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MAMMALS OF THE CRAG AND FOREST BED

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SUMMARY. In the Red and Norwich Crags mastodonts gradually give way to the southern elephant, large caballine horses and deer of the *Euctenoceros* group become common. Large rodents are represented by *Castor*, *Trogontherium* and rarely *Hystrix*; small forms include species of *Mimomys*. Carnivores include hyaena, sabre-toothed cat, leopard, polecat, otter, bear, seal and walrus.
The Cromer Forest Bed Series had steppe and forest forms of the southern elephant and the mastodont has been lost. Several species of giant deer become widespread and among the many rodents are a number of voles which develop rootless cheek teeth. The mole is common. Warmth indicators include a monkey, and more commonly hippopotamus. Possible indicators of cold include glutton and musk ox. Rhinoceros is widespread, and it is a time of rapid evolution for the elk. Carnivores include hyaena, bear, glutton, polecat, marten, wold and seal.

The interpretation of mammalian finds from the Crags and Forest Bed is not an easy matter. A proportion of the remains have been derived from earlier horizons, others are discovered loose in modern coastal deposits, and early collectors often kept inadequate records. Owing to the uncertain processes of fossilisation or inadequate collecting there are many gaps in our knowledge of the mammalian faunas of these times.

Order Insectivora

Three shrews have been recorded from the Cromer Forest Bed Series, one, *Sorex savini* Hinton, as large as any known fossil or living form, a second, *Sorex runtonensis* Hinton, about the size of the modern pygmy shrew, and the third, *Neomys newtoni* Hinton, similar to our modern water shrew and possibly its predecessor.

A mole, similar to *Talpa europaea* L. is common in the temperate freshwater beds of the Cromerian, and is mainly represented by its relatively robust and characteristically shaped humerus, though other bones and mandibles are known. The European desman, *Desmana moschata* Pallas, now restricted to south-east Russia and central western Asia, is represented by bones which resemble the mole remains but are about twice their size.

Order Primates

The order is represented at this period in England by a single record of *Macaca* sp., the distal end of a left humerus from a sandy horizon of the Cromerian at West Runton, Norfolk. Most workers feel grave doubts about the alleged Crag date of the human jaw found at Foxhall near Ipswich, but as the bone has been lost for more than a century fully conclusive evidence is not available.

Order Carnivora

In the Lower and early Middle Pleistocene of East Anglia more than twenty species of carnivore have been recorded, though nowhere are they common.

The typical Lower Pleistocene hyaena, *Hyaena perrieri* CROIZET & JOBERT, is found in the Crags, and a much larger species, *Hyaena brevirostris* Aymard, is typical of the early Forest Bed where it is soon replaced by the spotted hyaena, *Crocuta crocuta* Erxleben.

There were two sabre-toothed cats; a larger

species of Crag date, *Homotherium sainzelli* Aymard, recorded as far north as Derbyshire in a cave deposit, and a smaller species, *Homotherium latidens* Owen, known in the Cromerian by a few fine canines. A single cat tooth from the same horizon resembles *Felis lunensis* Martelli rather than the modern wild cat, and a leopard, *Felis pardoides* Owen, has been recorded from the Red and Norwich Crag. The lion, *Felis leo* L., first reached this country in the Forest Bed as a spectacularly large form.

Several mustelids are known from East Anglian deposits but they are rather rare. A glutton, probably *Gulo schlosseri* Kormos, rather than *Gulo gulo* L., has been found in Forest Bed strata; unlike the latter species its presence may not indicate cold conditions. The probable ancestor of the pine marten occurs in the Forest Bed as *Martes vetus* Kretzoi, with a large polecat, *Pannoniotis pliocaenica* Kormos, first found in a late Pliocene forest fauna in Hungary. A second polecat, *Enhydrictis ardea* Bravard, has been recorded from the Red Crag, but polecats of modern type are first found in the Forest Bed, possibly *Mustela putorius* L. itself. Remains of the weasel, or possibly its predecessor *Mustela praenivalis* Kormos have also been found, and in the Norwich Crag there occurs an otter, *Aonyx resvei* Newton.

Wolf, *Canis lupus* L., is undoubtedly present in the Forest Bed, but earlier records, and those of a fox from this period of the Crags are rather uncertain.

An unusual mammal recorded from three localities of the Red Crag is a panda, *Parailurus anglicus* Boyd Dawkins, evidently closely related to the modern lesser panda which is now restricted to bamboo forests on the slopes of the Himalayas.

Although bear remains, probably *Ursus arvernensis* Croizet & Jobert, are known from two Red Crag localities it is not until Forest Bed times that representatives of this family become relatively common. The fossils can be separated into two species, *Ursus deningeri* Reichenau, and *Ursus savini* Andrews, with the possibility of a third species, *Ursus spelaeus* Rosenmuller & Heinroth. The boundaries between these species in the Forest Bed are rather blurred.

