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## The vertebrates of the Last Cold Stage in Britain and Ireland

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Until many more dated records are available it will not be possible to follow in much detail the faunal changes through the Last Cold Stage.

Some of the mammal taxa characteristic of the Devensian were already present in the second half of the Ipswichian, probably in response to decreasing forest cover. The Early and Middle Devensian English faunas include extinct animals (e.g. mammoth, woolly rhinoceros) and living animals whose ranges do not overlap at the present day. Many now live in tundra or tundra and boreal forest (e.g. lemmings, reindeer), others in steppe (e.g. red-cheeked suslik, horse), while others have very southern distributions (lion, spotted hyaena). Some animals (e.g. elk) may have been confined to woodland interstadials, but the fauna as a whole is consistent with treeless herbaceous vegetation. Many taxa (e.g. woolly rhinoceros) failed to reach Ireland.

At some time in the Late Devensian before Zone II several large mammals (e.g. spotted hyaena, mammoth) became locally or totally extinct. The elk failed to reach Ireland in the Late Devensian, and reindeer and giant deer are the only known fauna. The beginning of the Flandrian saw the rapid replacement of the northern and steppe fauna by forest animals.

### 1. INTRODUCTION

On the whole the vertebrates of the Last Cold Stage have received relatively little attention in recent years in comparison with the faunas of earlier stages. Consequently the number of reliably stratified and dated records of fossil vertebrates at present available is not adequate as a basis for any detailed analysis of faunal change during this time. Moreover, the faunal lists from many sites need critical revision.

In view of the emerging complex patterns of climatic and vegetational changes during the Devensian this lack of data is unfortunate, since it seems very probable that the history of the vertebrate fauna was correspondingly complex.

In this paper I have tried to make the best use of such information as we have. The data and conclusions presented here should be regarded as provisional and likely to be much modified by future work.

### 2. THE OCCURRENCE OF FOSSIL VERTEBRATES

Fossil vertebrate material (mostly mammalian) of Devensian age is known from most parts of the British Isles, and is abundantly represented in museum collections. The finds come from river terrace, lacustrine and cave and fissure deposits. At present, however, only the material from a limited number of sites is of very much value because of the considerable uncertainties in dating most of the finds.

The low terrace sands and gravels of many rivers have yielded bones of mammoth and other animals. In a few cases the fossil vertebrate records are more or less associated with radiocarbon-dated organic horizons which have yielded pollen, macroscopic plant remains and beetles.

Lacustrine deposits with fossil vertebrates are known from the Late Devensian. Records from these deposits are ideal in that the sediments are clearly and simply stratified, contain pollen and are generally dateable by radiocarbon.

Cave and fissure deposits are usually far richer in fossil vertebrates than are the deposits of open sites. Carnivora are much better represented in proportion to herbivores than would be expected from the relative population densities of living animals. This is because carnivorous mammals, e.g. spotted hyaena, bear, commonly used caves as dens and when they died contributed their remains to those of their prey accumulating on the cave floor. As a result of this bias and the overall abundance of remains many records of Devensian vertebrates are available only from cave and fissure deposits. Unfortunately there are serious difficulties in dating these fossil assemblages. Very few caves have been excavated with careful regard to the usually complex stratigraphy, and the fossils from different horizons have therefore been confused. In the few cases where cave deposits have been carefully excavated, however, the age of a faunal assemblage can be approximately estimated from the stratigraphical relationships to other fossiliferous horizons, and by comparison with faunas from other sites. Radiocarbon dates on bone collagen are available from a few sites. These are obviously of value, but inherently less reliable than radiocarbon dates based on plant material.

### 3. IPSWICHIAN

The faunal history of the preceding Ipswichian stage has recently been described by the author (Stuart 1976). It seems relevant here to mention certain aspects of the faunas of this interglacial as they in some ways anticipate those of the Devensian.

The fauna of zone Ip II included temperate mammals such as a rhinoceros (*Dicerorhinus hemitoechus*), straight-tusked elephant (*Palaeoloxodon antiquus*), hippopotamus (*Hippopotamus amphibius*) and fallow deer (*Dama dama*) in association with regional mixed oak forest vegetation. During the second half of the interglacial the temperate taxa were gradually replaced by taxa usually considered to be characteristic of cold stages. At for example Aveley, Essex, both mammoth (*Mammuthus primigenius*) and horse (*Equus caballus*) were present as early as the beginning of zone Ip III. The fauna of the Lower Brickearth at Crayford, Kent, is considered (Stuart 1976) to be of probable late Ipswichian age, possibly late zone Ip IV. If this is correct then northern vole (*Microtus oeconomus*), arctic lemming (*Dicrostonyx torquatus*), Norway lemming (*Lemmus lemmus*), woolly rhinoceros (*Coelodonta antiquitatis*) and musk ox (*Ovibos moschatus*) were present before the end of the interglacial. The fauna, however, differs from those of Devensian age in the continued presence of temperate mammals such as *D. hemitoechus*, the absence of reindeer (*Rangifer tarandus*), and the occurrence throughout the deposits of abundant temperate and southern molluscs, notably *Corbicula fluminalis*, which suggest that summer temperatures were still high. The early occurrence of such animals as lemmings and woolly rhinoceros may have been related to a regional or local vegetation that was largely open, rather than giving any direct indication of climatic deterioration.

