Pleistocene vertebrates in the British Isles

A. J. Stuart *University of Cambridge*

Longman *London and New York*

agent in breaking bones, especially as many are far too large to have been passed through the gut of another animal, or to have been broken by its teeth. The question needs much further investigation in view of its implications for the taphonomy of vertebrate assemblages (Ch. 4).

Small-mammal bones from the pellets regurgitated by modern diurnal birds of prey (raptors) show corrosion, which appears to be of a characteristic type and can be matched in Pleistocene fossil assemblages (Mayhew 1977). Mayhew describes and illustrates a number of recent and fossil examples. In vole molars, for example, corrosion is confined to the enamel ridges near the crowns, the rest of the tooth having been protected by the bone of the jaw.

Material recovered from the pellets of owls shows no such corrosion and little breakage, and is therefore not readily recognizable in fossil assemblages. Nevertheless, most of the fossil small-mammal bones and teeth from cave deposits at least almost certainly originated from pellets dropped by owls. Occasionally, discrete patches of fossil small-mammal material have been observed, sometimes with traces of organic matter, evidently representing owl pellets, as at Angel Road, North London (Devensian). The pellets contained bones and teeth of arctic lemming *Dicrostonyx torquatus* in an excellent state of preservation (Hinton 1912).

Palaeopathology

Pathological abnormalities are occasionally observed in Pleistocene fossil mammal material. For example, Wells and Lawrence (1976) describe a metatarsal of giant deer *Megaceros verticornis*, from the Cromerian of West Runton, Norfolk, which has a large bone tumour, with a central pit, on the antero-medial surface. The lesion is thought most likely to have been caused by ossification of a sub-periosteal haematoma resulting from injury.

Pathological elephant molars, showing twisting, distortion and eruption at abnormal angles, are fairly common. Bone tumours and direct injury have been cited as causes of these lesions (McWilliams 1967).

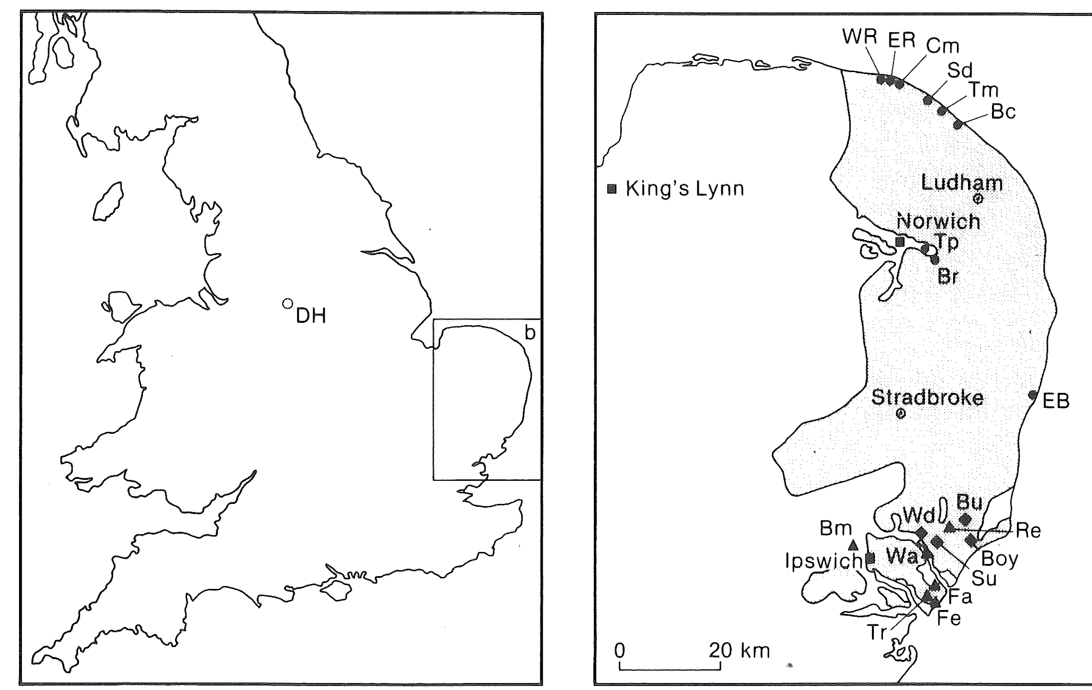
Lesions due to physical injury by weapons have been described in detail from Star Carr, Yorkshire (early Flandrian), and Blackpool, Lancashire (Late Devensian). Two scapulae, one of red deer *Cervus elaphus*, the other of elk *Alces alces*, from Star Carr, show partly-healed fractures produced by flint-tipped projectile weapons or barbed points (Noe-Nygaard 1975). A complete elk skeleton from Blackpool (Ch. 8) bears a variety of unhealed lesions resulting from the impact of flint-tipped projectile weapons, together with what appear to be axe cuts on one of the metacarpals, all dating from immediately prior to the death of the animal. In addition, however, there are a few lesions with accompanying reaction – osteoporosis of the bone due to bacterial infection which must have dated from some time before the elk's death. In particular, a barbed bone projectile point was excavated *in situ* resting in a broad groove in the distal end of the left metatarsal (Hallam *et al.* 1973) (see Figs 8.6, 8.7). The groove had evidently been eroded by the point which was embedded in the animal's foot, an estimated two to three weeks before death. Noe-Nygaard's (1975) dismissal of the lesions as caused by earth pressure and by damage during excavation appears to be based on misunderstandings of the nature of the site and the state of preservation of the bones (Stuart 1976b).

6 Lower Pleistocene faunas

With the exception of one cave assemblage, the Lower Pleistocene vertebrates of the British Isles come from the predominantly marine crags of East Anglia. The record is therefore not surprisingly patchy and unsatisfactory in comparison with the 'Villafranchian' faunas of southern and eastern Europe.

Due to the combination of sparse material and imprecise stratigraphical information for many finds, there is little prospect of detecting faunal changes within stages for the Lower Pleistocene. The overall faunal history for the period is discussed in Chapter 9.

The main sites with Lower Pleistocene vertebrate faunas are shown in Fig. 6.1



a b

Fig. 6.1. Location map of the main Pliocene and Lower Pleistocene vertebrate sites. ◆, Red Crag Nodule Bed (Pliocene); ▲, Red Crag; ●, other crags; ○, cave sites. The extent of the Pliocene Coralline Crag (hatched) and the Lower Pleistocene crags (stippled) are indicated, together with the locations of the Ludham and Stradbroke boreholes. Bc, Bacton; Bm, Bramford; Boy, Boyton; Br, Bramerton; Bu, Butley; Cm, Cromer; DH, Doveholes; EB, Easton Bavents; ER, East Runton; Fa, Falkenham; Fe, Felixstowe; Re, Rendlesham; Sd, Sidestrand; Su, Sutton; Tm, Trimingham; Tp, Thorpe, Norwich; Tr, Trimley; Wa, Waldringfield; Wd, Woodbridge; WR, West Runton.

Upper Pliocene (Red Crag Nodule Bed)

The Red Crag occurs over much of south-east Suffolk and as small outliers in north-east Essex. At its base at a number of localities, (notably Woodbridge, Boyton, Sutton and Butley, all in Suffolk) is found a condensed deposit – comprising flint pebbles and phosphatic nodules. Vertebrate fossils from this horizon are generally heavily mineralized, and often well rolled and polished, imparting an attractive glass, so that specimens were much prized by nineteenth-century, and later, collectors.

Some of the fossil vertebrate material has clearly been reworked from much older strata. In particular, remains of *Coryphodon* and *Hyracotherium* were derived from Eocene London Clay which occurs over much of the area. Comparison with Continental faunas suggests that the bulk of the vertebrate material is of broadly Upper Pliocene ('Lower Villafranchian') age. The Pliocene age strictly puts the Red Crag Nodule Bed fauna outside the scope of this chapter, but it is nevertheless briefly considered here as a prelude to the faunas of the Lower Pleistocene. Little modern work has been done on this material, which was, however, extensively described and figured by Newton (1891).

