Pleistocene terrestrial mammal faunas from the North Sea

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Abstract

Many thousands of (sub)fossil mammalian remains have been collected from the bottom of the North Sea by fishermen using beamtrawls. The larger mammal fossils have been found mainly in a restricted area in the southern part of the North Sea notably the Deep Water Channel and the Brown Bank.

The list of mammal species are divided into two main groups: a group which live in a marine environment and a group of terrestrial mammals. The terrestrial mammals from the North Sea are divided in four fauna-associations which are regarded as groups of larger mammals with a comparable age although not necessarily regarded as contemporaneous. Heavily mineralized mammalian remains are referred to fauna-associations I and II. Fauna-association I, with Anancus arvernensis and Mammuthus meridionalis, of Early or Middle Villafranchian age is correlated with the Tiglian. Fauna-association II with e.g. Mammuthus meridionalis (advanced type), Mammuthus trogontherii, Hippopotamus antiquus and Cervalces latifrons, of Late Villafranchian age is correlated with the late Early/early Middle Pleistocene. The fossil remains referred to fauna-association I originate most probably from the IJmuiden Ground Formation and fauna-association II from the Yarmouth Roads Formation.

Fauna-association III, with e.g. Elephas antiquus, Mammuthus primigenius, Coelodonta antiquitatis and Ovibos moschatus, of Late Pleistocene age originates from the Brown Bank Formation. Fauna-association IV with e.g. Sus scrofa, Alces alces and Bos primigenius of early Holocene age originates from the Elbow Formation which occurs in the eastern part of the Flemish Bight area.

Introduction

Since historical times many towns along the coast of the North Sea and the former "Zuiderzee" had their own fishery fleets. The fishing technique employed to catch flatfish was the beamtrawl, the use of which dates from the Middle Ages when sailing boats with tiny gears fished over the sea bed in the coastal areas. Up until the late fifties of this century most fishing boats had small engines and the fishing gears used were not heavy. With the replacement of the fishing fleet by much heavier modern vessels (Figure 1), more sophisticated fishing gear towed over the sea bottom resulted in a higher pressure to be exerted on the sea bed. The amount of material collected off the sea bed (in addition to fish!) including much man-derived debris and (sub)fossil remains of mammals has increased considerably since the fishery fleet was modernised. Only remains of larger mammals (Figure 2) are collected by the beamtrawls due to the large diameter (about 5 cm) of the meshes of the nets; the occurrence of smaller mammal molars is largely restricted to sediments obtained from boreholes.

Trawling over the sea bed (Figure 3) takes on average about 1 hours at a speed of 5 to 7 knots, the tracklength varying between 10 and 13 kilometres, fishing mostly being carried out in loops. The penetration depth of a beamtrawl into the sea bed varies between 4 and about 8 centimetres, depending on the composition of the sea bed and the weight of the fishing gear used (Laban & Lindeboom, 1990). Below a depth of up to 8 centimetres no deformation of the sedimentary structures is visible. Studies carried out by other institutes have also pointed to a penetration depth of about 7 cm (Bridger, 1970, 1972; De Groot, 1973); during one of these studies a video camera mounted on one of the gears confirmed that the penetration was indeed only some centimetres.The mammal remains that have been exposed at the sea bed are overgrown by algae and bryozoa and are saturated by seawater. After desalination the bones are impregnated with a solution of

Figure 1
Beamtrawlers in the harbour of Stellendam (Delta area, Province of South-Holland, the Netherlands).

glue and acetone to prevent the remains disintegrating into pieces. The acetone evaporates while the glue remains in the pores, thus ensuring preservation.

Many thousands of fossils have been collected during the past 30 years and most of the material is stored in a large number of mainly small private collections. A restricted number of fossils have found their way into the National Museum of Natural History, Leiden, the Netherlands which houses the largest national collection. The most important private collections are owned respectively by D. Mol (Hoofddorp, Netherlands), H. van Essen (Dieren), C.F.G. van Tuyll van Serooskerken (Oostkapelle) and L.C.J. Stolzenbach (St. Michielsgestel). There is much interest in the mammal fossils from the North Sea and they are sold all over the world, especially in Europe, the U.S.A. and Japan.

