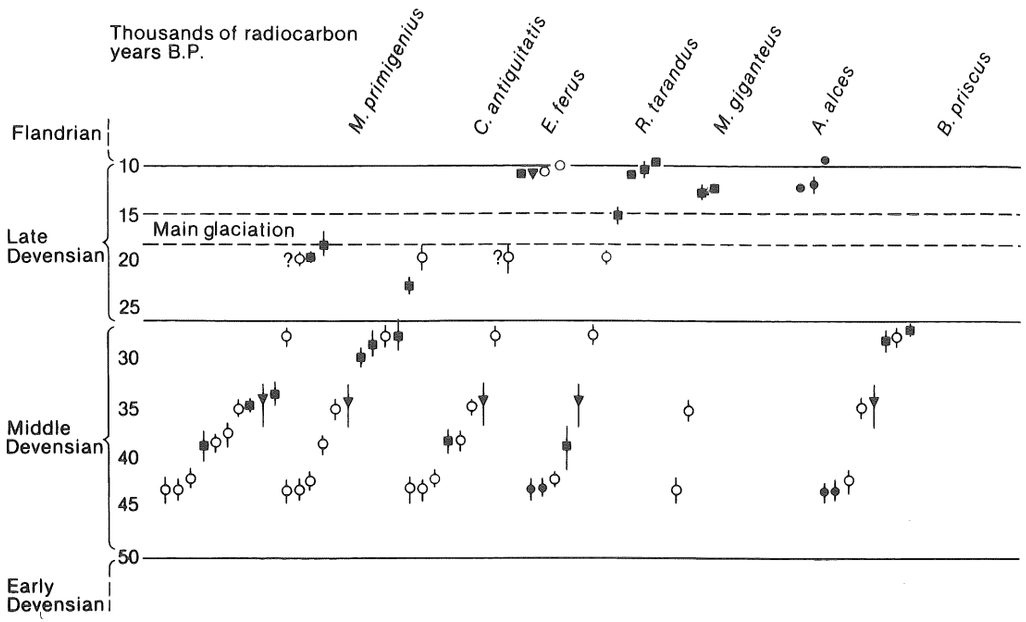

Fig. 8.5. Chart of radiocarbon dates, showing time-stratigraphical ranges of major species of large mammals during the Devensian Cold Stage (data from *Radiocarbon*, and Campbell 1977). ●, date on plant material from same horizon; ○, date on plant material broadly associated with mammal bones; ■, date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

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	+	+	+	+	–

vertebrate faunas from the cave or rock shelter called Picken's Hole, Compton Bishop, Somerset, was given by Tratman (1964). Revised faunal lists were given by Stuart (1974, 1977a). At this locality two quite distinct cave earths were seen sandwiched between and separated by frost-shattered angular limestone breccias. The fauna of the earlier fossiliferous cave earth, Layer 5, includes wolf *Canis lupus*, red fox *Vulpes vulpes*, bear *Ursus* sp., *C. elaphus* and *R. tarandus*; whereas that of the younger horizon has in addition a suslik *Spermophilus* sp., arctic fox *Alopex lagopus*, hyaena *C. crocuta*, mammoth *Mammuthus primigenius*, woolly rhino *Coelodonta antiquitatis*, and horse *Equus ferus* (Table 8.4). A few nondescript worked flints and some human teeth indicate that man *Homo sapiens* was also present. The Layer 5 assemblage was perhaps partly accumulated by wolves. Bears dying in winter hibernation also contributed their remains. The more species-rich assemblage of layer 3 was, in contrast, largely accumulated by hyaenas, as is shown by the characteristic bone damage (see Ch. 4).

Bone collagen from Layer 3 gave an acceptable radiocarbon date of 34 265 $\pm \frac{2\,600}{1\,950}$ years B.P. (BM-654), but the date for the earlier fauna from Layer 5 is considerably younger at 26 650 $\pm \frac{1\,700}{1\,400}$ years B.P. (BM-655A). A further assay made to check this result gave a very similar figure of 27 000 $\pm \frac{1\,850}{1\,500}$ years B.P. (BM-655B). The reasons for these anomalous results are unclear, but they certainly warn against the uncritical acceptance of isolated radiocarbon dates, especially those based on bone collagen.

In the last century mammalian remains were discovered in 'brickearths' at Fisherton near Salisbury, Wiltshire. Species represented include *Mammuthus primigenius, Coelodonta antiquitatis, Rangifer tarandus, Ovibus moschatus* and a suslik *Spermophilus* sp. (Dawkins & Reynolds 1872–1939; Simons 1962). The fauna is presumably of Devensian age.

A unique and very interesting record of saiga antelope *Saiga tartarica* is known from River Thames gravels at Twickenham, London (Dawkins & Reynolds 1872–1939). The age of these gravels is very probably Middle Devensian, broadly equivalent to the Upton Warren Interstadial (Coope & Angus 1975).