Taxa recorded include porcupine *Hystrix* sp., beaver *Castor fiber*, a small beaver-like rodent *Trogontherium minus*, a bear-like carnivore *Agriotherium* sp., extinct hyaena *Hyaena perrieri*, an extinct panda *Parailurus anglicus*, gomphothere mastodont *Anancus arvernensis*, true mastodon *Zygolophodon borsoni*, extinct elephant *Archidiskodon meridionalis*, horse *Equus* sp., extinct three-toed horse *Hipparion* sp., extinct tapir *Tapirus arvernensis*, extinct rhinoceros *Dicerorhinus megarhinus* and an extinct bovid cf. *Leptobos* sp.

Marine vertebrate remains also occur abundantly. Taxa represented include fishes, turtles, a sirenian, a walrus and several whales (Newton 1891).

Pre-Ludhamian Stage (Red Crag)

Comparison of the foraminifers and marine molluscs from surface outcrops of Red Crag, with faunas from the Ludham and Stradbroke boreholes strongly suggest that the Red Crag was deposited largely or entirely within the first stage of the British Pleistocene, the Pre-Ludhamian (Funnell & West 1977). Most fossil terrestrial vertebrates recorded from the Red Crag probably originate from the Red Crag Nodule Bed. A few specimens appear from their less mineralized condition, and/or where they were found, to have come from the Red Crag proper (Spencer 1964, 1966) and are therefore probably of Pre-Ludhamian age, if not reworked from older strata. Taxa represented include beaver *C. fiber*, gomphothere *Anancus arvernensis*, extinct elephant *Archidiskodon meridionalis*, horses including both *Equus* cf. *stenonis* and a 'caballine' species *Equus bressanus*, a deer *Eucladoceros* sp., a gazelle *Gazella* sp., and albatross *Diomedea* sp. Marine vertebrates are also recorded (Newton 1891).

Antian and Baventian Stages (Norwich Crag, in part)

It is uncertain to what extent the Ludhamian and Thurnian stages, which occur in the Ludham and Stradbroke boreholes, can be recognized in surface exposures of deposits assigned to the Red or Norwich Crag. Vertebrate records from the Norwich Crag so far available can be assigned to one or more of the stages from the Antian to the Pre-Pastonian.

The cliff section at Easton Bavents, north of Southwold, Suffolk, includes at least 2.8 m of Norwich Crag (Fig. 6.2), overlain by more than 2 m of laminated grey and blue clays (Funnell & West 1962). Pollen analyses of silt bands within the basal metre of crag indicates temperate forests with hemlock *Tsuga*, and the deposits are assigned to the Antian Stage with Easton Bavents as the type locality. A single pollen spectrum obtained from the upper part of the crag is of intermediate character and was assigned to the early part of the Baventian (zone Lp4a of Ludham). The crag therefore ranges from the Antian to the early Baventian in age.

The marine mollusc faunas (Norton & Beck 1972) record changes within the crag from open-coast littoral conditions at the base to sublittoral conditions towards the top.

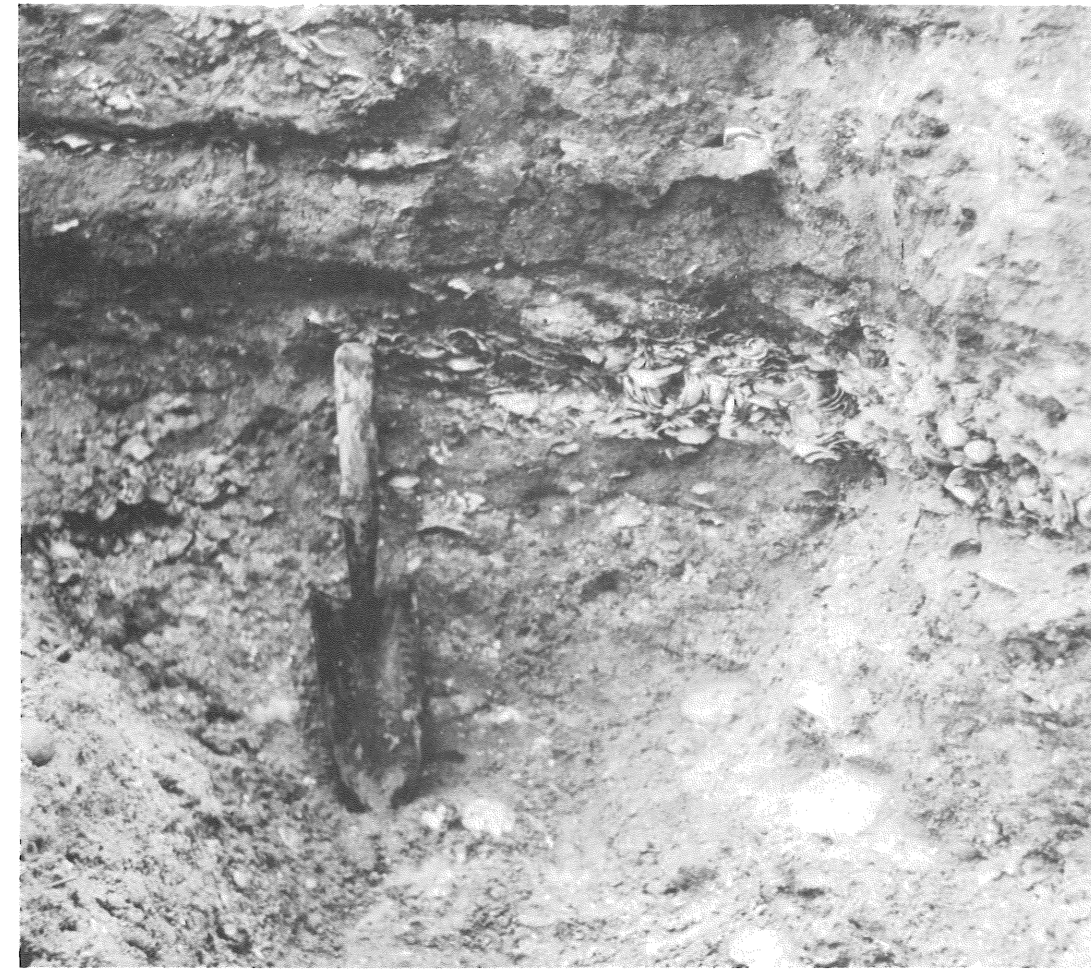


Fig. 6.2. Shelly marine sands ('crag') of Antian/early Baventian age at Easton Bavents, Suffolk.

Marine fish material is common in the crag, but remains of non-marine vertebrates are sparse, and much of our knowledge results from patient collecting over many years by Mr T. H. Gardner. Taxa recorded from the rarely exposed 'Lower Shell Bed', of probable Antian age, include *Equus* cf. *stenonis* and *Archidiskodon meridionalis*. Large mammals from the 'Upper Shell Bed' of early Baventian, or late Antian age, include *E.* cf. *stenonis, A. meridionalis, Eucladoceros falconeri, Eucladoceros* sp. and *Anancus arvernensis*. Teeth of the extinct water vole *Mimomys pliocaenicus* were described by Carreck (1966), and more recently collected material includes also the smaller species *Mimomys blanci* (Mayhew & Stuart, in preparation).

Bramertonian Stage and Pre-Pastonian *a* Substage (Norwich Crag, in part)

The pit at Bramerton Common, near Norwich, Norfolk, has long been regarded as the type section for the Norwich Crag, and dates from the early nineteenth century. A later excavation, Blake's Pit, 300 m to the east, was first noted in 1870. The stratigraphy, pollen, foraminifers and marine molluscs from both localities have recently been described in detail by Funnell, Norton and West (1979).

At Bramerton shelly sands with silt bands overlie Chalk. Pollen analyses from silty bands within the

6 m of crag at Blake's Pit allow the recognition of an *Alnus-Quercus-Carpinus* pollen assemblage zone, covering the bottom 4 m, indicating temperate forest. These spectra are assigned to a new stage, the Bramertonian with Blake's Pit as the type locality. A single sample from about 5 m above the Chalk is assigned to a *Pinus*-Ericales-Gramineae pollen assemblage zone, representing heath and herbaceous communities and a cold climate, and is correlated with the Pre-Pastonian *a* substage of the Norfolk coast succession.

The foraminferan and molluscan assemblages at Blake's Pit confirm the climatic history based on pollen evidence and also allow a fairly firm correlation with the Bramerton Common section. The Mollusca indicate littoral and sublittoral depositional environments, with periods with brackish sheltered tidal flat conditions marked by a 'fluviomarine' molluscan assemblage which includes non-marine taxa washed in to the sea.