The faunal remains have never been studied and described properly to any great extent apart from some of the more spectacular finds. Erdbrink (e.g. 1981, 1983b, 1983c, 1985) published a large number of fossil remains mainly from large carnivores and Hooijer (1984a, 1984b, 1985) described some mammoth and ass remains from the North Sea. More general reviews of the faunas from the North Sea have been published by Kortenbout van der Sluijs (1970-71; 1983), Drees (1986) and Van Kolfschoten & Van der Meulen (1986).

The study of the fossils from the North Sea is hampered by the fact that although the number of fossils is very large they are dispersed over many collections. In addition, and possibly of more importance, however, was the lack, until recently, of adequate stratigraphical information. With the publication by the Geological Survey of the Netherlands and the British Geological Survey of the Quaternary map of the Flemish Bight (Cameron et al., 1984), a much better insight into the outcrop of formations has now been obtained. Combination of the available information of the locations where the material was obtained from the seafloor together with the recent geo-

Figure 2
Fossils from the bottom of the North Sea collected by Mr. P. van Es, Stellendam within a period of a few weeks.

logical data, enable conclusions to be drawn about the possible age of the faunal remains and the environment in which the sediments were deposited. The geological setting of the south-west part of the North Sea, the composition of the different faunal assemblages and their bio- and chronostratigraphical position are discussed below.

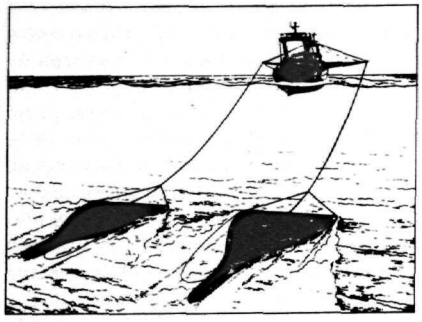


Figure 3
A schematic impression of a beamtrawler trawling over the sea bed.

Geological setting of the south-west part of the North sea

The Neogene, Early and Middle Pleistocene deposits in the south-west part of Flemish Bight, the area between the coordinates 52° - 53° N/2° - 4° E, form a complex sequence of marine, brackish-marine, deltaic and fluviatile sediments (Cameron et al. 1984, 1989) (Figure 4-6). Late Pleistocene and Holocene deposits cover most of the area and are up to 30 metres thick. Pliocene and Early Pleistocene sediments crop out or subcrop close to the sea bed only in the extreme south-west part of the area.

The oldest sediments exposed belong to different formations notably the Brielle Ground Formation (Pliocene, Reuverian), the Red Crag Formation (Praetiglian), the Westkapelle Ground Formation (Praetiglian to early Tiglian), the Smith's Knoll Formation and the IJmuiden Ground Formation (both Tiglian). All these formations were mainly deposited in a marine pro-deltaic environment. The succeeding Winterton Shoal Formation (late Tiglian to Eburonian), which partly covers the Smith's Knoll and the IJmuiden Formations, may include fluviatile, delta and pro-delta facies of the Rhine, Meuse and North German river systems. The Winterton Shoal Formation is mainly covered by younger deposits al-