The sole record of polar bear *Ursus maritimus* is based on a specimen from a railway cutting in low terrace gravels of the River Thames near Kew Bridge, London (Kurtén 1964). Bones of *R. tarandus* have also been found in the same general area. A Middle or Late Devensian age is likely for these finds.

Robin Hood's Cave and Pin Hole Cave, in the Permian Magnesian Limestone of Creswell Crags, Derbyshire, contain abundant vertebrate remains of Devensian age. Radiocarbon dates (Table 8.3) indicate the presence of Late-Devensian horizons, but the deposits date back at least to well into the Middle Devensian. Radiocarbon dates for Kent's Cavern, Torquay, Devon, indicate a similar time range for the younger sequence of deposits at that locality. All three sites have yielded generally similar faunas resembling those of broadly Middle Devensian age from elsewhere. Of particular interest, however, is the presence of a large red deer *Cervus elaphus* at Kent's Cavern and probably also the other two sites, apparently in association with a 'cold' fauna. Even more intriguing are the records of sabre-tooth *Homotherium latidens* from these three sites, since the species is otherwise unknown from Britain and Continental Europe later than the Middle Pleistocene. The Kent's Cavern specimen can be dismissed because deposits of Middle Pleistocene age also occur within the cave, but at Robin Hood's Cave an *H. latidens* canine was excavated (in the presence of W. B. Dawkins), in direct association with material of *M. primigenius, C. antiquitatis*, etc., and flint artefacts (Dawkins 1877). Late survival of *H. latidens* in Britain, as suggested by Kurtén (1968), seems highly improbable, however, but a possible explanation is that the specimens are actually of Middle Pleistocene date and being distinctive were collected by man in Devensian times.

Leopard *Panthera pardus* is known from Robin Hood's cave (Dawkins 1877) and also from Banwell and Bleadon Caves, Somerset. Finds attributed to cave bear *Ursus spelaeus*, from Kent's Cavern, Wookey Hole, Mendip, Somerset and elsewhere in south-west England, are probably of Middle or Early Devensian age.

The Devensian mammal faunas of Scotland have not received very much attention and would repay detailed study. Arctic lemming *Dicrostonyx torquatus* is recorded from Corstorphine Edinburgh (Sutcliffe & Kowalski 1976). Delair (1969) lists *M. primigenius, C. antiquitatis, R. tarandus* and *M. giganteus*, some of which could be of Late Devensian age. A specimen of *C. antiquitatis* from Bishopbriggs, Lanarkshire is dated to near the end of the Middle Devensian (Table 8.3). *M. primigenius* and *R. tarandus* are recorded from beneath till at Kilmaurs, Ayrshire (Gregory & Currie, 1928) (see Table 8.3).

Castlepook Cave, County Cork, provides the principal evidence of pre-Late Devensian vertebrates in Ireland (Scharff, Seymour & Newton 1918). Unfortunately, the fossils were recovered from a series of sands and stalagmite floors and may not all be of the same age. Flandrian mammals including domestic species were found in later deposits within the cave, and the presence of wood mouse *Apodemus sylvaticus* in association with the older fauna strongly suggests contamination with later material. A list of the fauna believed to be of Midlandian (Devensian) age is given in Table 8.4. A radiocarbon date of 33 400 ± 1 200 years B.P. (D-122) on collagen from a mammoth bone suggests a Middle Devensian age for this faunal assemblage, which includes both species of lemming *Dicrostonyx torquatus* and *Lemmus lemmus*, wolf *Canis lupus*, fox *Vulpes vulpes*, arctic fox *Alopex lagopus*, bear *Ursus* sp., spotted hyaena *C. crocuta*, mammoth *M. primigenius*, giant deer *Megaceros giganteus* and reindeer *R. tarandus*. Conspicuously absent at Castlepook, and elsewhere in Ireland, are any species of vole, woolly rhino *C. antiquitatis* and bison *Bison priscus*. Horse *Equus ferus*, although absent at Castlepook, is recorded elsewhere in Ireland at Shandon Cave, County Waterford, in association with mammoth and reindeer (Brenan 1860; Carte 1860).

Lynx *Felis lynx* is recorded from Kilgreany Cave, County Waterford (Savage 1966). The age of the find is uncertain.

Bones and teeth of *M. primigenius, C. antiquitatis*, and other cold stage species, are from time to time dredged from the sea bed in the English Channel and southern North Sea, especially from the Dogger Bank. These finds graphically illustrate the depressed sea level of at least certain phases of the Devensian in comparison with that of the present day (Ch. 2).

Late Devensian (26 000 to 10 000 radiocarbon years B.P.)