Most of the vertebrate material from Bramerton was found during the last century, notably by Reeve. The exact localities and horizons of most specimens are unclear, but most of the material probably comes from Bramerton Common pit. It seems fairly certain, however, that specimes from the 'Lower Shell Bed' at either pit are of Bramertonian age, whereas those labelled 'Upper Shell Bed' are likely to date from the Pre-Pastonian *a* substage, or perhaps from the end of the Bramertonian.

Recently a very valuable collection of vole material has been made from the type Bramertonian Lower Shell Bed of Blake's Pit by P.G. Cambridge.

The faunal list from the 'Lower Shell Bed' (based on Mayhew 1979) includes the voles *Mimomys pliocaenicus, Mimomys reidi* and *Mimomys newtoni*, the extinct clawless otter *Aonyx reevei*, and from the basal stone bed the extinct elephant *Archidiskodon meridionalis* and deer *Eucladoceros* cf. *sedgwicki*. Taxa recorded from the 'Upper Shell Bed' include *Aonyx reevei, M. pliocaenicus* and the large vole *Mimomys rex*. The horizon of the gomphothere *Anancus arvernensis* is unfortunately unknown. The vole *Mimomys blanci*, known from several Lower Pleistocene localities, is strangely absent at Bramerton. Marine fishes and a seal *Phoca* sp. are also recorded.

One of the best available collections of crag vertebrates is from the Norwich Crag of Thorpe Norwich, collected during the last century, mainly by Fitch. The crag at this locality, which is only 5 km from Bramerton, is probably of approximately Bramertonian/Pre-Pastonian age. Taxa recorded include the extinct beaver *Trogontherium cuvieri*, voles *M. pliocaenicus, M. newtoni, M. blanci* and *M. reidi*, horse *Equus stenonis*, deer *Eucladoceros falconeri* and gazelle *Gazella anglica*.

Pre-Pastonian Stage ('Weybourne Crag' facies of Cromer Forest-bed Formation, in part)

Most of the older Cromer Forest-bed Formation finds unfortunately can be only broadly assigned to the Pre-Pastonian and Pastonian stages. These include the fine antler of *Eucladoceros sedgwicki* from Bacton, Norfolk, much of the large-mammal material from East Runton, Norfolk, where beds of both ages occur together. At a few sites, however, the stratigraphical evidence is good enough to assign finds to particular stages or substages.

At Sidestrand, Norfolk, locality SSB (West 1980a) shelly crag overlying chalk (Fig. 6.3) yielded teeth of the voles *Mimomys pliocaenicus, Mimomys reidi* and *Mimomys blanci*. Associated pollen spectra have been correlated by West with the Pre-Pastonian *a* substage, and a cold climate park-tundra vegetation is indicated.

A molar of the extinct elephant *Archidiskodon meridionalis*, found by R. G. West at West Runton cemented on to the surface of the Stone Bed, is probably of Pre-Pastonian *a* age and an antler of extinct elk *Alces gallicus* from West Runton is also attributable to this stage. At East Runton, Norfolk, teeth of voles *M. pliocaenicus, M. newtoni, M. blanci, M. reidi* and *Mimomys pitymyoides* are recorded from the 'Weybourne Crag'. This crag is overlain by freshwater muds giving a Pre-Pastonian *d* spectrum (West 1980a) and is almost certainly of Pre-Pastonian age.

Pastonian Stage (Cromer Forest-bed Formation, in part)

At East Runton a bed of clay conglomerate, (Bed e) probably 2–3 m thick containing marine shells, rests on an eroded surface of the crag described in the previous section, and is in turn overlaid conformably by marine silts yielding Pastonian zone Pa II pollen spectra. Bed *e* is therefore probably of Pastonian age. Antlers of deer are reported to have come from this horizon by Reid (1882), but unfortunately it is not clear to which specimens he was referring. A few vole teeth recorded from East Runton appear to have come from this horizon.

Excavations for sea defences at West Runton in 1975 exposed up to 2 m of shelly crag (bed d) (Fig. 6.4), the upper part of which was seen to interdigitate with Pastonian (zone Pa II) marine silts and must therefore be of this age (West 1980a). Samples of small-vertebrate remains were collected from both this horizon, and the crag beneath. The former is therefore of Pastonian age, and the latter could be of Pre-Pastonian or Pastonian age, although a Pastonian is much more probable. Taxa recorded include an unnamed species of desman, and the voles *Mimomys pliocaenicus, Mimomys newtoni, Mimomys blanci, Mimomys reidi* and *Mimomys pitymyoides* (Mayhew & Stuart, in preparation). On the assumption that there has been no reworking, all these species probably lived in association with regional temperate forest. Marine fishes also occur.

Fig. 6.3. Section in deposits of the Cromer Forest-bed Formation at Sidestrand, Norfolk. The Pleistocene deposits overlie domes of Chalk which have been thrust upwards by several metres. Pre-Pastonian and Pastonian crag and sands are unconformably overlain by Cromerian sediments, which are seen to channel into the older beds in the left of the photo, about halfway up the cliff. Site SSB, which yielded vole teeth from Pre-Pastonian crag immediately overlying the Chalk, is near the extreme right of the picture (see text).

Cave Sites

An assemblage of Pleistocene mammal, remains from a cave, at about 351 m O.D., in carboniferous limestone at Doveholes, Bibbington, Derbyshire, was originally described by Dawkins (1903). The fauna, recently reassessed and figured by Spencer and Melville (1974), includes a hyaena

Fig. 6.4. Marine silts and crag of Pastonian age exposed beneath the beach, in the course of constructing sea defences at West Runton, Norfolk, to the west side of Woman Hythe. (Cromerian freshwater deposits occur at a higher level in the base of the cliff – see Figs. 7.2, 7.3, 7.4).

Hyaena sp., sabre-tooth *Homotherium sainzelli*, gomphothere mastodont *Anancus arvernensis*, extinct elephant *Archidiskodon meridionalis*, extinct horse *Equus* cf. *bressanus*, and a deer. The presence of *A. arvernensis* indicates an age not later than Bramertonian.

Comparison with Continental faunas

The 'Villafranchian' deposits of southern Europe are subdivided, on the basis of their mammalian faunas, into Lower ('Pliocene'), Middle (earlier Lower Pleistocene) and Upper (later Lower Pleistocene) units. Finer divisions are also made using faunas of individual sites. The earliest Villafranchian faunas (Triversa Faunal Unit) of Italy (Azzaroli 1970, 1977b; Azzaroli & Vialli 1971) include mastodon *Zygolophodon borsoni*, the vole *Mimomys polonicus*, and other characteristically Pliocene taxa. The later Lower Villafranchian fauna (Montopoli fauna) lacks these elements, but includes the earliest elephant and horse in Italy. The Suffolk Red Crag Nodule Bed assemblage may therefore include a mixture of fossils of broadly Lower Villafranchian age.

The Middle Villafranchian, not found in Italy, is represented by the French Saint Vallier fauna. Azzaroli (1977b) equates it with that of the English Red Crag. The earliest faunas from Italy attributed to the Late Villafranchian (Olivola Faunal Unit) still include the gomphothere mastodont *Anancus arvernensis*, but this species is absent from the later faunas (Tasso and Farneta Faunal Units). This corresponds to the pattern of faunal change seen in the British Lower Pleistocene. An interesting feature of the Italian faunas is the occurrence of the extinct hippopotamus *Hippopotamus major*.

The deer faunas from Villafranchian localities in France and Spain (Heintz 1970) show considerable change from the Pliocene through the Lower Pleistocene. In particular, *Eucladoceros* spp. occur only in the Middle and Upper Villafranchian (Lower Pleistocene) and *Alces* (*Libralces*) *gallicus* is restricted to the Upper Villafranchian only, again corresponding to the British sequence. Villafranchian records of other taxa can be found in Lumley (1976).

The Upper Pliocene and Lower Pleistocene assemblages of central and eastern Europe are known mainly from cave and fissure deposits, and are generally restricted to small-mammal material.