### 4. EARLY AND MIDDLE DEVENSIAN

A list of Early and Middle Devensian mammal taxa and their occurrences at some of the more important sites are given in table 1.

*(a) Britain*

An Early Devensian fauna is available from terrace deposits of the River Wissey at Wretton, Norfolk (West *et al.* 1974). The vertebrate material is being studied by K. A. Joysey, and only a preliminary faunal list is so far available. The vertebrates recorded (K. A. Joysey, personal communication) include arctic fox (*Alopex lagopus*), mammoth (*Mammuthus primigenius*), horse (*Equus caballus*) (not included in earlier lists), reindeer (*Rangifer tarandus*) and bison (*Bison priscus*). The pollen spectra record a long period of herbaceous vegetation, interrupted by two (pollen-based) interstadials with boreal forest. It should prove possible to relate many of the vertebrate finds to the stratigraphy. The fauna seems consistent with open herb vegetation and includes no characteristically woodland animals.

A skull of *Bison priscus* was recovered from deposits of probable Early Devensian age at Sidgwick Avenue, Cambridge (Lambert, Pearson & Sparks 1963).

Middle Devensian faunas are available from a number of sites, of which the most important described so far is Upton Warren, Worcestershire (Coope, Shotton & Strachan 1961). At this site numerous bones and teeth of large mammals were found in terrace deposits of the River Salwarpe. Remains of small vertebrates were recovered from silt bands, one of which gave a radiocarbon date of 42 000 a B.P. Only a few stickleback remains were, however, actually found in the dated horizon and the large-mammal remains were mostly found in the gravels by workmen. The date can only, therefore, be taken as a general indication of the age of the faunal assemblage. The fauna includes arctic lemming (*Dicrostonyx torquatus*), mammoth, horse, woolly rhinoceros (*Coelodonta antiquitatis*), reindeer and bison. Pollen spectra from the silt bands indicate a treeless herbaceous vegetation.

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

A mammoth tusk from Oxbow near Leeds was recovered from organic silts which gave a radiocarbon date of about 38 600 a B.P. (Gaunt, Coope & Franks 1970). The pollen again indicates open herbaceous vegetation.

At Fladbury, Worcestershire, finds of mammoth, woolly rhinoceros and horse from river gravels are broadly associated with a radiocarbon date of about 38 000 a B.P. from a peat horizon within the gravels (Coope 1962).

Many cave deposits, probably covering Early and/or Middle Devensian time, are known from Britain.

The series of deposits in Tornewton Cave, Devon (Sutcliffe & Zeuner 1962; Kowalski 1967) apparently spans the time from the Wolstonian to the Flandrian. Overlying a horizon of Ipswichian age with hippopotamus and other temperate mammals is a series of deposits of probable Devensian age. The Elk Stratum, a cave earth resting on frost-shattered limestone breccia, has yielded arctic lemming, northern vole (*Microtus oeconomus*), spotted hyaena, woolly rhinoceros, horse, reindeer, red deer (*Cervus elaphus*) and elk (*Alces alces*). Man is represented by a few nondescript artefacts.

The fauna of the overlying Reindeer Stratum is rather similar but lacks both elk and red deer. On the other hand bank vole (*Clethrionomys glareolus*) and mole (*Talpa europaea*) are recorded. Man is represented by flint flakes and an incisor.

A preliminary account of the stratigraphy and vertebrate remains of the cave or rock shelter at Picken's Hole, Compton Bishop, Somerset, was given by Tratman (1964). The faunas were

TABLE 1. MAMMALS RECORDED FROM THE EARLY AND MIDDLE DEVENSIAN

	Wretton (Early Devensian)	Upton Warren (Middle Devensian)	Tornewton Cave, Elk Stratum	Tornewton Cave, Reindeer Stratum	Picken's Hole, Layer 5	Picken's Hole, Layer 3	Castlepook Cave, Ireland	other sites	Ponders End
<b>Insectivora</b>									
1. <i>Sorex cf. araneus</i> L., common shrew	—	—	—	—	—	—	—	—	—
2. <i>Talpa europaea</i> L., mole	—	—	—	—	—	—	—	—	—
<b>Primates</b>									
3. <i>Homo sapiens</i> L., man (bones or artefacts)	—	—	—	—	—	—	—	—	—
<b>Lagomorpha</b>									
4. <i>Lepus timidus</i> L., mountain hare	—	—	—	—	—	—	—	—	—
<b>Rodentia</b>									
5. <i>Spermophilus major</i> Pallas, red-cheeked suslik	—	—	—	—	—	—	—	—	—
6. <i>Dicrostonyx torquatus</i> (Pallas), arctic lemming	—	—	—	—	—	—	—	—	—
7. <i>Lemmus lenanus</i> (L.), Norway lemming	—	—	—	—	—	—	—	—	—
8. <i>Clethrionomys glareolus</i> (Schreber), bank vole	—	—	—	—	—	—	—	—	—
9. <i>Arvicola terrestris</i> L., water vole	—	—	—	—	—	—	—	—	—
10. <i>Microtus oeconomus</i> (Pallas) northern vole	—	—	—	—	—	—	—	—	—
11. <i>Microtus gregalis</i> (Pallas), tundra vole	—	—	—	—	—	—	—	—	—
12. <i>Microtus agrestis</i> (L.), field vole	—	—	—	—	—	—	—	—	—
13. <i>Microtus</i> sp., a vole	—	—	—	—	—	—	—	—	—
<b>Carnivora</b>									
14. <i>Canis lupus</i> L., wolf	+	—	—	—	—	—	—	—	—
15. <i>Alopex lagopus</i> (L.), arctic fox	—	—	—	—	—	—	—	—	—
16. <i>Vulpes vulpes</i> (L.), red fox	—	—	—	—	—	—	—	—	—
17. <i>Ursus arctos</i> L., brown bear	—	—	—	—	—	—	—	—	—
18. <i>Ursus maritimus</i> Phipps, polar bear	—	—	—	—	—	—	—	—	—