The present state of knowledge on the Late Devensian vertebrate faunas is far from satisfactory. Most of the material ascribed to this period is from various cave deposits, most of which were not properly excavated, so that it is impossible to be sure which of the species represented actually lived at any given time. More reliable faunal records are, however, available from a few cave sites, often in association with radiocarbon dates, usually based on bone collagen.

There are also a few sparse faunas available from fluviatile deposits in association with radiocarbon dates and/or pollen spectra. Remarkably complete large-mammal material is available in accurately known stratigraphical context from lacustrine deposits in both Britain and Ireland, but the finds are of one or two species only.

Sands and gravels about 1.5 m thick overlying Gault Clay were exposed near Barnwell Station, Cambridge, early in the present century (Marr & Gardner 1916). These deposits form part of the second terrace of the River Cam. Peaty seams within the sands yielded plant macrofossils and beetles. The former were re-examined by Bell and Dickson (1971) and indicate a rich herbaceous vegetation, together with the shrubs *Betula nana* and *Salix* spp. (willows). Coope (1968b) reappraised the beetle fauna, which he says suggests an open habitat devoid of trees. An arctic climate is indicated by the limited number of species and presence of arctic and arctic-alpine beetles. The radiocarbon date of 19 500 ± 650 years B.P. (Q-590) on plant detritus, which puts these deposits into the early part of the Late Devensian, contradicts Coope's correlation of the Barnwell Station Beds with the closing phases of the Upton Warren interstadial complex (i.e. about 28 000 years B.P.). It is possible, as pointed out by Coope, that the radiocarbon date is too young, as it was made on a peat sample stored for many years previously.

Large-mammal remains found by workmen in the sands and gravels and listed by Marr and Gardner include *M. primigenius, E. ferus, C. antiquitatis* and *R. tarandus* (Table 8.2), of which only the last two species are represented in the collections of the Sedgwick Museum, Cambridge. Red deer *Cervus elaphus* was also mentioned by these authors, but antlers of this species labelled from nearby pits adjacent to Newmarket Road are included in the Sedgwick Museum collection, and significantly Marr omitted this species from the Barnwell Station lists in subsequent publications.

With the principal exception of the Barnwell Station material, nearly all assemblages of Late Devensian age, appear to date from the end of the substage, conveniently termed 'late-glacial' (*c.* 15 000 to 10 000 years B.P.).

In 1970 an entire associated skeleton of a male elk *Alces alces* was found *in situ* in detritus muds, within a sequence of lacustrine sediments, at High

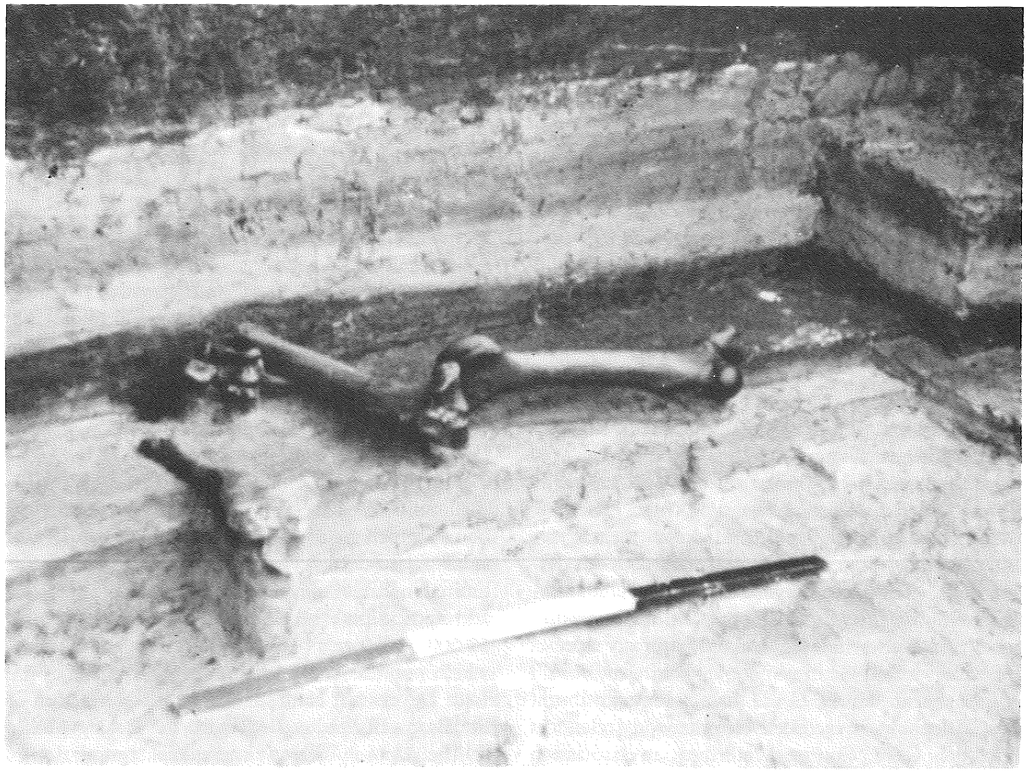

Fig. 8.6. Hind limb bones of elk *Alces alces in situ* in Late Devensian zone II, lacustrine deposits at High Furlong, Blackpool, Lancashire. (Scale in feet)