The fauna from the Tegelen Clay, south Netherlands, is of great importance because it can be dated to the late part of the Tiglian temperate stage in the detailed pollen-biostratigraphical scheme for the Dutch Lower Pleistocene. The large mammals need revision, but include *Anancus arvernensis*, extinct tapir *Tapirus arvernensis* (both dating from the beginning of the succeeding Eburonian cold stage), and a species of *Eucladoceros* (*E. tegelensis*) resembling the British *E. tetraceros* (Kortenbout van der Sluijs & Zagwijn 1962). The small mammals (from Tiglian zone Tc 5) include *Mimomys reidi*, *Mimomys blanci* and *Mimomys pliocaenicus* (Freudenthal *et al.* 1976). The fauna indicates a probable correlation with the Antian or Bramertonian temperate stages of the East Anglian sequence.

A. correlation of European Lower Pleistocene deposits based on pollen biostratigraphy, palaeomagnetic data and vertebrate faunas is given by Zagwijn (1974).

7 Middle and Upper Pleistocene interglacial faunas

General

As discussed in Chapter 2 the interglacial periods appear to have been relatively short, each of the order of 10–20 000 years, compared with the Middle and Upper Pleistocene as a whole. It should be stressed that the various interglacials were not all of the same duration.

Each interglacial had a broadly similar vegetational cycle with the development of temperate deciduous forests in the middle of the stage (pollen zones II, III – see Ch. 2), when warm summers and mild winters are indicated from the evidence of various fossil invertebrates and plants. Coniferous and birch woodland and more extensive herbaceous vegetation characterize the beginning and end of each interglacial (zones I and IV).

Faunal change within the stage largely reflecting climatic and vegetational changes can be detected for each of the interglacials, but is particularly evident in the Ipswichian, which is also represented by a comparatively large number of sites.

The faunas from the middle and generally warmest parts (pollen zones II and III) of the interglacials from the Cromerian to the present day each comprise a mixture of species nowadays either: (a) extinct; (b) widespread in the Palaearctic and commonly beyond; (c) characteristic of the temperate regions only; or (d) restricted to areas to the south of the British Isles. Although the general character of the faunas from each of the interglacials is similar, they nevertheless differ in detail, reflecting complex patterns of evolution, extinction and immigration.

Faunas dated more or less certainly to the closing phases of the Cromerian, Hoxnian and Ipswichian interglacials, each seem to show the appearance of nowadays arctic-boreal taxa in association with surviving temperate and southern taxa. This phenomenon may be related to the prevalence of continental climatic conditions with warm summers and cold winters.

Notwithstanding the higher sea levels reached in earlier interglacials, compared with that of the present day (Flandrian), Britain appears to have remained connected to the Continent throughout the Cromerian and Hoxnian interglacials. There is evidence, however, that England was separated from France by sea during part of the Ipswichian interglacial (Ch. 2), and the Flandrian flooding of the Straits of Dover probably dates from a time within pollen zone VI (Fl II).

It is not known whether or not Ireland was connected (presumably via south-west Scotland) to Britain during interglacials before the Flandrian. The Flandrian separation from Britain was probably as early as zone IV (Fl Ia).

Cromerian Stage

Sites and Faunas (Fig. 7.1, Table 7.1)

The Cromer Forest-bed Formation (CF-bF) has been famous for its fossil mammal remains since the early part of the last century, but unfortunately few finds can be accurately related to particular stages (see Ch. 2), largely because the exact locations and horizons of the fossils were not recorded at the time of discovery. Nevertheless a rich fauna is accurately recorded from the type locality of the Cromerian stage at West Runton, Norfolk, a few fossils have been found *in situ* at other CF-bF localities and it has proved possible to date certain other finds by pollen analyses of adhering sediment.

The West Runton Freshwater Bed occupies a broad shallow channel, cut in sands and gravels, more than 400 m across in section and crops out at the base of the cliff east of Woman Hythe (West Runton) (Figs. 7.2, 7.3). The channel filling with a maximum thickness of about 2 m constitutes the type section for the Cromerian Stage.

Table 7.1. Pollen-dated records of Cromerian mammals.

Sites:	West Runton	West Runton	West Runton	Sugworth	Trimingham	Mundesley Bacton	Ostend
Cromerian Pollen zones	?Ia	Ib–IIb	IIIa	IIIb	?IIIb	?IV	IV
MAMMALIA							
Insectivora							
1. *Erinaceus* cf. *europaeus* L., hedgehog	–	+	–	–	–	– –	–
2. *Sorex cf. minutus* L., pigmy shrew	–	–	–	+	–	– –	–
3. *Sorex runtonensis* Hinton, extinct shrew	–	+	–	–	–	– –	+
4. *Sorex savini* Hinton, extinct shrew	–	+	–	+	–	– –	+
5. *Neomys newtoni* Hinton, extinct water shrew	–	+	–	–	–	– –	–
6. *Beremendia* cf. *fissidens*	–	–	–	+	–	– –	–
7. *Talpa europaea* L., mole	–	+	–	–	–	– –	+
8. *Talpa minor* Freudenberg, extinct mole	–	+	–	+	–	– –	–
9. *Desmana moschata* Pallas, Russian desman	–	+	–	–	–	– –	+
Primates							
10. *Macaca* sp., macaque monkey	–	–	+	–	–	– –	–
Lagomorpha							
11. *Lepus* sp., hare	–	+	–	–	–	– –	–
Rodentia							
12. *Sciurus whitei* Hinton, extinct squirrel	–	–	+	–	–	– –	–
13. *Sciurus* sp., a squirrel	–	–	–	–	–	– –	+
14. *Trogontherium cuvieri* Fischer, extinct beaver	–	+	–	–	–	– –	+
15. *Castor fiber* L., beaver	–	+	–	–	–	– –	–
16. *Cricetus cricetus* (L.), common hamster	–	+	–	–	–	– –	–
17. *Clethrionomys glareolus* (Schreber), bank vole	–	+	–	+	–	– –	+
18. *Pliomys episcopalis* Méhely, extinct vole	–	–	–	+	–	– –	–
19. *Mimomys savini* Hinton, extinct water vole	+	+	+	+	–	– –	–
20. *Arvicola cantiana* (Hinton), extinct water vole	–	–	–	–	–	– –	+
21. *Pitymys arvaloides* Hinton, extinct pine vole	–	+	–	–	–	– –	–
22. *Pitymys gregaloides* Hinton, extinct pine vole	–	+	–	–	–	– –	–
23. *Microtus* cf. *arvalis* (Pallas), common vole	–	+	–	+	–	– –	+
24. *Microtus oeconomus* (Pallas), northern vole	–	+	–	–	–	– –	–
25. *Apodemus sylvaticus* (L.), wood mouse	–	+	+	+	–	– –	–
Carnivora							
26. *Canis lupus* L., wolf	–	+	–	–	–	– –	–
27. *Ursus deningeri* v. Reichenau, extinct bear	–	+	–	–	–	– –	–
28. *Mustela nivalis* L., weasel	–	+	–	–	–	– –	–
29. *Martes* sp., marten	–	+	–	–	–	– –	–
30. *Pannonictis* sp., extinct mustelid	–	+	–	–	–	– –	–
31. *Lutra* sp., otter	–	+	–	–	–	– –	–
32. *Crocuta crocuta* Erxleben, spotted hyaena	–	+	–	–	–	– –	–
33. *Felis* cf. *lunensis* Martelli, extinct cat	–	+	–	–	–	– –	–
34. Undetermined large felid	–	+	–	–	–	– –	–
Proboscidea							
35. cf. *Mammuthus trogontherii* Pohlig, extinct elephant	–	–	–	–	–	– –	+
36. Undetermined elephant	–	+	–	–	–	– –	–
Perissodactyla							
37. *Equus* sp. (caballine), a horse	–	+	–	–	–	– –	+
38. *Dicerorhinus etruscus* (Falconer), extinct rhinoceros	–	+	–	–	–	– –	–
Artiodactyla							
39. *Sus scrofa* L., wild boar	–	+	–	–	–	– –	–
40. *Hippopotamus* sp., hippopotamus	–	–	–	–	+	+ +	–
41. *Megaceros verticornis* Dawkins, giant deer	–	+	–	–	–	– –	–
42. *Megaceros dawkinsi* (Newton), extinct giant deer	–	–	–	–	–	– –	–
43. *Megaceros* sp., giant deer	–	–	–	+	–	+ –	–
44. *Dama dama* (L.), fallow deer	–	+	–	–	–	– –	–
45. *Cervus elaphus* L., red deer	–	+	–	+	–	– –	–
46. *Alces latifrons* Johnson, extinct elk	–	+	–	–	–	– –	–
47. *Capreolus capreolus* (L.), roe deer	–	+	–	–	–	– –	+
48. *Bison* cf. *schoetensacki* Freudenberg, extinct bison	–	+	–	+	–	– –	–