Kew Bridge†



later revised by the author (see list in Stuart 1974). At this site two fossiliferous cave earths are sandwiched between, and separated by, frost-shattered limestone breccias. The fauna of the earlier horizon, Layer 5, includes wolf (*Canis lupus*), red fox (*Vulpes vulpes*), brown bear (*Ursus arctos*), red deer and reindeer. The fauna of the younger horizon, Layer 3, includes red-cheeked ground squirrel (*Spermophilus major*) (identified by D. F. Mayhew 1975), arctic fox, brown bear, spotted hyaena, lion (*Panthera leo*), mammoth, horse, woolly rhinoceros, red deer, and reindeer. The presence of man is attested by a few indeterminate artefacts and two incisor teeth. The faunas from the sites discussed above are fairly typical and include nearly all the taxa recorded from the Early and Middle Devensian. A few additional sites are, however, also worth mentioning as they have produced records of rare taxa.

The 'Arctic Bed' peats and gravels of the River Lea flood plain terrace of Enfield and Edmonton, North London, have yielded arctic lemming, from Angel Road, Edmonton, mammoth, woolly rhinoceros and horse (Warren 1912; Hinton 1912) and a record of shrew (*Sorex* cf. *araneus*, equals *S. kennardi* Hinton) (Hinton 1911) from Ponders End, Enfield.

In the last century a number of mammalian remains were discovered at Fisherton, near Salisbury, Wiltshire. The finds included mammoth, woolly rhinoceros, reindeer and others, and of particular interest: red-cheeked suslik (identified by D. F. Mayhew 1975) and musk ox (Dawkins & Reynolds 1872–1939; Simons 1962). An Early or Middle Devensian age seems probable for this faunal assemblage.

A single record of saiga antelope (*Saiga tartarica*) is known from River Thames gravels at Twickenham, London (Dawkins & Reynolds 1872–1939). There appears to have been no associated fauna.

The record of polar bear (*Ursus maritimus*) is based solely on an ulna from a railway cutting in low terrace gravels of the River Thames near Kew Bridge, London. The bone was compared in detail with a number of fossil and recent bears by Kurtén (1964) who found it differed from recent polar bear only in its greater size. A number of reindeer remains have also been found at Kew.

Fissures in Lower Greensand at Ightham, Kent, have produced large numbers of vertebrate remains (Newton 1894), probably covering much of Devensian and Flandrian time. The material from different periods appears to have been mixed together when found, but the records of red-cheeked suslik, woolly rhinoceros and others are most probably of Early or Middle Devensian age. Simons (1962) mentioned a vertebra of musk ox from this site.

The caves of Creswell Crags, Derbyshire, have yielded abundant vertebrate remains, apparently in the main of Early or Middle Devensian age. The records of sabre-tooth cat (*Homotherium latidens*) from Robin Hood and Pin Hole Caves, seem out of place, since this genus is not otherwise recorded in Europe later than the Middle Pleistocene. The third English record from Kent's Hole, Devon, could well be of Middle Pleistocene age. The record from Robin Hood Cave is based on the crown of a canine (Dawkins 1877) which was excavated in Dawkins' presence and was directly associated with woolly rhinoceros, mammoth, etc. and man-made flint flakes. A possible explanation is that the sabre-tooth cat remains were collected by man, and are actually much older than the deposits in which they were found.

Remains of gnutton (*Gulo gulo*) are known from a very few cave sites in Britain. At Plas Heaton Cave, near Cefn St Asaph, North Wales, it was recorded in association with wolf, bear, horse and reindeer (Dawkins 1871). A Devensian age seems probable, but by no means certain.

Leopard (*Panthera pardus*) is recorded from Robin Hood Cave (Dawkins 1877) and also Banwell and Bleadon Caves, Somerset (Dawkins & Sanford 1866–72).

Some of the finds of cave bear (*Ursus spelaeus*) from south-west England, e.g. Kent's Hole, Torquay, Devon, and Wookey Hole, Mendip, Somerset, are possibly of Devensian age.

Giant deer (*Megaloceros giganteus*) is included in a number of faunal lists from various sites in England, e.g. Robin Hood Cave (Dawkins 1877), although many of these records are suspect because of likely confusion of giant deer remains with these of large red deer or with elk.

Most of the fossil localities are in England, although a number of records, mostly from cave deposits, are known for Wales. The sparse list from Scotland includes arctic lemming, mammoth, woolly rhinoceros, reindeer and giant deer (Delair 1969), some of which could be of Late Devensian age.