Furlong, Blackpool, Lancashire (Hallam *et al.* 1973) (Figs 8.6, 8.7). Pollen analyses showed that the sequence represented pollen zones I to III of the Late Devensian plus part of the Flandrian. The detritus mud bed yielded pollen spectra characteristic of zone L-DeII, and gave radiocarbon dates of 11 665 ± 140 and 12 200 ± 160 years B.P. (IGS-C14/134, IGS-C14/135) which are rather too high. The contemporary vegetation appears to have been birch woodland (tree birch leaves were also found) with juniper, grasses, sedges and other open-ground herbs. Two barbed projectile points were found with the skeleton, which also bears numerous lesions due to injuries by weapons (see Ch. 5). The occurrence of the skeleton, which was clearly not butchered by the hunters, in lacustrine deposits suggests that it may have perished by breaking through thin ice and subsequently drowning, as has been observed to happen with modern animals. This hypothesis finds support from the fact that the antlers were nearly parted from the pedicles at the time of death, i.e. were about to be shed, which indicates winter as the season when the animal died (see Ch. 5).

Another skeleton of *A. alces* was discovered in 1939 at Neasham near Darlington, County Durham (Trechmann 1939). Blackburn (1952) later established that, like the Blackpool specimen, this specimen also came from Late Devensian zone II muds of a former pond or lake. Radiocarbon dates of 11 011 ± 230 and 11 561 ± 250 years B.P. (Q-207, Q-208) were obtained from the muds. The Neasham specimen is also male, but in this case the antlers were found firmly united to the skull (see Hallam *et al.* 1973), so that the season of death is uncertain.

The Pleistocene of Ireland is renowned for the many hundreds of giant deer *Megaceros giganteus* skulls and skeletons which have been found beneath the peat bogs (Figs. 8.8, 8.9). The fossils

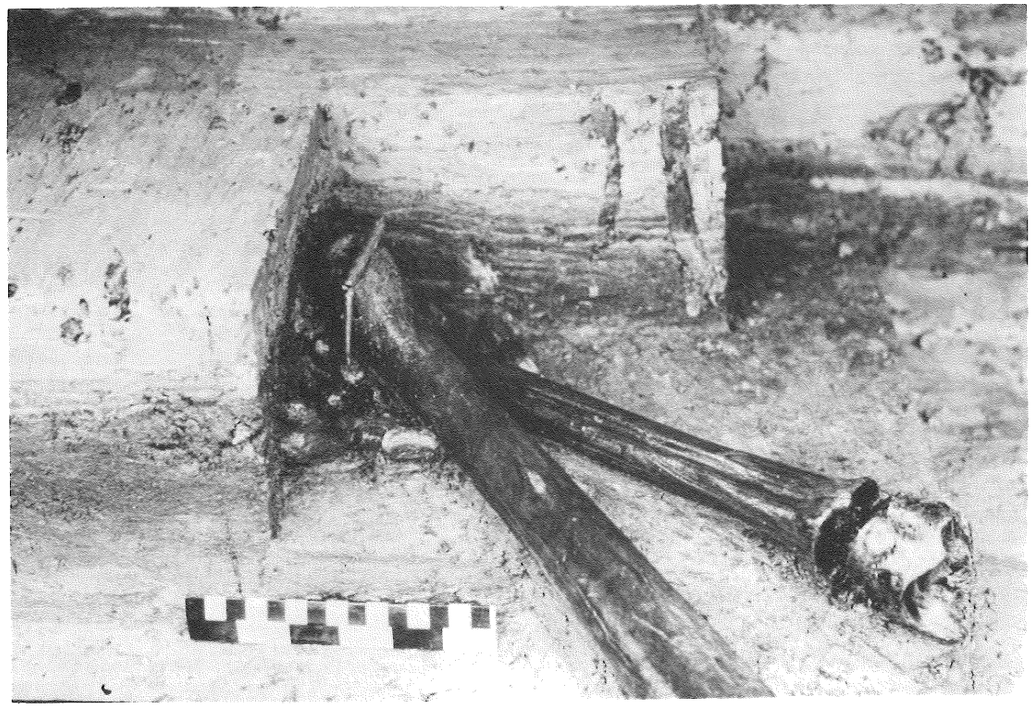

Fig. 8.7. Close-up of metatarsals of High Furlong *Alces alces*, showing barbed projectile point *in situ*.