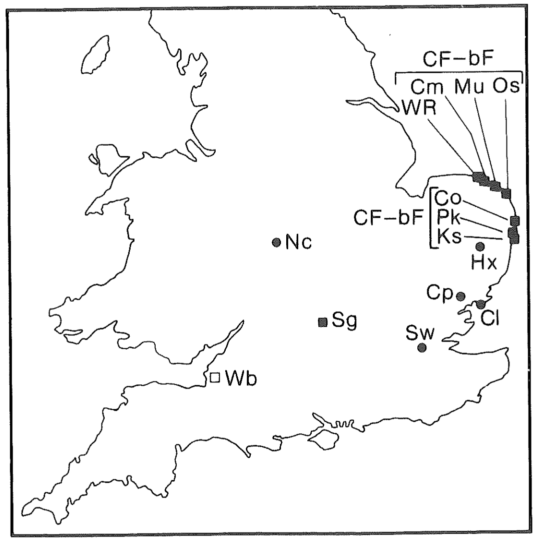


Fig. 7.1. Location map of Cromerian and Hoxnian vertebrate sites. ■, Cromerian; ●, Hoxnian; (cave site shown by open symbol). Cl, Clacton; Cm, Cromer; Co, Corton; Cp, Copford; Hx, Hoxne; Ks, Kessingland; Mu, Mundesley; Nc, Nechells Birmingham; Os, Ostend near Bacton; Pk, Pakefield; Sg, Sugworth; Sw, Swanscombe and Ingress Vale; Wb, Westbury-sub-Mendip; WR, West Runton.

The basal bed of the channel filling, West's Bed a, comprising marls and detritus muds, is of Late Beestonian and Cromerian subzone Cr Ia age (West 1980a). On its eroded surface rest beds c–e: comprising fluviatile shelly sands and organic muds containing lumps of marl reworked from the underlying deposit. Pollen analyses demonstrate that these beds essentially cover subzones Cr Ib to Cr IIa. The bulk of the West Runton Freshwater Bed consists of detritus muds, leached at the top, and covers subzone Cr IIb.

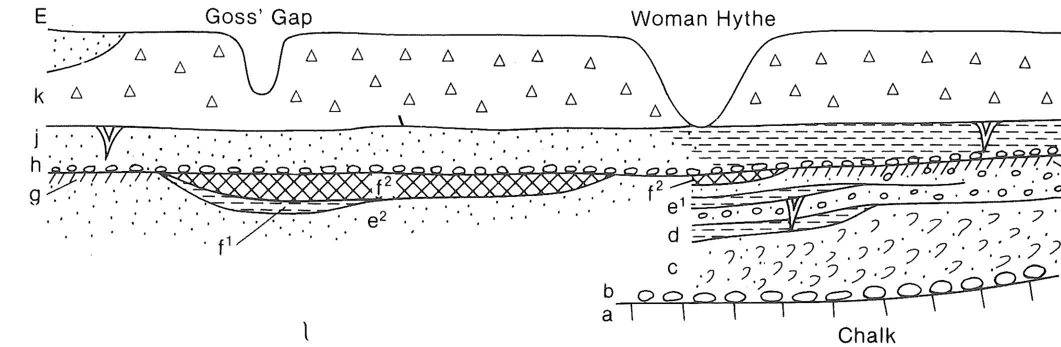
These deposits have yielded a rich vertebrate fauna (Table 7.1), although the records of the larger mammals are based on relatively sparse material. Much of the collecting was done by A. C. Savin, a local amateur, from about 1880 to 1945. These finds can be dated only rather broadly to the range subzones Cr Ib to Cr IIb (i.e. not restricted to Cr II as previously stated, e.g. Stuart 1975), since vertebrate remains are extremely rare in the earlier horizon. It is apparent, however, both from material collected *in situ* by the author, and examination of museum material with attached sediment matrix, that all large-mammal finds come from the coarser basal units. With minor exceptions, therefore, the age of the vast majority of the fauna can be narrowed to subzones Cr Ib to Cr IIa. Bulk samples of small vertebrates were collected by the author from three separate lithological units, corresponding fairly closely with subzones Cr Ib, Cr IIa and Cr IIb, at West's locality AJS. All three assemblages are almost identical, although the concentration of terrestrial vertebrate material for a given weight of sediment decreases sharply from bottom to top (Stuart 1975).

The fossil pollen and macroscopic plant remains (West 1980a) record changes from a pine–elm–birch woodland with extensive herb vegetation and restricted fen and reed swamp in subzone Cr Ib (*Pinus–Ulmus* pollen-assemblage biozone: p.a.b.), to a more diverse woodland with oak and other thermophilous genera more widespread, persistent local open habitats with herbaceous vegetation, and fen and reedswamp, in subzone Cr IIa (*Pinus–Quercus–Ulmus* p.a.b.). During subzone Cr IIb (*Quercus–Ulmus–Tilia* p.a.b.) mixed oak forest dominated, but again with persistent local open herb vegetation and even indications of heath. A rich aquatic and reedswamp flora is indicated.

Taking the sedimentological and palaeontological evidence together, one can picture a slow-flowing river, rich in aquatic plants and fringed by fen, supporting a wide variety of fishes, such as is found in a typical English lowland river today, plus frogs and toads, grass snake *Natrix* sp., water birds, and mammals of waterside habitats, including Russian desman *Desmana moschata*, beaver *Castor fiber*, extinct beaver *Trogontherium cuvieri* and extinct water vole *Mimomys savini*. Local herb-dominated vegetation on the floodplain appears to have supported grassland voles *Microtus* spp. and *Pitymys* spp., and common hamster *Cricetus cricetus*.

Two species of mole, *Talpa europaea*, and the smaller extinct *T. minor*, made their tunnels in the floodplain.

Much of the fauna, including wood mouse *Apodemus sylvaticus*, bank vole *Clethrionomys glareolus*, extinct rhinoceros *Dicerorhinus etruscus*, wild boar *Sus scrofa*, fallow deer *Dama dama* and roe deer *Capeolus capreolus*, is consistent with the presence of temperate forest, although many of these animals probably obtained much of their food at the forest edge on the floodplain, or in glades within the forest. The presence of the large deer *Megaceros verticornis* and *Alces latifrons*, in which the males carried enormous outspread antlers,



Stage		*Sediments*	*Environment*
Anglian (cold stage)	k	Till and contorted drift (ice-wedge casts below) Sands	Glacial Permafrost
Cromerian (temperate stage)	i	Silts zones Cr III, IV	Estuarine
	h	*Mya* Bed	
	g	Soil overlain by gravel	Subaerial
	f²	Detritus mud, zones Cr Ib to IIb	Freshwater
	f¹	Marl, zones 1–Be to Cr Ia	
Beestonian (cold stage)	e²	Gravels and sands with shells	Marine
	e¹	Laminated silts (ice wedge casts below)	Freshwater Permafrost
Pastonian (temperate stage)	d	Silts	Marine
	c	Shelly sand	
Pre-Pastonian (cold-stage)	b	Stone Bed	
	a	Combe rock, on Chalk (*U. Cretaceous*)	Permafrost

Fig. 7.2. Sketch section at West Runton, Norfolk (not to scale). (Adapted from West 1977a) Length of section approximately 450 m; depth of deposits below till approximately 7 m. The V-shaped vertical structures are ice-wedge casts. Vertebrates are recorded from beds b, c, f^2 and h.

together with horse *Equus* sp. and probably certain other large-mammal taxa, suggests that the forest was not very dense. Carnivores preying on the wide variety of available herbivores included wolf *Canis lupus*, the omnivorous extinct bear *Ursus deningeri*, weasel *Mustela nivalis*, spotted hyaena *Crocuta crocuta*, extinct cat *Felis* cf. *lunensis* and an undetermined large cat (Stuart 1975, 1981).