#### (b) Ireland

Without doubt the most important pre-Late Devensian fossil vertebrate site in Ireland is Castlepook Cave, County Cork. The fauna from this cave was listed by Scharff, Seymour & Newton (1918). The site and fauna have recently been reassessed by A. J. Sutcliffe (in preparation). The mammals believed to come from an earlier set of deposits include arctic lemming, Norway lemming, wolf, red fox, arctic fox, brown bear, spotted hyaena, mammoth, reindeer and giant deer. The fossils were recovered from a series of sands and stalagmite floors, and are probably not contemporaneous. Remains of animals of Flandrian age, including domestic animals, were recovered from later deposits within the cave. Wood mouse (*Apodemus sylvaticus*), an animal characteristic of temperate woodland, was listed by Scharff *et al.* from the earlier deposits, but it seems much more likely to date from the Flandrian and I have therefore not included it in table 1. A radiocarbon date of about 33 500 years from collagen of a mammoth femur suggests a Middle Devensian age for the older faunal assemblage.

One animal not recorded from Castlepook Cave, but apparently present in Ireland during the Early or Middle Devensian is horse. Bones of horse in association with remains of hare, bear, mammoth and reindeer were found in stalagmite in a quarry at Shandon Cave, near Dunganarven in County Waterford (Brenan 1860; Carte 1860). Lynx (*Lynx lynx*) is recorded from Kilgreany Cave, County Waterford (Savage 1966). It could be either Devensian or Flandrian.

The Devensian mammals of Ireland have been discussed by Savage (1966) and Mitchell (1969).

#### (c) Distributions and ecology

Many of the mammals represented as fossils in the Early and Middle Devensian of Britain have very different distributions at the present day.

##### (i) Arctic and boreal animals

The arctic fox (*Alopex lagopus*) has a holarctic circumpolar distribution (figure 1). It is essentially confined to the tundra but its range extends southwards to the northern part of the boreal forest zone in winter (Corbet 1966). It overlaps the northern part of the range of red fox (*Vulpes vulpes*). Voles, and lemmings are an important source of food.

The arctic lemming (*Dicrostonyx torquatus*) also has a holarctic circumpolar distribution confined to the tundra but entirely absent from Fennoscandia (figure 2). The Norway lemming (*Lemmus lemmus*) together with the Siberian and North American forms, often regarded as a different closely-related species *Lemmus sibericus* Kerr, has a similar distribution to the arctic



lemming but extends further south into the northern part of the boreal forest zone, and does occur in Fennoscandia (Corbet 1966; Ellerman & Morrison-Scott 1966). Both lemmings burrow extensively and eat grasses, sedges and other available plant food (Banfield 1974; Corbet 1966).

The northern vole (*Microtus oeconomus*) occurs in tundra, boreal forest, wooded steppe and the northern part of the deciduous forest in Eurasia, and also the tundra of northwest North America (Corbet 1966; Banfield 1974). The tundra vole *Microtus gregalis* has a wide distribution in Asia, apparently occurring in tundra, boreal forest and steppe (Ellerman & Morrison-Scott 1966). This, or a closely-related species (*Microtus miurus* Osgood) occurs also in northwest North America (Banfield 1974).

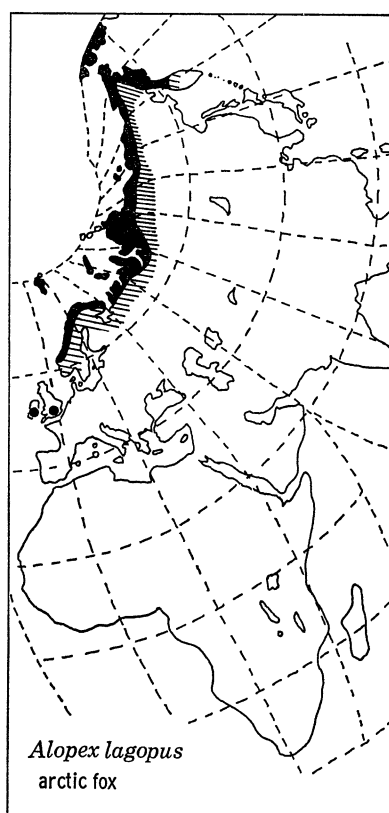


FIGURE 1. Present Old World distribution of arctic fox (after Corbet 1966). Summer range shown in solid black, winter extension hatched. Fossil occurrences in England and Ireland indicated by dots.

The reindeer (*Rangifer tarandus*), a very characteristic animal of Devensian faunas, is nowadays a holarctic circumpolar species, occurring in tundra, boreal forest and mountain regions (figure 3). It has been extensively domesticated in the southern part of the Eurasian range but the distribution of the species has probably been little altered. The tundra populations commonly migrate long distances, up to 300 km, south in winter (Banfield 1974). From the small size of the shed antlers in Tornewton Cave Reindeer Stratum, Sutcliffe & Zeuner (1962) concluded that reindeer were only present at the site in the summer when the females and young shed their antlers. Presumably they migrated south to the Continent for the winter. Reindeer feed on sedges, grasses, other herbs and the shoots of shrubs in summer. Lichens, often dug from under the snow, are very important in the winter diet (Corbet 1966; Banfield 1974).