almost invariably occur in calcareous lacustrine muds which date from Late Midlandian (= Late Devensian) pollen zone II (Mitchell & Parkes 1949). Remains of reindeer *Rangifer tarandus* also occur in the same deposits but are much less common than those of *M. giganteus* (Mitchell 1941). Most specimens were recovered for ornamental purposes, and many are to be seen in Irish country houses as well as in museums throughout the British Isles and elsewhere. Since nearly all the existing specimens are of stags with fine antlers, it is probable that the less spectacular material including skulls of females (the latter probably also confused with domestic horse) was not readily collected. The occurrence of *M. giganteus* remains suggests that the animals perished by being mired in soft mud at the edge of lakes, or perhaps sometimes breaking through thin ice and drowning. This situation would result in a bias towards males which are encumbered by their large antlers, and also explains the relative rarity of *R. tarandus* finds, since the latter are very much smaller and lighter animals. Whole *M. giganteus* skeletons do occur but portions of the skeleton, or detached skull and antlers are usual, suggesting break-up of floating carcasses. The three small bogs in a small steep-sided valley at Ballybetagh near Dublin yielded remains of over 60 individuals, and no doubt more are still entombed in the deposits.

The large numbers of *M. giganteus* remains found have led many authors to conclude that this animal was especially common in Ireland near the end of the Last Cold Stage. This apparent abundance may, however, be simply a result of the widespread existence of such natural traps and the calcareous nature of these lacustrine deposits which has preserved the bones. *M. giganteus* is also recorded from zone L-De II deposits at Ballaugh, Isle of Man (Mitchell & Parkes 1949).

There has been no up-to-date study of an *M. giganteus* find in conjunction with palaeobotanical work, so that the precise history of this animal in Ireland in relation to the vegetational history is unknown. The occurrences of *M. giganteus* and *R. tarandus*, however, most probably correspond to the Gramineae (grass) phase, dating from approx-

imately 12 000 to 10 900 years B.P. The plant assemblage suggests predominant short grassland with small herbs and shrubs and stands of the tree birch *Betula pubescens* (Watts 1977).

Rangifer tarandus, *M. giganteus* and a duck *Anas* sp., mentioned by Jessen and Farrington (1938), are the only taxa of zone II age known from Ireland. A few finds of *R. tarandus* are recorded from overlying horizons, presumably dating from zone III. Very probably, many cave finds also date from the end of the Late Midlandian, although this has yet to be demonstrated since no Irish cave deposits of this age have been properly excavated.

At Flixton near Star Carr, Yorkshire, Late Devensian muds yielded pollen suggesting a date towards the end of pollen zone II. Overlying muds with an early pollen zone III spectrum gave a radiocarbon date of 10 413 ± 210 years B.P. (Q-66). Partial skeletons of three individuals of horse *Equus ferus* were found in the zone II horizon accompanied by a flint point and some bird bones (Clark 1954). The associated pollen spectra indicate open grassy vegetation with perhaps some tree birch.

At Nazeing, Essex, a series of deposits of Late Devensian and Flandrian age occupy a channel cut in Devensian gravels of the River Lea (Allison, Godwin & Warren 1952). The gravels have yielded remains of *M. primigenius*, *C. antiquitatis*, *R. tarandus* and other large mammals. Peat rafts, within these gravels ('Arctic Plant Bed') at Broxbourne near Nazeing, have been radiocarbon dated to about 28 000 years B.P., so that the mammal bones probably represent the late Middle Devensian and the early part of the Late Devensian. Remains of arctic lemming *Dicrostonyx torquatus* and a vole *Microtus* sp. have been found in the same terrace at Angel Road, Edmonton (Warren 1912). The 'Arctic Bed' yielded macroscopic plant fossils indicating a tundra-like flora with sedges, grasses and a variety of other open-ground herbs.

The earliest channel deposits ('peaty muds' of beds AB4, B4) appear to be of Late Devensian pollen zone II age or slightly earlier. Small mammals from this bed include Norway lemming *Lemmus lemmus* and northern vole *Microtus oeconomus*. The pollen indicates grass sedge tundra or park tundra. Overlying calcareous muds (Beds 'M' in part) pollen dated to the end of zone L-De III yielded remains of *D. torquatus*, tundra vole *Microtus gregalis*, *M. oeconomus*, frog *Rana* sp., toad *Bufo* sp. and common lizard *Lacerta vivipara*. Fossil pollen and

