giving way to an unwooded environment dominated by grasses and sedges. A correlation with the end of the Early Devensian Chelford interstadial seems very probable. Ipswichian interglacial deposits also occur in the gravel pit and a hippopotamus *Hippopotamus amphibius* tooth has been recorded from the site, although not *in situ*.

The majority of large-mammal bones from Coston are of *Bison priscus*. Other taxa, represented by a few specimens each, comprise *Coelodonta antiquitatis*, *Mammuthus primigenius*, *Rangifer tarandus*, and red deer *Cervus elaphus*. All of these species were recorded *in situ* in the organic deposits, although many unstratified finds have also been made. Small-vertebrate remains collected *in situ* by the author include: three-spined stickleback *Gasterosteus aculeatus*, frog *Rana* sp. and/or *Bufo* sp., toad, short-tailed vole *Microtus agrestis* and extinct water vole *Arvicola cantiana*.

A basal antler fragment of *C. elaphus* has been found in deposits attributed to a post Chelford interstadial at Brimpton, Berkshire (Bryant & Holyoak 1980).

Middle Devensian (50 000 to 26 000 radiocarbon years B.P.)

Middle Devensian vertebrate faunas are available from a number of open sites in association with radiocarbon dates, beetle faunas and pollen (Table 8.2).

At Tattershall Castle, Lincolnshire, several metres of fluviatile gravel, deposited by the River Witham, overlie fossiliferous organic deposits dated by pollen analyses to the Ipswichian interglacial (Girling 1974) (Fig. 8.4). A thin silt band near the base of the gravels has yielded a fossil beetle fauna of arctic type and radiocarbon dates of 44 300 $\pm \frac{1\,600}{1\,300}$ and 42 100 $\pm \frac{1\,400}{1\,100}$ years B.P. (Lab. no. Birm-408, 398. A higher silt band up to 2 m thick has, in contrast, yielded a temperate beetle fauna, and radiocarbon dates of 43 000 $\pm \frac{1\,300}{1\,100}$ and 42 200 $\pm$ 1 000 years B.P. (Birm-341, 409). Numerous large-mammal bones have been found at this site, of which as at Wretton the majority are of *Bison priscus*, with *Rangifer tarandus* in second place (Rackham 1978). Bones of both these species have been found *in situ* in the upper silt bed, but most finds are not stratigraphically located and may cover several thousands of years, within which there may have been considerable changes in climate. The presence of abundant shed male antlers at the site indicates that *Rangifer tarandus* was present in the winter months (Ch. 5).

Of particular interest is the occurrence of numerous dung beetles in the upper silt bed coleopteran fauna, indicating the presence of large herbivores in the area during the summer months as well.

Numerous large-mammal remains were discovered in the late 1950s and early 1960s at Willment's Pit, Isleworth, Middlesex, and collected by J. W. Simons. The deposits, laid down by the River Thames, comprise a sequence about 5 m thick of gravels, sands and organic silty clays, the latter giving a radiocarbon date of 43 140 $\pm \frac{1\,520}{1\,280}$ years B.P. (Birm-319) (Coope & Angus 1975). The vertebrate fauna (Table 8.2) includes fishes, amphibians, and the voles *Microtus oeconomus* and *Microtus gregalis* from the dated silty clay bed. Of the far more abundant large-mammal remains, bear *Ursus* sp., reindeer *Rangifer tarandus* and bison *Bison priscus* are definitely recorded from the silty clay bed, while the majority of finds are from the gravels and sands, and are therefore less precisely dated.

The vertebrate assemblage is dominated by the remains of *Bison priscus*. Remains of *Rangifer tarandus* are also conspicuous, though much less abundant than *Bison*; but this impression is exaggerated since they include many shed antlers, and each reindeer produces several pairs of antlers in its lifetime. The other taxa are each represented by one or a few specimens only.

The organic silty clay bed has produced a rich beetle fauna, described by Coope and Angus, with representatives of aquatic pool, riparian and terrestrial environments. The latter were interpreted as comprising an adjacent marshy area with lush herbaceous vegetation, and patchy vegetation includ-

Fig. 8.4. Section showing sequence of Middle Devensian deposits at Tattershall Castle, Lincolnshire. A fossiliferous organic rich channel fill (dark) near the base, is succeeded by cross-bedded sands and gravels (the holes were made by sand martins).

ing heath on higher and drier ground. More recent pollen analyses, by P. L. Gibbard, show typical Devensian herb pollen spectra dominated by grasses and sedges. According to Coope and Angus, the beetle fauna consists of temperate species now found in Britain plus a smaller number of more southern or eastern distribution, indicating mean July temperatures of 18 °C or more, i.e. higher than at the present day. The absence of trees was attributed to the climatic amelioration having been too short for trees to immigrate. The possibility of grazing pressure by the large herbivores, preventing tree growth, was also mentioned. Tree growth may, however, have been restricted by severe winters (West 1977b).