The musk ox (*Ovibos moschatus*) no longer occurs in Eurasia but is confined to the tundra of North America and Greenland. The food includes grasses, sedges and various shrubs (Banfield 1974).

The polar bear (*Ursus maritimus*) is essentially a marine animal confined to the Arctic Ocean and adjacent coasts. It is seldom reported more than about 100–200 km from the sea (Corbet 1966; Banfield 1974). Very few fossil occurrences are known, although it has been found in Denmark and Scania (Kurtén 1964). The single record from Kew Bridge may represent a solitary wandering individual, perhaps dating from a glacial maximum.

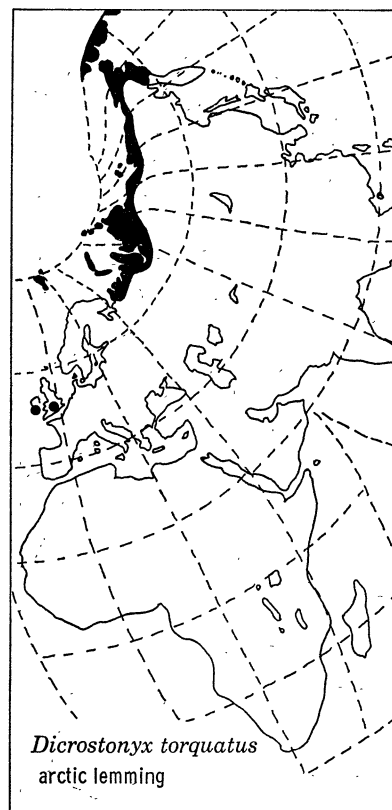


FIGURE 2. Present Old World distribution of arctic lemming (after Banfield 1974). Fossil occurrences in England and Ireland indicated by dots.

The elk, or moose in North America (*Alces alces*), has a holarctic distribution (figure 4) and is mostly confined to boreal forest areas at the present day, although Roman writers record it from North Germany and France about 2000 years ago. It is especially associated with water and marshy forested country. In summer elk feed on herbs, aquatic and riverside plants, and browse on shrubs and deciduous trees. In winter they subsist on shoots and the bark of trees (Corbet 1966). The record of this species from the Elk Stratum of Tornewton Cave (Sutcliffe & Zeuner 1962) therefore seems incompatible with open herbaceous vegetational conditions and suggests that woodland grew in the area at this time.

The glutton or wolverine (*Gulo gulo*) is also primarily found in boreal forest, although migrating northwards onto the tundra in summer (Corbet 1966). It has a circumpolar holarctic distribution.

(ii) *Steppe animals*

The red-cheeked suslik (*Spermophilus major*) has a well-defined steppe distribution at the present day (figure 5). Other species of *Spermophilus* occur in steppe, tundra and mountain areas of Eurasia and North America (Ellerman & Morrison-Scott 1966).

The saiga antelope (*Saiga tartarica*) is found nowadays in the dry steppe and subdesert areas of the southern U.S.S.R. Kahlke (1975) has plotted the recent and fossil occurrences, and his map indicates that during the Last Cold Stage its range was extended westwards across Europe to England, and northwards and eastwards to Siberia and northwest North America.

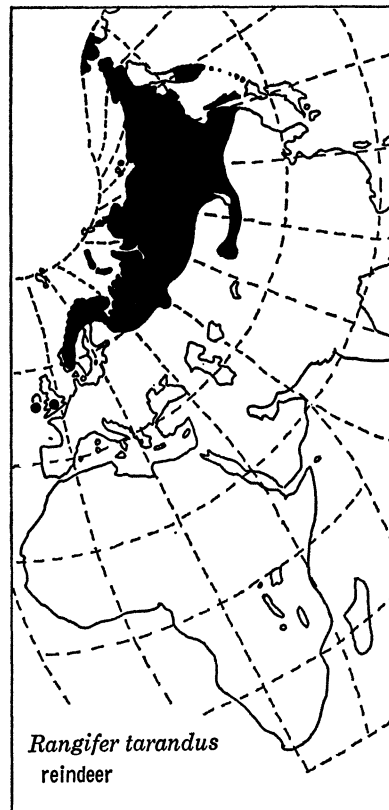


FIGURE 3. Present Old World distribution of reindeer (modified from Banfield 1974). Fossil occurrences in England and Ireland indicated by dots.

The original distribution of the horse (*Equus caballus*) seems impossible to reconstruct with any precision and it is virtually extinct as a wild animal. It appears to have been primarily a steppe-dweller, although according to some authors (e.g. Brink 1967) there may have been a woodland ecotype living in the forest of Poland and elsewhere to within the last hundred years or so. An engraving made by Upper Palaeolithic man on a bone from Robin Hood Cave (Dawkins 1877) shows a horse with an erect mane, very similar to those depicted in French cave paintings and to the living Mongolian wild horse (*Equus caballus*, or *E. przewalskii* Poliakov).