Seal fossils occur throughout the Crags and Forest Bed but in the absence of cranial remains little can be said of their specific identity. When limb-bones are compared with modern North Sea forms they show no recognisable differences. A few walrus tusks and bones described under the name *Trichechus huxleyi* Lankester have been found in both Crags and Forest Bed but three mineralised crania dredged off the Norfolk coast are presumably more recent.

Order Proboscidea

The central element of the Crag and Forest Bed fauna are the mastodonts and elephants, which were widely distributed and show evolutionary trends in the structure of their teeth which can be matched with environmental changes which characterise the Pleistocene itself.

Two mastodonts survived from the Pliocene in Europe, but one, *Zygolophodon borsoni* Hays, died out early in the Pleistocene and is only represented in the Red Crag by a few very worn molars in the basement bed which are obivously derived. The second mastodont, *Anancus arvernensis* Croizet & Jobert, was the characteristic proboscidean of the early Pleistocene and occurs in both the Red and Norwich Crags but by the end of the Lower Pleistocene was extinct in this country and the southern elephant, *Archidiskodon meridionalis* Nesti was common. Molars of the southern elephant are found in the Red and Norwich Crags, and in the latter are as numerous as those of the mastodont. Limb bones and vertebrae become better represented in the younger Crag sands and by Forest Bed times are abundant at several localities. It is at this period that the species begins to show a division into presumed forest and steppe forms which diverge into the temperate straight-tusked elephant, *Palaeoloxodon antiquus* Falconer & Cautley, and the steppe mammoth, *Mammuthus trogontherii* Pohlig. The southern elephant ranged through Europe as far as the Black Sea and North Africa and is disting-

guished by its large, gently-curving tusks, wide molars with short, broad grinding surfaces enclosing relatively few widely spaced lamellae. The adults reached a shoulder height of over 12 ft. and have correspondingly massive limb bones.

The forest form of the southern elephant appears to have become a distinct species by Forest Bed times. *Palaeoloxodon antiquus* FALCONER & CAUTLEY has rather narrow deep molars, the lamellae in the grinding surface of the lower molars in particular tend towards a lozenge-shaped pattern of wear with relatively thick, coarsely folded enamel. The tusks are large and gently curved.

Forms transitional between the southern elephant and the steppe mammoth, *Mammuthus trogontherii* POHLIG, are first found in the Forest Bed. Molars of this species have a relatively large number of lamellae which tend towards a division into three parts in the posterior part of the grinding surface. At its acme this species attained a shoulder height of over 14 feet and later in the Pleistocene gave rise to the woolly mammoth, *Mammuthus primigenius* BOJANUS.

Order Perissodactyla

A number of tapir teeth described under the species *Tapirus arvernensis* CROIZET & JOBERT have been found in the nodule bed of the Red Crag, these may have been derived from a Pliocene source.

There are a few records of rhinoceros from the Crags, but not until Forest Bed times are remains common, where a single species, *Dicerorhinus etruscus* FALCONER is present. This rather small rhinoceros extended over most of southern Europe and was close to its northern limit in Norfolk. Most Forest Bed localities of Norfolk and Suffolk have yielded mandibles of which more than twenty are preserved in Norwich Castle Museum.

Equine remains occur throughout the Crags and more commonly in the Forest Bed. Caballine horses, *Equus robustus* POMEL, are distinguished by their large size compared with the zebrine horse, *Equus stenonis* COCCHI, which may be absent in the Forest Bed, but the systematics of this family are rather confused. Rolled teeth of *Hipparion* cf. *gracile* KAUP occur in the Red Crag, obviously derived from an older horizon.

Order Artiodactyla

Pig fossils from the Red Crag are scarce and may belong to *Sus strozzii* MENEGHINI. The first satisfactory remains come from the Forest Bed of Norfolk. These include a fine skull and mandible from one individual which appears to be a large form of the modern wild hog, *Sus scrofa* L.

The hippopotamus which reached this country by Forest Bed times has often been thought of as a separate species from the modern *Hippopotamus amphibius* L., but the only difference is in size, the early form being rather larger than the modern animal. Hippopotamus is absent until the last interglacial, the Ipswichian, where it occurs in some abundance.

Deer remains form an important part of the fauna of the Crags and Forest Bed but are a difficult family to work on as most identifications are based on the antlers. Other parts of the skeleton are grouped with antlers mainly on size because associated bones are rare. Where similar sized deer occur together the problems are formidable.