It is not known whether *Bison priscus* was present at Isleworth throughout the year. Provisional study of the numerous *Rangifer tarandus* antlers from the site suggests that most of the shed antlers are from males, indicating presence of the herds in the winter months (see Ch. 5).

As at Tattershall Castle the large and varied dung-beetle fauna indicates that large herbivores were present during the summer. Carrion beetles are also recorded.

At Upton Warren, Worcestershire, many bones and teeth of large mammals were found in terrace deposits of the River Salwarpe (Coope, Shotton & Strachan 1961). Silt bands within the sands and gravels yielded pollen spectra indicative of treeless herb-dominated vegetation. One of these silt bands gave a radiocarbon date of 42 100 ± 800 years B.P. (GrN-1245). Only a few remains of three-spined stickleback *Gasterosteus aculeatus* were, however, actually found in this dated silt. Bones assigned to common frog *Rana temporaria*, arctic lemming *Dicrostonyx torquatus* and a vole *Microtus* sp. were recovered from the other silt bands. The large-mammal bones were mostly found by workmen in the sands and gravels so that the majority of records are only broadly associated with the radiocarbon date. Mammoth *Mammuthus primigenius* is much better represented than in the faunas from Isleworth and Tattershall Castle, although both *Bison priscus* and *Rangifer tarandus* are still very abundant.

From the abundance of both dung and carcass beetles, Coope *et al.* suggested that the pools on the floodplain, represented by fossiliferous silt bands, were used as waterholes by large mammals.

An organic silt horizon at Oxbow near Leeds yielded a tusk of *Mammuthus primigenius* together with insects and pollen and a radiocarbon date of 38 600 $\pm^{1\,720}_{1\,420}$ years B.P. (NPL-163B) (Gaunt, Coope & Franks 1970). The pollen indicates a thin herbaceous plant cover with patches of bare ground, and the beetles also point to arctic conditions.

River sands and gravels at Fladbury, Worcestershire, include a peat horizon radiocarbon dated to 38 200 ± 600 years B.P. (GrN-1269). The vertebrate fauna from the gravels comprises only *Mammuthus primigenius*, *Coelodonta antiquitatis* and horse *Equus ferus* (Coope 1962). The beetles from the peat again indicate an arctic environment.

At Kirkby-on-Bain (Tattershall Thorpe) Lincolnshire, only some 4 km from Tattershall Castle in the valley of the River Witham, several metres of sands and gravels (Fig. 8.4) have produced a number of large-mammal bones. A silt band, radiocarbon dated to 34 800 ± 1 000 years B.P. (Birm-250), has yielded an arctic beetle fauna (Girling 1974). Rackham (1978) has listed the fauna (Table 8.2) and pointed out the striking differences when compared with the earlier sites. At Kirkby *Bison priscus* is virtually absent, and no remains of *Rangifer tarandus* have been found. The faunal assemblage is here dominated by remains of mammoth *Mammuthus primigenius* and rarer woolly rhinoceros *Coelodonta antiquitatis*.

At Brandon, Warwickshire, organic silts, radiocarbon dated to about 28 200 years B.P., occur at the base of gravels of the River Avon number 2 terrace (Shotton 1968). They contain plant and insect fossils (Kelly 1968; Coope 1968a) both of which indicate an open, herb-rich, treeless environment. Dwarf birch *Betula nana* and dwarf willow *Salix herbacea* were also present. The beetles imply a severe arctic climate. The single vertebrate record from the silt deposits is of arctic lemming *Dicrostonyx torquatus*.

Organic silt bands within terrace sands and gravels of the Carrant Brook at Beckford, Worcestershire, gave a radiocarbon date of 27 650 ± 250 years B.P. (Birm-293) (Briggs, Coope & Gilbertson 1975). Non-marine molluscs from the silt were thought to suggest marshy ground and exposed open environments with lack of continuous grass cover. The beetle assemblage is of arctic tundra type, again suggesting sparse vegetation. One species of carcass beetle occurs. According to Whitehead (in Shotton, 1977c) the large-mammal bones from the sands and gravels, and therefore only broadly associated with the radiocarbon date, in-

Table 8.3. Devensian radiocarbon-dated mammal records based on bone collagen. (Data from *Radiocarbon* 1959–79; Campbell 1977)