A sparse fauna is recorded from the marine or estuarine gravel which immediately overlies the West Runton Freshwater Bed (Fig. 7.4). This horizon ('Monkey Gravel' of Hinton 1908) is overlain by marine silts with pollen of subzones Cr IIIa and Cr IIIb (West 1980a). The faunal list includes *Mimomys savini*, *Apodemus sylvaticus*, and two taxa not recorded from the older bed: macaque monkey *Macaca* sp. (Hinton 1908) and extinct squirrel *Sciurus whitei* (Hinton 1914, 1915). The pollen spectra from the overlying deposits indicate that these animals probably lived in temperate forest (West 1980a).

Harrison (1979a) records 20 bird taxa from the West Runton Freshwater Bed. These comprise water fowl and others closely associated with water, e.g. cormorant *Phalacrocorax carbo*, Bewick's swan *Cygnus bewicki*, greylag goose *Anser anser* and various ducks (genera *Anas*, *Netta*, *Athya*, *Bucephala* and *Mergus*). The only non-British species recorded are mandarin duck *Aix galericulata*, nowadays indigenous to China, and an eider duck considered by Harrison to represent an extinct species *Somateria gravipes*.

The Rev. C. Green and Anna Gurney collected a limited fauna, mainly small mammals, from Ostend near Bacton, Norfolk, in the early part of the last century. Taxa recorded (Table 7.1) include extinct shrews *Sorex runtonensis* and *S. savini*, *Desmana moschata*, extinct water vole *Arvicola cantiana* and

Fig. 7.3a. View of cliff at West Runton, Norfolk, looking eastwards from Woman Hythe. The Cromerian Freshwater Bed can be seen as a dark band at the foot of the cliff.

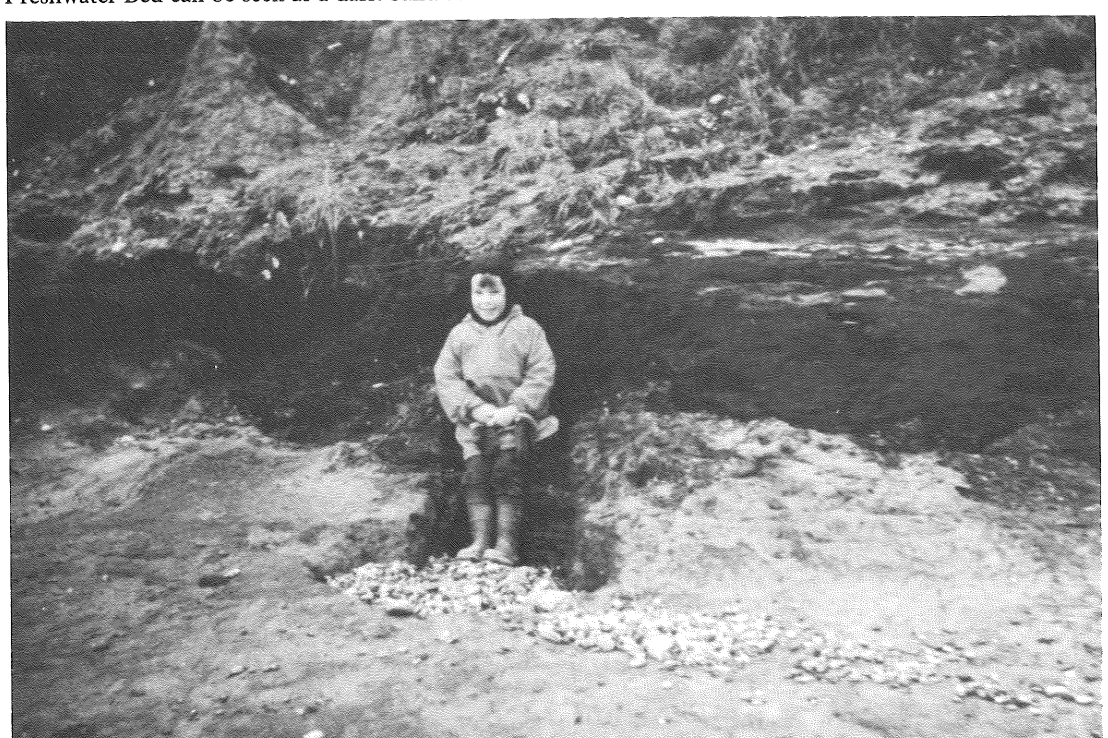


Fig. 7.3b. Cliff section showing the Cromerian West Runton Freshwater Bed (subzones Cr Ib–IIb) resting on lacustrine marls of Late Beestonian and early Cromerian (subzone Cr Ia) age.

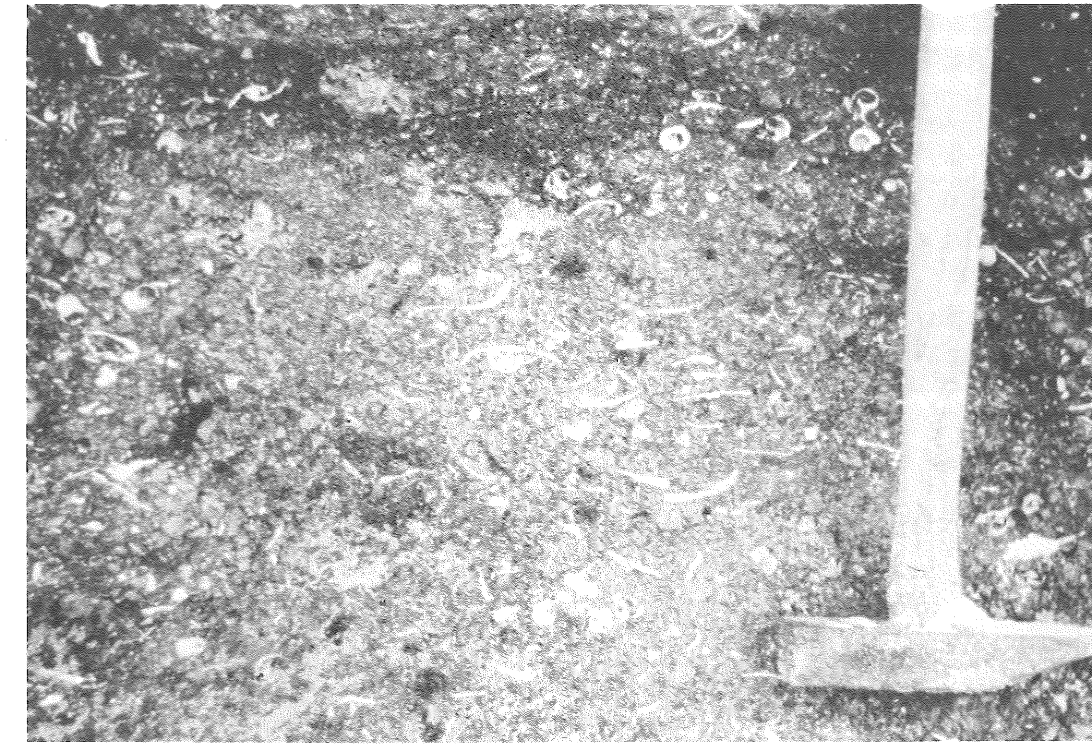


Fig. 7.3c. Detail of base of West Runton Freshwater Bed, showing reworked marl lumps and non-marine molluscan shells.

sparse large mammals. Pollen analyses of sediment matrix of some of the specimens showed that they dated from pollen zone Cr IV (Stuart & West 1976). The contemporary vegetation, towards the end of the interglacial, had reverted to coniferous forest. Of particular interest is the occurrence at Ostend of *Arvicola cantiana*, an extinct water vole with permanently growing (rootless) cheek teeth, replacing the earlier species *Mimomys savini* in which the cheek teeth became rooted (see Ch. 11). Harrison (1979a) records an extinct species of jungle fowl *Gallus europaeus* from this locality.

Pollen obtained from sediment within fossil *Hippopotamus* bones from the CF-bF has shown that this animal was present in England during pollen zones Cr IIIb and Cr IV (Gibbard, in Stuart 1982). The inferred contemporaneous vegetation was regional conifer-dominated forest with only local areas of herb vegetation.