(iii) *Temperate animals*

The red deer (*Cervus elaphus*) is widely distributed in Eurasia, but its original range is difficult to reconstruct accurately because of interference by man (figure 6). It is or was present in the deciduous woodland of Europe, montane woodland and the transition between steppe and boreal forest in Asia. It is entirely absent from tundra and most of the boreal forest zones. This distribution is paralleled in North America, where the red deer is also known as 'elk' or wapiti (Banfield 1974). It feeds largely by grazing and browsing on the leaves of deciduous trees (Corbet 1966).

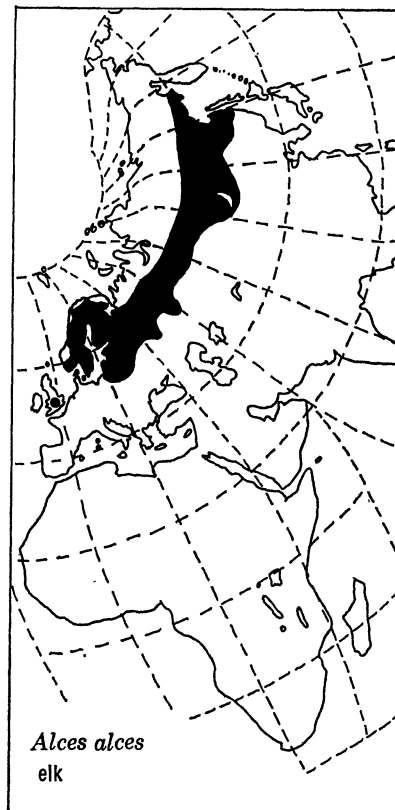


FIGURE 4. Present Old World distribution of elk (from data in Ellerman & Morrison-Scott 1966). The fossil occurrences in England are indicated by a dot.

The Early or Middle Devensian records of red deer pose some interesting problems. Perhaps it migrated into England only during woodland interstadials. Alternatively it may have been adapted to the treeless herb vegetation of much of the stage, possible in the form of a distinct ecotype. The survival of red deer on the Scottish moors at the present day gives some insight into the potential adaptability of this species.

The record of mole (*Talpa europaea*) from Tornewton Cave Reindeer Stratum is rather surprising since nowadays it does not occur further north than southern Scandinavia (Brink 1967). Since the animal lives a subterranean existence feeding on soil invertebrates, its occurrence implies that the ground was not permanently frozen at that time.

(iv) *Southern animals*

The lion (*Panthera leo*) is now found only in Africa south of the Sahara, and a small area of India (figure 7). As also shown in the map it formerly occurred over most of Africa except areas of desert and tropical rain forest across southwest Asia to India. According to Herodotus and other classical writers it occurred in northern Greece about 2500 years ago. It is an animal of open or lightly wooded grassland, avoiding dense forest and it preys on a variety of large ungulates (Dorst & Dandelot 1970).

The spotted hyaena (*Crocuta crocuta*), both a predator and scavenger, has a very similar distribution to the lion, but is restricted to Africa south of the Sahara (Dorst & Dandelot 1970).

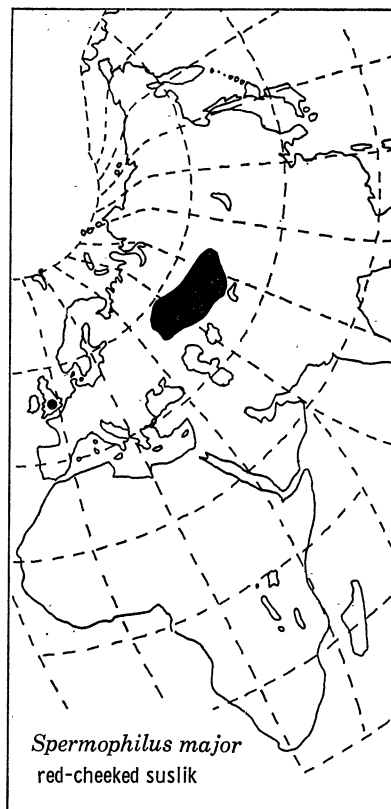


FIGURE 5. Present distribution of red-cheeked suslik (from data in Ellerman & Morrison-Scott 1966). The fossil occurrences in England are indicated by a dot.

(v) *Extinct animals*

There were also four extinct species of large mammals present during the Devensian: mammoth, woolly rhinoceros, giant deer and bison (*Bison priscus*). Of these at least the first two were probably tolerant of extreme cold conditions since we know from finds of carcasses in Siberia and Poland that both animals were protected by long shaggy coats. Nevertheless mammoth, bison and giant deer are also recorded from the temperate parts of interglacials, e.g. at Barrington, Cambridgeshire, they were present in zone IIb of the Ipswichian in association with local deforestation of the river floodplain (Gibbard & Stuart 1975).

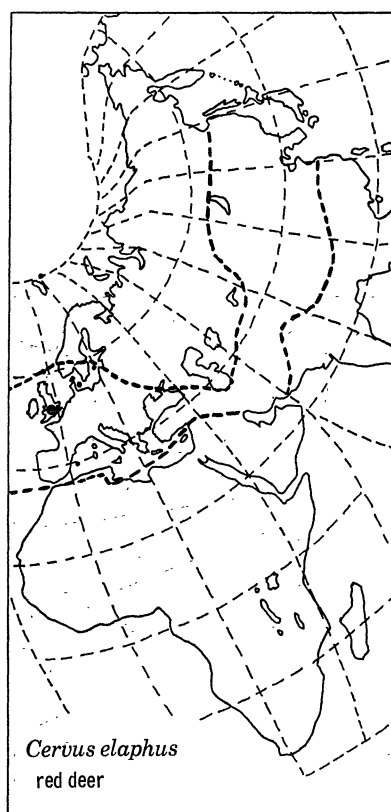


FIGURE 6. Present Old World distribution of red deer (from data in Ellerman & Morrison-Scott 1966). Only the approximate northern and southern limits are shown. The fossil occurrences in England are indicated by a dot.