	Lab. and assay no.	Date in radiocarbon years B.P.
Homo sapiens, man		
Paviland, Glamorganshire ('Red Lady')	BM-374	18 460 ± 340
Ursus arctos, brown bear		
Sun Hole, Somersetshire	BM-524	12 378 ± 150
Kent's Cavern, Devonshire	GrN-6203	14 275 ±120
Robin Hood's Cave, Derbyshire	BM-602	28 500 $\pm^{1\,600}_{1\,300}$
Kent's Cavern, Devonshire	GrN-6202	28 720 ± 450
Mammuthus primigenius, mammoth		
Cae Gwyn Cave, Flintshire	Birm-146	18 000 $\pm^{1\,400}_{1\,200}$
English Channel off Sussex	Gif.-1110	19 300 ± 700
Castlepook Cave, County Cork	D-122	33 500 ± 1 200
Little Rissington, Gloucestershire	Birm-466	34 500 ± 500
Oxbow, near Leeds	NPL-162B	38 600 $\pm^{1\,720}_{1\,420}$
Coelodonta antiquitatis, woolly rhino		
Ogof-yr-Ichen, Caldey Island, Pembrokeshire	Birm-340	22 350 ± 620
Bishopbriggs, Lanarkshire	GX	27 550 $\pm^{1\,370}_{1\,680}$
Kent's Cavern, Devonshire	GrN-6201	28 160 ± 435
Leadenhall Street, London	GrN-4630	29 450 ± 350
Equus ferus, horse		
Robin Hood's Cave, Derbyshire	BM-604	10 590 ± 90
Kent's Cavern, Devonshire	GrN-6324	38 270 $\pm^{1\,470}_{1\,240}$
Megaceros giganteus, giant deer		
Kent's Cavern, Devonshire	GrN-6204	12 180 ± 100
Brandesburton, Yorkshire (reworked)	Birm-55	12 850 ± 250
Rangifer tarandus, reindeer		
Dead Man's Cave, Anston, Yorkshire	BM-440b	9 750 ± 110
Rodden's Port, County Down	LJ-658	10 250 ± 350
Ossoms Cave, Staffordshire	GrN-7400	10 590 ± 70
Cattedown Cave, Plymouth, Devonshire	BM-729	15 125 ± 390
Coygan Cave, Camarthenshire	BM-499	38 684 $\pm^{2\,713}_{2\,024}$
Kilmaurs, Ayrshire	Birm-93	>40 000
cf. *Bison priscus*, extinct bison		
Broadway, Worcestershire	Birm-656	26 600 $\pm^{700}_{650}$
Kent's Cavern	GN-6325	27 730 ± 350
Ovibos moschatus, musk ox		
Clifford Hill, Northamptonshire	BM-725	18 213 ± 310

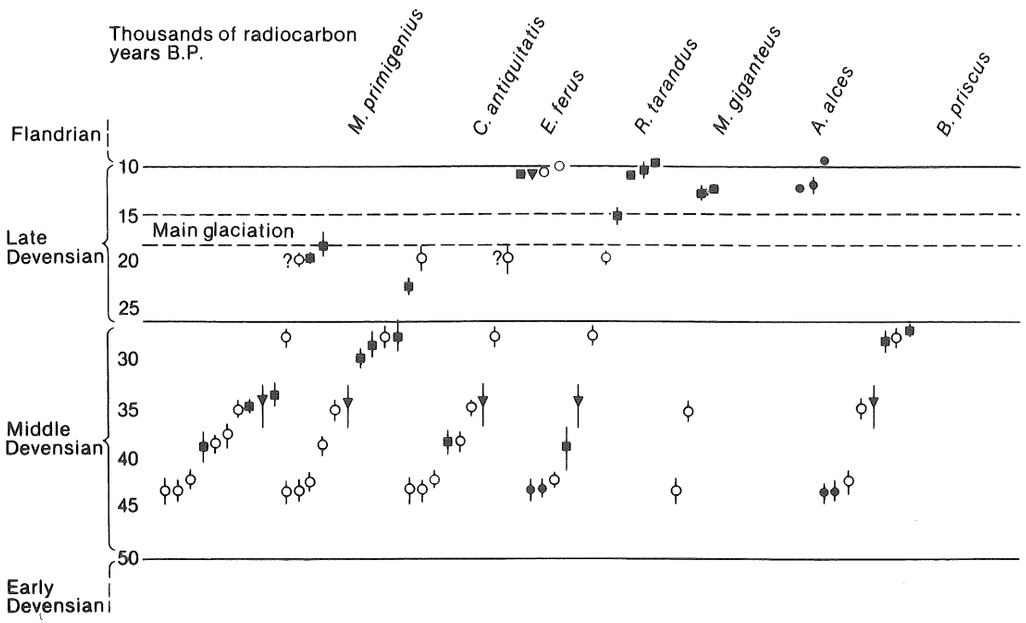


Fig. 8.5. Chart of radiocarbon dates, showing time-stratigraphical ranges of major species of large mammals during the Devensian Cold Stage (data from *Radiocarbon*, and Campbell 1977). ●, date on plant material from same horizon; ○, date on plant material broadly associated with mammal bones; ■, date on bone collagen from this species; ▼, bone collagen date on material from same horizon.

clude *Mammuthus primigenius, Coelodonta antiquitatis, Equus ferus, Rangifer tarandus, Bison priscus*, and one specimen of musk ox *Ovibos moschatus*. Molar teeth of small voles from this site attributed by Sutcliffe and Kowalski (1976) to *Microtus arvalis* are very probably of tundra vole *Microtus gregalis* as suggested by Hall and Yalden (1978).