An antler of the extinct giant deer *Megaceros dawkinsi* from Mundesley has similarly been assigned to zone Cr III or Cr IV.

As mentioned above, the majority of CF-bF finds do not have accompanying stratigraphical data. Nevertheless, the faunas of the Pre-Pastonian and Pastonian stages (Ch. 6) include few taxa which also occur in the Cromerian and *vice versa* so that, for example, nearly all specimens of *Megaceros verticornis* probably date from the Cromerian, with perhaps some from the Beestonian and Early Anglian stages. Moreover, at a few sites, e.g. Pakefield, Corton, Kessingland, Mundesley, most of the recorded fauna is of Cromerian type so that at these localities the earlier deposits are probably not very fossiliferous.

The following taxa, not included in Table 7.1 because they lack precise stratigraphical data, may be in part of Cromerian or approximately Cromerian age: extinct glutton *Gulo schlosseri* (Mundesley); extinct hyaena *Hyaena brevirostris* (Mundesley); lion *Panthera leo* (Pakefield); sabre tooth *Homotherium latidens* (Kessingland); straight-tusked elephant *Palaeoloxodon antiquus* (e.g. Corton, Mundesley); extinct elephant *Archidiskodon meridionalis* (Mundesley); extinct giant deer *Megaceros savini* (Mundesley, Pakefield) and extinct musk ox *Praeovibos priscus* (Walcott).

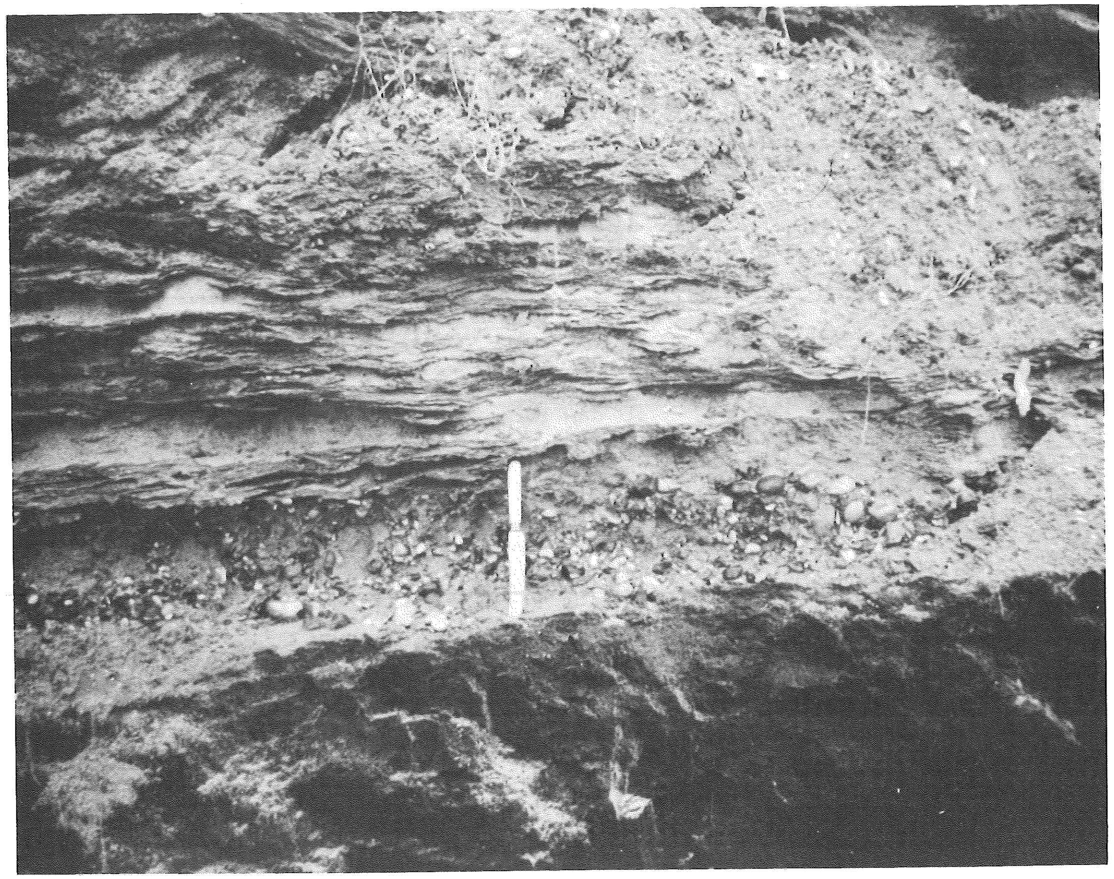


Fig. 7.4. Cliff section showing estuarine gravel and alternating sands and silts (Cromerian zone Cr III) resting on the West Runton Freshwater Bed.

Until a few years ago no fossil vertebrate sites of definite Cromerian age were known outside East Anglia. In 1972, however, fossiliferous sediments filling a river channel cut in the Jurassic Kimmeridge Clay were discovered at Sugworth near Oxford, 40 m above the modern River Thames (Briggs *et al*: 1975). The palaeontological evidence taken together indicates a Cromerian age, and the pollen and macroscopic plant remains indicate pollen assemblage subzone Cr IIIb (Gibbard & Pettit 1978). The vegetation is interpreted as regional mixed coniferous-deciduous forest in the river valley with alder fen carr bordering the river. Both wet and dry ground herb communities probably grew on the floodplain immediately adjacent to the river and on the point bar.

The collection of Sugworth vertebrate material (Stuart 1980) is much less extensive than that from West Runton, as the deposits were only exposed for a short time. The fish and amphibian fauna is consistent with West Runton, but several small mammals, pigmy shrew *Sorex minutus*, large extinct shrew *Beremendia* cf. *fissidens* and extinct vole *Pliomys episcopalis*, are not recorded from West Runton, although the rest of the Sugworth mammals, including *Sorex savini*, *Mimomys savini* and *Dicerorhinus etruscus*, have been found at the type site.

In contrast to West Runton, the Sugworth small-mammal assemblage, with high percentages of *Apodemus sylvaticus* and *Clethrionomys glareolus*, is consistent with forested habitats predominating close to the depositional site (see Ch. 5).

In 1969 extensive cave deposits containing very large numbers of vertebrate fossils were discovered in the course of quarrying the Carboniferous limestone near Westbury-sub-Mendip, Somerset (Fig. 7.5). The stratigraphy and fauna are being

Fig. 7.5. View of quarry face at Westbury-sub-Mendip showing fossiliferous early Middle Pleistocene cave deposits (foreground and middle distance) in the carboniferous limestone.

studied by Bishop (1974, 1975, 1982) and also by a team from the British Museum (Natural History), London, directed by P. Andrews. The stratigraphy of the deposits is extremely complex and at present the only reliable evidence for the relative age of these deposits seems to be the vertebrate assemblage itself.

Disregarding the lowest beds ('Siliceous Group' Bed 1 of Bishop 1974) which have a fauna no younger than Cromerian in age, the bulk of the deposits ('Calcareous Group', including the 'Rodent Earth' Beds 3–10) will be considered here as a whole. The deposits, however, may span a considerable period of time.

The fauna includes many elements occurring at West Runton, e.g. *Sorex savini*, *Desmana moschata*, *Ursus deningeri*, *Dicerorhinus etruscus* and extinct pine vole *Pitymys gregaloides*. However, it also includes *Pliomys episcopalis*, recorded elsewhere only at Sugworth, and significantly *Arvicola cantiana*, which has been found in the CF-bF only at Ostend, Norfolk (zone Cr IV), although very rare specimens attributed to *Mimomys savini* do occur in Bed 1 (Bishop, 1982). Like many cave assemblages, the Westbury fauna is rich in Carnivora. These include extinct leopard *Panthera gombazogensis*, extinct dhole *Xenocyon lycaonoides* – both unique records for the British Pleistocene, and sabre-tooth *Homotherium latidens*. Unfortunately, large herbivores are rather sparsely represented, complicating comparisons with open-site faunas.

Other interesting records from Beds 3–10 include the now arctic-boreal Norway lemming *Lemmus lemmus* and arctic lemming *Dicrostonyx torquatus*, the steppe-dwelling pika *Ochotona pusilla*, and in contrast European pond tortoise *Emys orbicularis* (Stuart 1979) which requires mean July temperatures in excess of 17–18 °C for its eggs to hatch (Ch. 5).