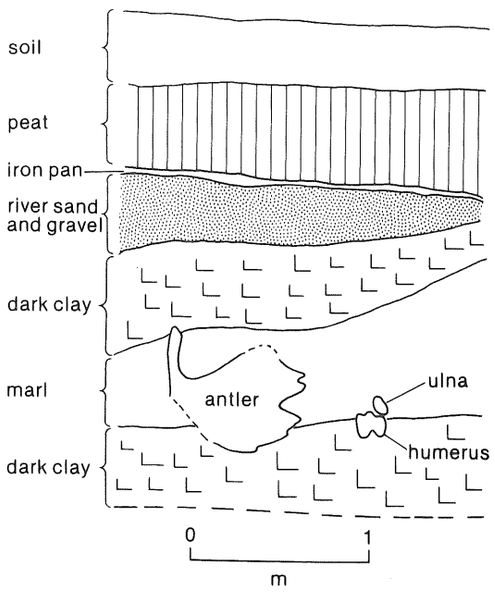

Fig. 8.8. Field sketch (after J. P. O'Connor) showing stratigraphical position of *in situ* find of giant deer *Megaceros giganteus* at Craddanstown, Co. Meath, Ireland, in 1976.

macroscopic plant remains indicate a typical late-glacial flora with many herbs and dwarf birch *Betula nana*.

The faunas of the Flandrian deposits at Nazeing are discussed in Chapter 7.

Gravels and sands of the River Gipping at Sproughton near Ipswich, Suffolk, have yielded barbed projectile points and remains of horse *Equus ferus* and reindeer *Rangifer tarandus* (Wymer *et al.* 1975). A find of the former species was bracketed between radiocarbon dates of 9 880 and 11 370 years B.P., lying stratigraphically much closer to the younger date, i.e. probably towards the end of pollen zone III. The *R. tarandus* finds probably date from zone III or possibly a little earlier.

A fossil vertebrate assemblage of probable Late Devensian age was found in a series of sands and limestone breccias banked up against a 'fossil' Pleistocene sea cliff at Brean Down near Weston–Super-Mare, Somerset (Apsimon, Donovan & Taylor 1961). The fauna includes arctic fox *Alopex lagopus*, horse *Equus ferus* and reindeer *Rangifer tarandus*.

The faunas from a number of cave deposits in England are distinctive in lacking *M. primigenius*, *C. antiquitatis*, etc., whereas the steppe pika *Ochotona pusilla* is commonly present. Unfortunately, few of these faunas can be relied upon to date from a single horizon, largely because of contamination with younger material, but in a few cases carefully excavated material is available. The fauna from a single horizon in Ossom's Cave in the Manifold Valley, Staffordshire, *identified by D. Bramwell* (personal communication) includes: *D. torquatus; L. lemmus*; several voles, *E. ferus; R. tarandus*; red deer *C. elaphus*; eagle owl *Bubo bubo*; grouse *Lagopus lagopus*; ptarmigan *Lagopus mutus*; black grouse *Lyrurus tetrix*; corncrake *Crex crex*; jackdaw *Corvus monedula*; and missel thrush *Turdus viscivorus*. A radiocarbon date of 10 590 ± 70 years B.P. obtained from bone collagen suggests that the fauna was associated with the harsh climatic conditions of Devensian late-glacial pollen zone III.

Birds of probable Late Devensian age from a number of cave sites were discussed by Bramwell (1960), and more recently the same author has listed the Late Devensian avian and mammalian cave faunas of the Peak District, Derbyshire (Bramwell 1977). Campbell (1977) also lists faunas attributed to Late Devensian horizons from several caves in central and south-western England. These faunal lists generally resemble those from Ossom's Cave and other sites dating from the end of the Late Devensian. The records of temperate taxa, if correctly attributed to this time range, may largely date from the Windermere Interstadial. Remains of glutton *Gulo gulo*, known from a few sites in Britain including: Plas Heaton Cave, N. Wales (Dawkins, 1871); Wetton Mill Rock Shelter, Staffordshire and Chelm's Coombe Rock Shelter, Mendip (Bramwell, 1976); may be entirely or partly of Late Devensian age.

One find of musk ox *Ovibos moschatus* has been dated to the Late Devensian. (Table 8.3). The record from Maidenhead, Berkshire from the low terrace of the River Thames (Owen, 1856) is very probably also of Devensian age.

Fig. 8.9. Excavation of skull of *Megaceros giganteus* at Craddanstown.

Devensian Faunal History

The faunal history of the Devensian is much more complex than those of the interglacial stages, be-

cause of the much longer time span and the multiple climatic cycles covered by this cold stage.