In addition to the open sites of Middle Devensian age described above, where vertebrate remains have been recovered in good or reasonably well-stratified contexts, there are numerous finds from caves, fissures and open sites where the evidence for dating is rather less satisfactory. Radiocarbon dates on bone collagen are, however, available from some of these sites, and in some cases serve to date many other finds from the same horizon.

Radiocarbon dates on isolated Devensian mammal records are given in Table 8.3, and dated finds of selected large mammals plotted in Fig. 8.5. The possibility of contamination of a sample by younger carbon, and the lack of independent evidence on the age of many finds, means that it is unwise to relie greatly on any single radiocarbon date, although the overall pattern of dates can be accepted more confidently.

At Tornewton Cave, Devon (Sutcliffe & Zeuner 1962; Sutcliffe & Kowalski 1976), a series of deposits containing cold-stage type faunas, overlie the Hyaena Stratum with its characteristically Ipswichian fauna (see Fig. 7.11). The two main faunas are from the Elk stratum (actually there is no *Alces* material from this site, the name resulting from a misidentification – Lister 1981) and the Reindeer Stratum. The mammals recorded are listed in Table 8.4. Notable occurrences are of red deer *Cervus elaphus* in the Elk Stratum, and of mole *Talpa europaea* and bank vole *Clethrionomys glareolus* in the Reindeer Stratum.

Birds from the latter horizon, according to Harrison (1980), include teal *Anas crecca*, ptarmigan *Lagopus mutus*, willow grouse *Lagopus lagopus*, little bustard *Otis tetrax*, skylark, *Alauda arvensis*, fieldfare *Turdus pilaris*, starling *Turdus vulgaris* and carrion crow *Corvus corone*.

The main agents responsible for accumulating the vertebrate remains were probably spotted

Table 8.4 Mammalian faunas of selected Middle and Upper Devensian cave deposits.

	Tornewton Cave Elk Stratum	Tornewton Cave Reindeer Stratum	Picken's Hole Layer 5	Picken's Hole Layer 3 (34 265 years B.P.)	Castlepook Cave Ireland, (33 500 years B.P.)
Insectivora					
Talpa europaea L., mole	–	+	–	–	–
Primates					
Homo sapiens L., man (B, bones; A, artefacts)	A	A,B	–	B	–
Rodentia					
Spermophilus sp., suslik	–	–	–	+	–
Dicrostonyx torquatus (Pallas), arctic lemming	+	–	–	–	+
Lemmus lemmus (L.), Norway lemming	–	–	–	–	+
Clethrionomys glareolus (Schreber), bank vole	+	+	–	–	–
Arvicola terrestris L., water vole	+	+	–	–	–
Microtus oeconomus (Pallas), northern vole	+	+	+	+	–
Microtus gregalis (Pallas), tundra vole	+	+	+	–	–
Microtus agrestis L., field vole	+	+	–	–	–
Carnivora					
Canis lupus L., wolf	+	–	+	–	+
Alopex lagopus (L.), arctic fox	–	–	–	+	+
Vulpes vulpes (L.), red fox	+	+	+	–	+
Ursus sp., bear	+	+	+	+	+
Mustela erminea L., stoat	–	–	–	–	+
Crocuta crocuta Erxleben, spotted hyaena	+	+	–	+	+
Panthera leo (L.), lion	–	–	–	+	–
Proboscidea					
Mammuthus primigenius Blumenbach, mammoth	–	–	–	+	+
Perissodactyla					
Coelodonta antiquitatis Blumenbach, woolly rhino	+	+	–	+	–
Equus ferus Boddaert, horse	+	+	–	+	–
Artiodactyla					
Megaceros giganteus Blumenbach, giant deer	–	–	–	–	+
Cervus elaphus L., red deer	+	–	+	+	–
Rangifer tarandus L., reindeer	+	+	+	+	+
Bison sp. or *Bos* sp., bison or aurochs	+	+	+	+	–

hyaena *Crocuta crocuta*, which may have used the cave as a den; man, whose presence is attested by some worked flints and teeth; and owls roosting near the cave entrance. No radiocarbon dates are available for these faunas, which on present evidence could date from two phases anywhere within the Devensian earlier than about 18 000 years B.P.

A preliminary account of the stratigraphy and