This mixture of temperate and cold-stage elements seems to characterize the ends of interglacial periods, and it is tempting to place Westbury at the end of the Cromerian, especially in view of the occurrence of *Arvicola cantiana*, suggesting an approximate correlation with the Ostend zone Cr

IV fauna. It is, however, possible that the Westbury deposits represent in part one or more interstadials within the Anglian, or even, as has been suggested on the grounds that many of the species are larger than at West Runton (Bishop, 1982), a distinct interglacial period. The available evidence does not, however, appear to be sufficient to justify the latter conclusion. The most economical solution for the present seems to be to provisionally place the main Westbury fauna within a period at the end of the Cromerian and perhaps also extending into beginning of the Anglian.

It is especially desirable to determine the age of the deposits because Westbury provides the earliest plausible evidence of man in the British Pleistocene (Bishop 1975) (Ch. 10).

Cromerian faunal history

Generally speaking there are rather few accurately dated records for the Cromerian (Table 7.1) on which to base an account of faunal history through the stage. It is difficult, for example, to judge whether the differences in small-mammal faunas between sites, particularly Sugworth and West Runton, are reflecting local habitat differences, or have some temporal or geographical significance. Faunal change through the interglacial is, however, suggested by the presence of *Hippopotamus* sp. and *Megaceros dawkinsi* in pollen zones Cr IIIb and IV, when these are absent from the rich fauna of temperate aspect from the type site, of Cr II age. Similarly, the replacement of *Mimomys savini*, recorded from zones Cr II, Cr III, by the phylogenetically more advanced *Arvicola cantiana* in zone Cr IV at Ostend may have regional significance. It is, however, possible that populations of both species co-existed in Britain and Europe at this time. We have no evidence for assuming that the replacement of one species by another was geologically instantaneous, even within a limited geographical area.

If all of the main Westbury deposits are considered to be of late Cromerian age, then lemmings and *Ochotona pusilla* had arrived before the close of the interglacial. The occurrence of *Emys orbicularis*, however, indicates that summer temperatures remained high.

Since there is no trace of undoubted man-made artefacts from the CF-bF or earlier, the Westbury material suggests that man first arrived in England towards the end of the Cromerian interglacial, and that at this period the human population was very sparse (Ch. 10).

Comparison with Continental faunas

Vertebrate faunas which can be broadly correlated with the type Cromerian are known from a number of localities in Continental Europe, especially from Germany (Kahlke 1975a).

The rich mammal fauna from Voigtstedt, Sangerhausen, Thüringia, East Germany (Kahlke 1965) comes from a restricted horizon immediately overlain by organic sediments yielding 'pollen spectra which can be correlated with zones Cr III and Cr IV of the type Cromerian. The Voigtstedt fauna is therefore virtually contemporaneous with that of the West Runton Freshwater Bed, and they are correspondingly remarkably similar (Stuart 1981). Two species, an extinct suslik *Spermophilus dietrichi* and extinct flying squirrel *Petauria voigtstedtensis*, which have not been found at West Runton, may reflect the more eastern continental situation of Voigtstedt.

The vertebrate material from another classic Thüringian locality, Süssenborn near Weimar, described in a series of papers edited by Kahlke (1969), includes reindeer *Rangifer tarandus* and musk ox *Ovibos moschatus* – both arctic species, as well as temperate Cromerian forms, and probably covers part of the preceding cold stage as well.

Comparison with the British sequence suggests that the rich faunas from the main vertebrate horizons at Mosbach, Wiesbaden, West Germany which include an extinct hippopotamus *Hippopotamus antiquus* and *Rangifer tarandus* (Kahlke 1975a; Brüning 1978) date from the end of the Cromerian interglacial and the beginning of the Elsterian (Anglian) cold stage. The more strictly temperate fauna from Mauer near Heidelberg, West Germany, also with *H. antiquus*, but including one of the earliest finds of man in Europe, a mandible attributed either to an advanced *Homo erectus* or an early form of *H. sapiens* may date rather earlier in the second half of the Cromerian. Other important faunas of approximate Cromerian age are known from Stránská Skála, Brno, Czechoslovakia, Vértesszöllös, Tata, Hungary, and Tiraspol, Moldavia, USSR. Vértesszöllös is of particular importance for its record of early man, both from bones and artefacts. The faunas of these and many other sites are listed by Kretzoi (1965), Kahlke (1975a) and Jánossy (1975).

Table 7.2. Records of mammals and *Emys orbicularis* from the Hoxnian (N.B. most records can only be tentatively or imprecisely related to pollen zones).

Site:	Clacton	Swanscombe a.	Hoxne a.	Hoxne b.	Ingress Vale	Hoxne c.	Hoxne d.	Swanscombe b.
Pollen zone:	c.IIb (I–IIIa)	?II	II	IIc	?III	?III–IV	?IV	
MAMMALIA								
Insectivora								
Sorex araneus L., common shrew	–	–	–	–	–	+	–	–
Talpa cf. *minor* Freudenberg, extinct mole	–	+	–	–	–	–	–	–
Desmana moschata Pallas, Russian desman	–	–	–	–	–	–	+	–
Primates								
Macaca sp., macaque monkey	–	+	–	–	–	+	–	–
Homo sp., man (skull)	–	–	–	–	–	–	–	+
Homo sp., man (artefacts) – C: Clactonian; A: Acheulian	C	C	–	A	A	A	A	A
Lagomorpha								
Oryctolagus cuniculus L., rabbit	–	+	–	–	–	–	–	–
Lepus timidus L., mountain hare	–	–	–	–	–	–	–	+
Rodentia								
Trogontherium cuvieri Fischer, extinct beaver	+[1]	–	+	–	+	+	+	–
Castor fiber L., beaver	?	+	–	–	–	+	–	–
Lemmus lemmus (L.), Norway lemming	–	–	–	–	–	–	+	+
Clethrionomys glareolus (Schreber), bank vole	+	–	–	–	+	–	–	
Arvicola cantiana (Hinton), extinct water vole	+	+	–	–	+	+	+	–
Pitymys arvaloides Hinton, extinct pine vole	–	+	–	–	–	–	–	–
Microtus cf. *arvalis* Pallas, common vole	(+)[1]	+	–	–	–	–	–	+
Microtus agrestis (L.), field vole	–	–	–	–	–	+	–	–
Microtus oeconomus (Pallas), northern vole	–	+	–	–	–	–	–	+
Apodemus sylvaticus (L.), wood mouse	–	–	–	–	+	–	–	–
Carnivora								
Canis lupus L., wolf	–	+	–	–	+	–	–	+
Ursus spelaeus Rosenmüller & Heinroth, (extinct) cave bear	–	+	–	–	–	–	–	–
Martes martes L., marten	–	+	–	–	–	–	–	–
Panthera leo (L.), lion	+	+	–	–	+	–	–	+
Felis sylvestris Schreber, wild cat	–	+	–	–	–	–	–	–
Proboscidea								
Palaeoloxodon antiquus Falconer & Cautley, (extinct) straight-tusked elephant	+	+	–	+	+	–	–	+
Perissodactyla								
Equus ferus Boddaert, horse	+	+	–	+	+	+	+	+
Dicerorhinus kirchbergensis (Jäger), extinct rhinoceros	+	+	–	–	+	–	–	+
Dicerorhinus hemitoechus (Falconer), extinct rhinoceros	+	+	–	–	+	–	–	–
Artiodactyla								
Sus scrofa L., wild boar	+	+	–	–	+	–	–	–
Megaceros giganteus Blumenbach, (extinct) giant deer	–	+	–	–	–	+	–	+
Dama dama (L.), fallow deer	+	+	–	–	+	+	–	+
Cervus elaphus L., red deer	+	+	–	–	+	+	–	+
Capreolus capreolus L., roe deer	–	+	–	–	–	+	–	–
Bos primigenius Bojanus, (extinct) aurochs	+	+	–	–	+	–	–	+
Bos sp., aurochs or *Bison* sp., bison	–	–	–	–	–	+	+	–
REPTILIA								
Chelonia								
Emys orbicularis L. European pond tortoise	–	–	–	–	+	–	–	–

1. Clacton Golf Course Excavation