Four species of the genus *Euctenoceros* have been separated on the basis of the forms of the antlers, which are quite large and have a few openly arranged slightly curved tines. *Euctenoceros ctenoides* NESTI is rare, possibly present in the Norwich Crag and recorded a few times from the Forest Bed. *Euctenoceros tetraceros* DAWKINS with four widely spaced tines is better known in the Forest Bed, though it has been recorded from the Norwich Crag and possibly also the Red Crag. *Euctenoceros falconeri* DAWKINS is a smaller species found in the Red and Norwich Crags but absent in later deposits. The largest of this group, *Euctenoceros sedgwicki* FALCONER has markedly flattened tines each of which is divided into three or four points. A fine antler from the Forest Bed at Bacton indicates a total span of over nine feet. This species has also been

recorded from the Norwich Crag and may be present in the Red Crag.

The true red deer, *Gervus elaphus* L., has been doubtfully recorded from the Forest Bed on the basis of a few antlers, some of which are beach specimens. Unfortunately the diagnostic terminal tines are invariably absent.

The commonest deer of Forest Bed times were the giant deer, two species of which can be traced back into the Crags. In *Praemegaceros verticornis* DAWKINS the antlers spread almost horizontally out on either side of the skull after the first tine which is almost circular in section and curved abruptly forwards and downwards. A number of antlers have a small extra tine just below this first tine, though often only one antler out of a pair possesses this additional feature. The beam is long and stout, and throws off a second forward facing tine followed by one at the rear, then the beam spreads out upwards into a large flat palmation which is rarely found intact. A peculiarity of the *Megaceros* group, which is especially marked in *M. verticornis*, is a strange thickening of the bone of the lower jaw, and to a lesser extent of the skull. This has been thought of as a mark of degeneration or a pathological character; perhaps the extra bone may have acted as a source of calcium required when new antlers were growing. *Megaloceros savini* DAWKINS has widely spread antlers in which the beam is flattened but does not terminate in a large palmate structure as in other giant deer. The first tine is short, almost fan-shaped, and is very close to the origin of the beam. There is a second rather small tine and a third backward-facing tine after which the beam curves upwards to a terminal fork. *Megaceros dwakinsi* NEWTON is common in the Forest Bed but there are no Crag records. The antlers are backward-pointing and spread rapidly into a broad fan with six or seven flat tines.

An early fallow deer. *Dama nestii* MAJOR, has been collected from both Crags but there are doubts about its presence in the Forest Bed as *Dama clactoniana* FALCONER may also be present. The roe deer, *Capreolus capreolus* L., first occurs in Forest Bed deposits.

Elk first reached this country in the form of *Alces gallicus* AZZAROLI in the Norwich Crag, by Forest Bed times considerable size variation had taken place and two further species, *Alces latifrons* JOHNSON and the very large *Alces reynoldsi* AZZAROLI, are distinguished. The antlers have long gently curved beams which end in a small palmation edged with small tines. The trend in this group is towards a large palmation and a shorter beam which is gently twisted along its length.

Bovids are first represented in this country by *Gazella anglica* NEWTON from the Red and Norwich Crags. The musk ox, *Ovibos moschatus* L., may be present in the Forest Bed, but most of the ovibovine remains are now referred to *Praeovibos priscus* Staudinger. There is no good evidence to suggest that musk ox was at this time adapted to cold conditions. The characteristic bison in the Forest Bed is the large steppe *Bison priscus* BOJANUS but a small species, *Bison schoetensacki* FREUDENBERG, probably a woodland animal, has also been found.

Order Rodentia

Fossil rodents have a potentially high value in stratigraphical studies because they are found in varied habitats and exhibited rapid evolution. About twenty species are known from Forest Bed deposits, perhaps only five from the *Crags*. Systematic collecting of small mammal remains in this area would tell us much of the details of past environments.

A squirrel, *Sciurus whitei* HINTON, probably ancestral to the modern red squirrel, has been found in the West Runton Cromerian deposts. Two types of beaver occur in the Crags and Forest Bed; a large form, *Trogontherium cuvieri* FISCHER, and the then less common *Castor fiber* L., to which is attributed a mass of gnawed branches in the Forest Bed near Bacton, Norfolk, part of a fossil dam. A porcupine, *Hystrix* sp., has been recognised from the Red Crag, and a second unusual rodent, a large hamster, *Cricetus cricetus runtonensis* HINTON is known from West Runton.