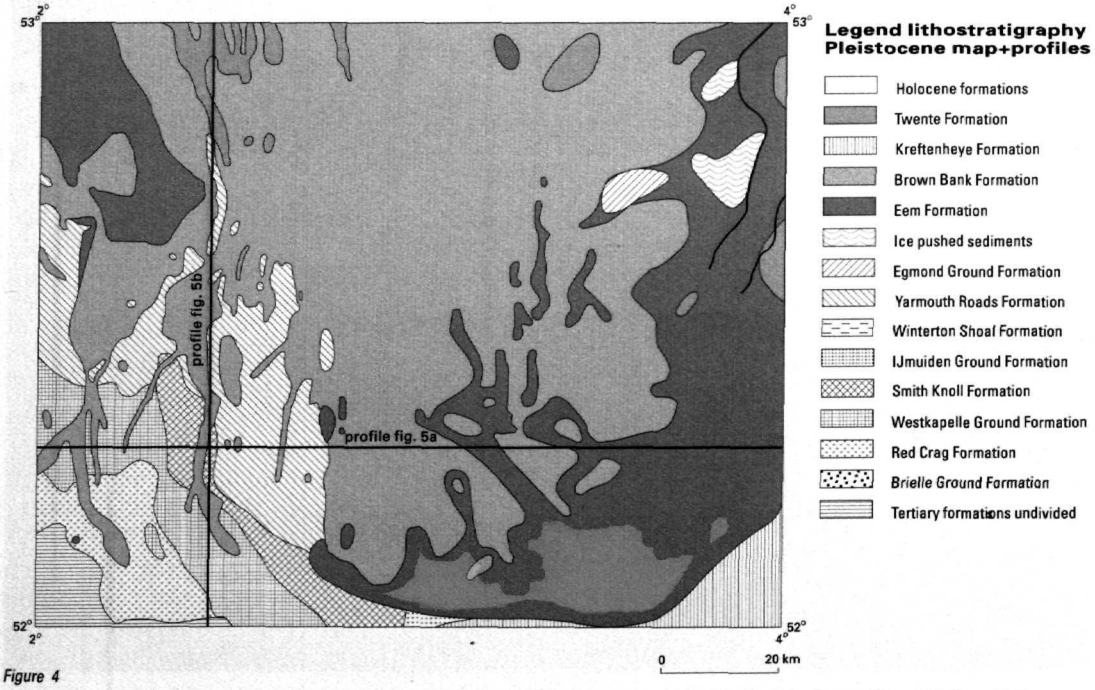


Figure 4
The lithostratigraphy of the top of the Pleistocene of the geological sheet Flemish Bight of the southern bight of the North Sea between 52° and 53°N/2° and 4° E. Location of sections shown in 5A and B.

though scattered outcrops occur in the south-east part of the North Sea. The overlying Yarmouth Roads Formation (late Tiglian to Elsterian) is composed of a predominantly non-marine sequence of fine or very fine-grained sands and clay. The surface outcrops of this formation are restricted to the western part of the Flemish Bight area. In the Dutch licence block P13, pollen analyses of a core indicate that deposition of sediments referred to the Yarmouth Road Formation occurred during the Cromerian III Interglacial (Zagwijn, 1983). Fluvioglacial deposits with an Elsterian age are found only locally in the Flemish Bight area. The maximum extension of the Elsterian ice sheet is thought to have crossed the area from roughly the NE to the SW corners and the Early Pleistocene deposits were pushed only locally by the ice cover.

Sediments deposited during the Holsteinian interglacial and the Saalian glaciation, with a marine and glacigenic origin respectively, are present only in the northern part of the Flemish Bight area. Early Pleistocene/early Middle Pleistocene deposits are overlain by sandy marine sediments (Eem Formation) with an Eemian age in a large part of the area (Zagwijn, 1983). Two to five metres of brackish-marine to continental clay deposits (Brown Bank Formation) from the late Eemian and early Weichselian occur in the entire central part of the Flemish Bight area.

Pollen analytical investigations on a number of cores show that deposition mainly took place during the early Weichselian, pollen zone EW1a (Zagwijn, 1983). The sediments were thought to have been initially deposited in a lacustrine environment during the sealevel lowering during the late Eemian at the onset of the Weichselian glaciation (Du Saar, 1970). The sediments were mainly transported by rivers emanating from the British east coast and were deposited in a depression in the central area of the Southern Bight. During the Weichselian interstadials a relatively dense vegetation existed. By contrast, however, during the cold stadials the vegetation was scarce and a windblown sand cover (Twente Formation) was deposited on top of the lacustrine clay. The Brown Bank Formation is present only locally at sea bed or below a cover of Holocene deposits. The Twente Formation has outcrops in channels in the northwest and locally in the east part of the Flemish Bight sheet.