Of the taxa represented, good fossil records are available for mammoth *Mammuthus primigenius*, woolly rhino *Coelodonta antiquitatis*, horse *Equus ferus*, reindeer *Rangifer tarandus*, extinct bison *Bison priscus* and, to a lesser extent, brown bear *Ursus arctos*. Fossil mammal assemblages from the Early Devensian and the peak of the Upton Warren Interstadial (early Middle Devensian – about 43 000 years B.P.) are dominated by remains of *B. priscus*. *Rangifer tarandus* also occurs but *E. ferus* and *M. primigenius* are only sparsely represented. In faunas from later in the Middle Devensian, however, *B. priscus* becomes much scarcer, with *M. primigenius* and *E. ferus* now abundant, and *B. priscus* may have become extinct in Britain soon after the beginning of the Late Devensian (Fig. 8.5). As noted by Rackham (1978) the relative abundance of *B. priscus* appears to correspond rather closely to the temperature curve inferred from beetle faunas constructed by Coope (see Fig. 2.4). This probably indicates, by analogy with modern species of bison (Ch. 5), that during relatively warm periods a richer growth of herbs was able to support large herds of grazing *B. priscus*, whereas the deteriorating climatic conditions of the later Middle Devensian, and much of the Late Devensian allowed the growth of only poorer quality graze, which was, however, sufficient for *M. primigenius*, *C. antiquitatis* and *E. ferus* (Ch. 5). The amelioration of climate of the Windermere Interstadial was, however, probably not accompanied by the return of *B. priscus*.

Mammuthus primigenius and *C. antiquitatis* are conspicuously absent from the numerous assemblages which can be attributed with varying precision to the end of the Late Devensian ('late glacial'), post-dating the main glaciation of about 18 000 to 15 000 years B.P. Both species, however, appear to have been present immediately prior to this event (Fig. 8.5).

The virtual absence of radiocarbon-dated records, including those of man (Ch. 10), suggests that few vertebrates were able to persist in those areas not covered by ice south of the ice sheets, and that the faunas from the 'late glacial' therefore resulted from re-immigration from the Continent, to which the British Isles would have been broadly connected at this time (Ch. 2).

Mammuthus primigenius and *C. antiquitatis* evidently failed to return after the main glaciation, probably because they had become rare or extinct on the Continent by this late date.

Other species which did not return in the Devensian 'late glacial' include the carnivores lion *Panthera leo* and spotted hyaena *Crocuta crocuta*.

On the other hand, the arctic fox *Alopex lagopus*, lemmings *Lemmus lemmus* and *Dicrostonyx torquatus*, together with *E. ferus* and *R. tarandus* survived until the very end of the Late Devensian (Fig. 8.5), and their disappearance by the beginning of Flandrian can readily be attributed to the amelioration of climate and spread of forests. Northern vole *Microtus oeconomus* lasted into the early Flandrian. Other species with wide tolerances, such as the red fox *Vulpes vulpes*, may have been present in Britain during much of the Devensian, as this animal was throughout the Flandrian.

Two species, the steppe pika *Ochotona pusilla* and elk *Alces alces*, appear to be unique in the Devensian to the period *c.* 15 000 to 10 000 years B.P. The giant deer *Megaceros giganteus*, like *A. alces* apparently restricted in the 'late glacial' to the milder interstadial conditions of zone L-De II in both Britain and Ireland, is however also sparsely recorded from the Middle Devensian (Fig. 8.5). Its scarcity suggests that it may have migrated into the British Isles only during interstadials.

Of particular interest is the Devensian history of red deer *Cervus elaphus*, which also has a sparse fossil record for this stage. It is recorded in association with the boreal forests of the Chelford Interstadial, but also appears to have been present during colder periods (e.g. at Picken's Hole *c.* 34 265 years B.P.). The latter may represent a distinct open-ground ecotype. Equally intriguing is the sparse record of musk ox *Ovibos moschatus*. The single radiocarbon date of 18 213 years B.P. suggests that this animal may have occurred in Britain only during the more arctic phases of the Last Cold Stage. The rarity of lion *Panthera leo*, spotted hyaena *Crocuta crocuta* (and possibly leopard *Panthera pardus*) in faunas of Devensian age also suggests that they also were present only at certain periods within the stage.

The Irish Devensian (Midlandian) faunas show some interesting differences and similarities to those of Britain. In the Middle Devensian, lion *Panthera leo*, *Coelodonta antiquitatis*, *Bison priscus* and the various species of vole were for some reason unable to cross over to Ireland via the link with south-west Scotland, while many other mammals were successful in doing so. Ireland was largely covered by ice within the Late Devensian so that the

Irish 'late glacial' fauna represents a fresh immigration of animals via Britain. Only two species – *Rangifer tarandus* and *Megaceros giganteus* – have been dated to this period, but the high probability that many cave deposits are of 'late glacial' age allows us to infer that certain species, well represented in Britain, were almost certainly absent from Ireland. These include elk *Alces alces*, *Ochotona pusilla*, and all species of voles.