Amongst the voles six species of the *Mimomys* group have been described from the

	R.C.	N.C.	W.C. & C.F.B.S.
SPECIES			
Insectivora			
Sorex savini Hinton.			×
Sorex runtonensis Hinton.			×
Neomys newtoni Hinton.			×
Talpa europaea L.			×
Desmana moschata Pallas.			×
Primates			
Macaca sp.			×
Carnivora			
Hyaena perrieri CROIZET & JOBERT.	×	×	
Hyaena brevirostris AYMARD.			×
Crocuta crocuta ERXLEBEN.			×
Homotherium sainzelli AYMARD.	×		
Homotherium latidens OWEN.		×	×
Felis cf. *lunensis* MARTELLI.			×
Felis pardoides OWEN.	×	×	
Felis leo L.			×
Gulo schlosseri KORMOS.			×
Martes vetus KRETZOI.			×
Enhydrictis ardea BRAVARD.	×		
Pannonictis pliocaenica KORMOS.			×
Mustela cf. *putorius* L.			×
Mustela praenivalis KORMOS.			×
Aonyx reevei NEWTON (Pomel)		×	
Canis lupus L.		?	×
Parailurus anglicus BOYD DAWKINS.	×		
Ursus deningeri REICHENAU.			×
Ursus savini ANDREWS.			×
Ursus spelaeus ROSENMULLER & HEINROTH.			?
Ursus cf. *arvernensis* CROIZET & JOBERT.	×		
Phoca sp.	×	×	×
Trichechus huxleyi LANKESTER	×	×	×
Proboscidea			
Anancus arvernensis CROIZET & JOBERT.	×	×	
Archidiskodon meridionalis NESTI.	×	×	×
Palaeoloxodon antiquus FALCONER & CAUTLEY.			×
Mammuthus trogontherii POHLIG.			×
Perissodactyla			
Tapirus arvernensis CROIZET & JOBERT.	×		
Dicerorhinus etruscus FALCONER.			×
Rhinoceros sp.	×	×	
Equus stenonis COCCHI.	×		
Equus robustus POMEL.	×	×	×
Hipparion cf. *gracile* KAUP.	×		
Artiodactyla			
Sus strozzii MENEGHINI.	×		

Sus scrofa L.			×
Hippopotamus amphibius L.			×
Euctenoceros ctenoides NESTI.		?	×
E. tetraceros DAWKINS.	?	×	×
E. falconeri DAWKINS.	×	×	
E. sedgwicki FALCONER.	×	×	×
Cervus cf. *elaphus* L.			×
Praemegaceros verticornis DAWKINS.	?	×	×
Megaloceros savini DAWKINS.	?	×	×
Megaceros dawkinsi NEWTON.			×
Dama nestii MAJOR.	×	×	×
Dama clactoniana FALCONER.			?
Capreolus capreolus L.			×
Alces gallicus AZZAROLI.		×	×
Alces latifrons JOHNSON.			×
Alces reynoldsi AZZAROLI.			×
Gazella anglica NEWTON.	×	×	
Praeovibos priscus STAUDINGER.			×
Ovibos moschatus L.			?
Ovis savini NEWTON.			×
Bison priscus BOJANUS.			×
Bison schoetensacki FREUDENBERG.			×
Rodentia			
Sciurus whitei HINTON.			×
Castor fiber L.	?	×	×
Trogontherium cuvieri FISCHER.	×	×	×
Hystrix sp.	×		
Cricetus c. runtonensis HINTON.			×
Clethrionomys cf. *glareolus* SCHREBER.			×
Mimomys newtoni MAJOR.		×	×
Mimomys reidi HINTON.			×
M. savini HINTON.			×
M. intermedius NEWTON.			×
M. pliocaenicus MAJOR.		×	×
M. majori HINTON.			×
Arvicola bactonensis HINTON.			×
A. greenii HINTON.			×
Pitymys gregaloides HINTON.			×
P. arvaloides HINTON.			×
Microtus arvalinus HINTON.			×
Microtus nivaloides FORSYTH MAJOR.			×
M. nivalinus HINTON.			×
M. ratticepoides HINTON.			×
Apodemus cf. *sylvaticus* L.			×
Lepus sp.	?		?
Cetacea include			
Balaena spp.	×	×	×
Megaptera sp.	×		
Balaenoptera spp.	×		×
Monodon monoceros L.	?		×
Delphinus sp.		×	×
Phocaena sp.			×

Forest Bed, two of which also occur in the Norwich Crag. During the early Middle Pleistocene the *Arvicola* group emerged with species of *Microtus* and *Pitymys*, characterised by their rootless high-crowned cheek teeth which grow throughout life.

The common field mouse, *Apodemus sylvaticus* L., is known from the Forest Bed at West Runton where a few cheek teeth very similar to the modern species have been found.

Order Cetacea

Many species of cetaceans are known from the nodule bed of the Red Crag but most are heavily mineralised, rolled and polished, the signs of derived fossils. Cetacean finds thought to be contemporaneous with the Red Crag are not as common as in the Norwich Crag where lightly mineralised bones have been referred to species of dolphin, fin and toothed whales. In addition to these the Forest Bed has yielded porpoise and narwhal.

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