(d) *Faunal history*

The faunas of the Early and Middle Devensian as a whole, and apparently the faunas of particular horizons, therefore comprise a mixture of faunal elements not found anywhere at the present day. Northern animals of tundra and boreal forest are especially well represented as might be expected, but steppe and southern animals were also present. Such animals as elk, mole and perhaps giant deer and red deer may have been confined to woodland episodes or warmer intervals. The rest of the fauna seems to fit in well with the picture of open herbaceous vegetation present throughout much of the Early and Middle Devensian (West 1977, this volume). The particular combination of climatic and vegetational conditions apparently suited animals now confined either to steppe, or tundra as well as the extinct taxa. Both lion and spotted hyena avoid dense forest at the present day and their present southern distribution may be due to the former existence of dense forest in much of Europe, or to the influence of man since both were present in England during the Ipswichian. Similar faunas to those from England are recorded from as far away as Siberia (Klein 1971).

As they are warm-blooded the distributions of mammals are probably not in most cases directly influenced by climate, but they are very much controlled by vegetational conditions. Throughout much of the Devensian one can picture herds of mammoth, woolly rhinoceros, horse, reindeer and bison grazing on the treeless herbaceous vegetation. No doubt many of them underwent considerable seasonal migrations. Woodland taxa such as elk and perhaps red deer

may have appeared during warmer interstadials, and on the other hand at times of increased cold and glacial maxima the variety of the fauna may have been reduced.

The faunas of Castlepook Cave and elsewhere in Ireland indicate that a number of taxa present in England during the Early and Middle Devensian failed to cross the land bridge to Ireland. Notable absences are lion, all species of voles, susliks, woolly rhinoceros, bison and red deer. Evidently the land bridge was filtering potential immigrants in some way.

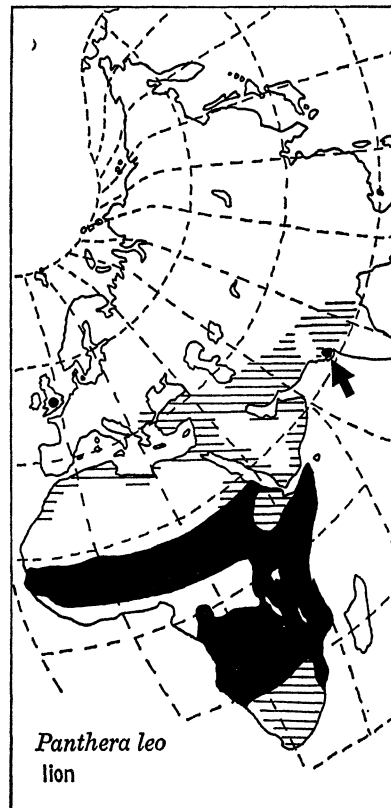


FIGURE 7. Present distribution of lion, shown in solid black (after Dorst & Dandelot 1970; Ellerman & Morrison-Scott 1966). The isolated population in India is arrowed. The hatched area is intended to give a general idea of the areas in which the lion has become extinct within the last 2500 years. The fossil occurrences in England are indicated by a dot.

## 5. LATE DEVENSIAN

### (a) Britain

A few years ago at High Furlong near Blackpool, Lancashire, an elk skeleton was discovered in Zone II lacustrine deposits (Hallam, Edwards, Barnes & Stuart 1973). Radiocarbon dates of about 12200 and 11700 a B.P. were obtained from plant material from the base and top respectively of the Zone II organic muds. A similar find had been made in 1939 at Neasham, County Durham (Trechmann 1939; Blackburn 1952). At both sites the pollen spectra indicate herb vegetation with some birch woods in zone L De II. The High Furlong elk had been hunted, but not butchered, by man. Two barbed points were found with the skeleton and there are numerous injuries on the bones.

Late Devensian muds, probably dating from the end of zone L De II, at Flixton near Star Carr, Yorkshire, yielded three partial skeletons of horse, together with bird bones and a few flint flakes (Clark 1954). The pollen spectra (Godwin, in Clark 1954) indicate open grassy vegetation with perhaps a little tree birch.

Calcareous muds of Late Devensian Zone III age, presenting former pools in the River Lea floodplain, at Nazeing, Essex, yielded frog (*Rana temporaria*), toad (*Bufo bufo* (L.)), common lizard (*Lacerta vivipara* Jacquin), arctic lemming, water vole (*Arvicola terrestris*), northern vole and tundra vole (Allison, Godwin & Warren 1952). The pollen spectra indicate open grassy vegetation. Norway lemming and northern vole are also recorded from muds older than the Zone III horizon.