The relative impoverishment of the Irish Devensian faunas in comparison with those of England could be due to climatic differences, or alternatively could reflect topographical, climatic or vegetational conditions in the vicinity of the land connection between Britain and Ireland, which could have filtered out potential immigrants.

Comparison with Continental faunas

Fossil vertebrates dating from the Last Cold Stage are known from numerous sites in Europe across to northern Asia and North America. Broadly similar assemblages with *Mammuthus primigenius, Equus ferus, Coelodonta antiquitatis, Rangifer tarandus, Dicrostonyx torquatus, Lemmus lemmus* and other species typical of the British Devensian, occur from southern France to Siberia (Klein 1971), but few faunas are precisely dated or can be accurately related to climatic and vegetational changes. Pre–late glacial faunas from central Europe show a stronger steppe component than those from Britain, with, for example, jerboa *Allactaga jaculus*, pika *Ochotona pusilla*, and a greater number of records of saiga *Saiga tartarica* (Kahlke 1975b).

Last Cold Stage ('Würmian') faunas from southern France, well represented in cave deposits, are conventionally assigned to phases Würm I, II, III and IV. Arctic species such as arctic fox *Alopex lagopus*, lemmings *D. torquatus* and *L. lemmus*, woolly rhino *C. antiquitatis*, mammoth *M. primigenius*, and even rare musk ox *Ovibos moschatus* occur, as in Britain. The southern French faunas, however, also include: red deer *Cervus elaphus*, from all four phases; aurochs *Bos primigenius*; ass *Equus hydruntinus*; rhinos *Dicerorhinus* spp.; fat dormouse *Glis glis*; and other temperate or southern species (Lumley 1976), reflecting milder climatic conditions than in Britain, probably accompanied by the growth of woodland.

Such elements are especially marked in, but by no means confined to, the earliest phase 'Würm I'. The montane ibex *Capra ibex* and chamois *Rupicapra rupicapra* are well represented in French 'Würmian' cave deposits, as in those of the previous cold stage.

European faunas dating from the 'late glacial' (i.e. between about 15 000 and 10 000 years B.P.) all appear to lack *C. antiquitatis*, *M. primigenius* and several other species represented earlier in the Last Cold Stage. There are, however, several isolated finds of *M. primigenius* with radiocarbon dates of about 13 000 years B.P. and even younger, from France, Switzerland, European Russia and Scandinavia (Berglund *et al.* 1976), which, if correct, indicate that mammoth survived until almost the end of the Last Cold stage in some areas.

The best-dated 'late glacial' (Late Weichselian) faunas are from Denmark and north Germany. Vertebrate assemblages mostly obtained from archaeological sites have been dated by pollen analyses to particular zones within the Late Weichselian (Degerbøl 1964). The faunas are generally very similar to those from the British Isles, although Russian desman *Desmana moschata* (zones Ia, III), *Spermophilus major* (Ia, III), and of particular interest European bison *Bison bonasus* (zone III) are recorded from north Germany and Denmark. The more continental situation of the Holstein sites is reflected in the occurrences of *Bos primigenius*, wild boar *Sus scrofa* and elk *Alces alces* in zone III.

seem to be invariably associated with shells of terrestrial molluscs and relatively coarse sediments, indicating erosion and transport of bank material.

For sieving, a mesh of stainless steel or brass wire, retaining everything exceeding 1 mm, has been found to be practicable. Some very small shrew and mouse teeth may be lost, but this is not serious, and a smaller mesh size produces considerable problems in the much larger amounts of concentrate retained and clogging during use. It is usually desirable to have above a second sieve with larger holes, say 1 cm square, to retain large stones, shells, etc., and to hold lumps of sediment while they are breaking down. A pair of sieves each about 60 cm square, used in conjunction, have been found adequate for work in the field and for many purposes also in the laboratory. Large models are useful for processing large quantities from one site in the laboratory.

Sieving is usually only possible in water, and is best done on site, in the sea, in a stream, or in pools in gravel pits. If water is not available on site, or if the sediment does not break down readily, it may be worth transporting it in sacks and subsequently sieving it using a hose.

Intractable clay-rich sediments are best disaggregated by thorough drying and then immersing in water. Other methods include boiling, and treatment with hydrogen peroxide or 'Calgon'.

The wet concentrate can be sun- or oven-dried. The author uses a specially constructed drying cabinet containing a stack of fitted drying trays with fine nylon mesh. A through draught of hot air is provided by a 1 kW electric fan heater and a pipe at the top of the cabinet connected to the outside.

The dried concentrate is spread in small quantities on paper under a desk lamp and systematically sorted for small-vertebrate material, all of which is retained. Conservation treatment is usually unnecessary and the fossils can be stored in labelled glass tubes in boxes, or embedded in strips of soft wax in transparent plastic containers.

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