A faunal assemblage of probable Late Devensian age, including arctic fox, horse and reindeer, was found in a series of sands and limestone breccias banked up against an old limestone sea cliff at Brean Down, Somerset (ApSimon, Donovan & Taylor 1961).

Many English cave deposits containing vertebrate remains of probable Late Devensian age have been excavated, but so far few of the published faunal lists can be relied on to date from a single horizon. One reason for this is the likelihood of contamination by Flandrian material. Animals recorded from Aveline's Hole, Somerset (Davies 1922; Hinton 1924) include varying hare (*Lepus timidus*), pika (*Ochotona pusilla* Pallas), arctic lemming, Norway lemming, brown bear, lynx (*Felis lynx* L.), horse, red deer and reindeer. A number of human skeletons and artefacts were recovered from this site.

D. Bramwell (personal communication) lists a number of animals from Ossom's Cave in the Manifold Valley, Derbyshire. A radiocarbon date of  $10\,590 \pm 70$  a B.P. (GrN 7000) has been obtained from the collagen of a reindeer bone. A preliminary faunal list from the same horizon as the dated bone includes eagle owl (*Bubo bubo*), grouse (*Lagopus lagopus*), ptarmigan (*Lagopus mutus*), black grouse (*Lyrurus tetrrix*), corncrake (*Crex crex*), jackdaw (*Corvus monedula*), mistle thrush (*Turdus viscivorus*), arctic lemming, Norway lemming, various voles, horse, reindeer and red deer. Birds of probable Late Devensian age from a number of English cave sites were discussed by Bramwell (1960).

#### (b) Ireland

Many finds of giant deer and reindeer have been made in the zone L De II marls beneath the peat bogs in Ireland, e.g. at Ballybetagh near Dublin. The occurrences were discussed in detail by Mitchell (1941) and Mitchell & Parkes (1949). There is no indication of the presence of man at any of these sites or indeed anywhere in Ireland before the Flandrian.

According to Jessen (1949) the Late Devensian Zone II vegetation of much of Ireland was almost treeless herb communities with *Empetrum* heaths in the west. Mitchell & Parkes suggested that the absence of giant deer and reindeer finds in the west was due to these animals avoiding the areas of heath vegetation. Giant deer is also recorded from Zone II deposits at Ballaugh, Isle of Man (Mitchell 1958).

#### (c) Faunal history

The most striking feature of faunas dating from the later part of the Late Devensian is the absence of many of the characteristic larger mammals of the Early and Middle Devensian, i.e. mammoth, woolly rhinoceros, bison, musk ox, lion and spotted hyaena. The first three appear to have been extinct in Europe by this time and mammoth and woolly rhinoceros were totally



extinct by the end of the Last Cold Stage. Other large mammals, e.g. horse, reindeer and giant deer, survived throughout all or much of the Late Devensian. The small-mammal fauna was little affected, and the pika, so prominent in Late Devensian cave deposits in Britain, has not so far been recorded from earlier in the stage. The much better known and dated Late Weichselian faunas from North Germany and Denmark (Degerbøl 1964) and numerous other continental sites similarly lack mammoth etc.

The almost total glaciation of Ireland at the beginning of the Late Devensian presumably exterminated most, if not all, of the Irish vertebrate fauna. Giant deer and reindeer therefore must have repopulated Ireland via Britain after the ice had retreated.

The extinction of many large mammals in Britain and Europe towards the end of the Last Cold Stage is best viewed in a wider context as part of the general phenomenon of the accelerated late Pleistocene extinction of large mammals in Eurasia, North America and elsewhere. Similar extinctions did not occur for example during the preceding (Wolstonian) cold stage (Stuart 1974). The hypothesis for man directly or indirectly exterminating many large mammals has been advocated by a number of authors, while others favour climatic and vegetational changes (see Martin & Wright 1967).

The Late Devensian fauna as a whole still had a major northern component including ptarmigan (now found in tundra and mountain areas of Europe including the Scottish Highlands), lemmings, northern vole, tundra vole and reindeer.

Steppe animals are represented by the pika, which has a somewhat similar distribution to the red-cheeked suslik (figure 5), and horse.

In England the northward spread of birch woodland in Zone II was accompanied by the immigration of elk. It was probably absent from the open herbaceous vegetation of Zone III, but returned with the trees at the beginning of the Flandrian, e.g. at Star Carr, Yorkshire (Clark 1954).

In Ireland the many finds of giant deer and reindeer from Zone II comprise all that is known of the Late Devensian fauna, although some of the cave finds are no doubt also of this age. The elk evidently failed to reach Ireland, suggesting that as in the Middle Devensian environmental conditions in the region of the land bridge were in some way unsuitable for elk, i.e. it was acting as a filter. Giant deer is not known from deposits later than Zone II. Presumably it could not adapt to the harsher climatic and vegetational conditions of Zone III.

The climatic amelioration and spread of forests at the beginning of the Flandrian saw the rapid disappearance of reindeer, lemmings, northern vole and tundra vole. Horse is recorded from the early Flandrian at Thatcham, Berkshire (Wymer 1962) and pika (*Ochotona* sp.) appears to have survived until Zone V (F1 Ib) at Nazeing, Essex, although the faunal remains may have been reworked from Late Devensian deposits (Allison, Godwin & Warren 1952).

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