At the beginning of the Holocene transgression marshes formed in the Pleistocene landscape. During the ongoing transgression the marshes were drowned and erosion of the Pleistocene sediments, mainly the Twente Formation, took place. The early Holocene sediments consist of muddy sand and clay deposited in a tidal flat environment with a basal peat layer locally (Elbow Formation) (Cameron et al., 1984; 1989). Sand from the deltas of the

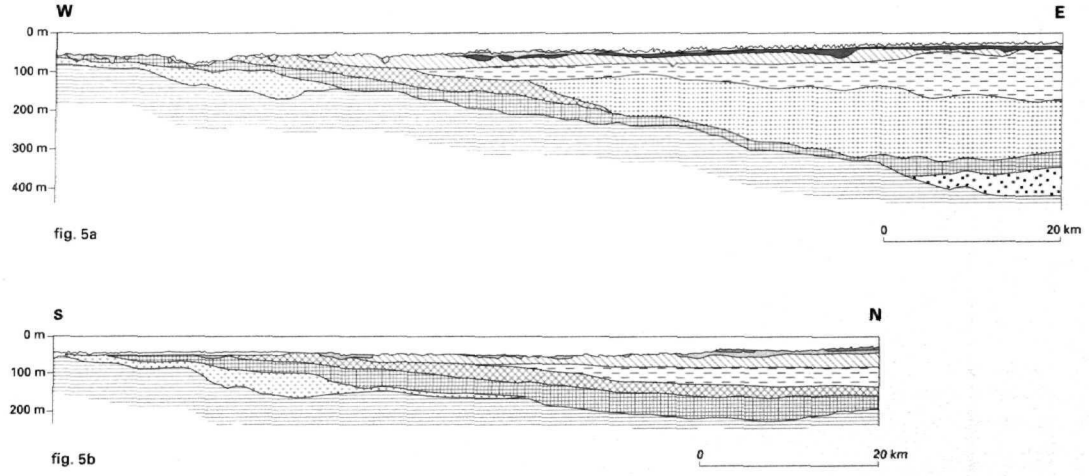


Figure 5a and b

An east/west and a south/north profile through the Flemish Bight sheet. At respectively the eastern and northern parts Upper Pleistocene formations subcrop beneath a Holocene cover. At the western and southern parts Lower Pleistocene formations subcrop.

Rhine and Meuse (Kreftenheye Formation, Saalian to Holocene) was transported into a northerly direction during the continuing Holocene sea level rise and covered the Pleistocene and early Holocene formations. These sands, which accumulated in extensive sandwave fields, form the Bligh Bank Formation.

Collection localities

The larger mammal fossils are found mainly in a restricted area in the southern part of the North Sea although some remains have been collected in the northeast of the North Sea (Post, 1992). A map with locations where concentrations of mammal fossils were found, and based on unpublished data by Mr. J. Mulder, was published by Drees (1986). The map shows that most of the mammalian remains were trawled by fishermen from the Deep Water Channel, an area located in the southern part of the North Sea between the Brown Bank area and the Norfolk coast (52°.30' - 53°.00' N/ 2°.30' - 3°.00' E) (Figure 7). Between sand waves in this area, there are a number of outcrops of the Yarmouth Roads Formation which yielded a number of the mammal fossils.

The area east of the Deep Water Channel is characterized by a series of north-south orientated sand ridges. One of these ridges, the Brown Bank, forms the eastern margin of the area where most of the mammalian fossils have been collected (Figure 7). The western margin of the Brown Bank Formation is located at or close to the sea bed east and northeast of the Deep Water Channel and there are extensive outcrops of the Brown Bank Formation between the Holocene sand waves. These outcrops yielded very large amounts of well preserved Late Pleistocene fossils. Some of the fossil specimens probably originate from the IJmuiden Ground Formation (Tiglian age) which has small and scattered outcrops in the south and more extensive outcrops in the west part of the sand bank in the central part of the area. Reports

Suggested correlation of sedimentary formations with the Pleistocene and Upper Pliocene stages of Britain and the Netherlands

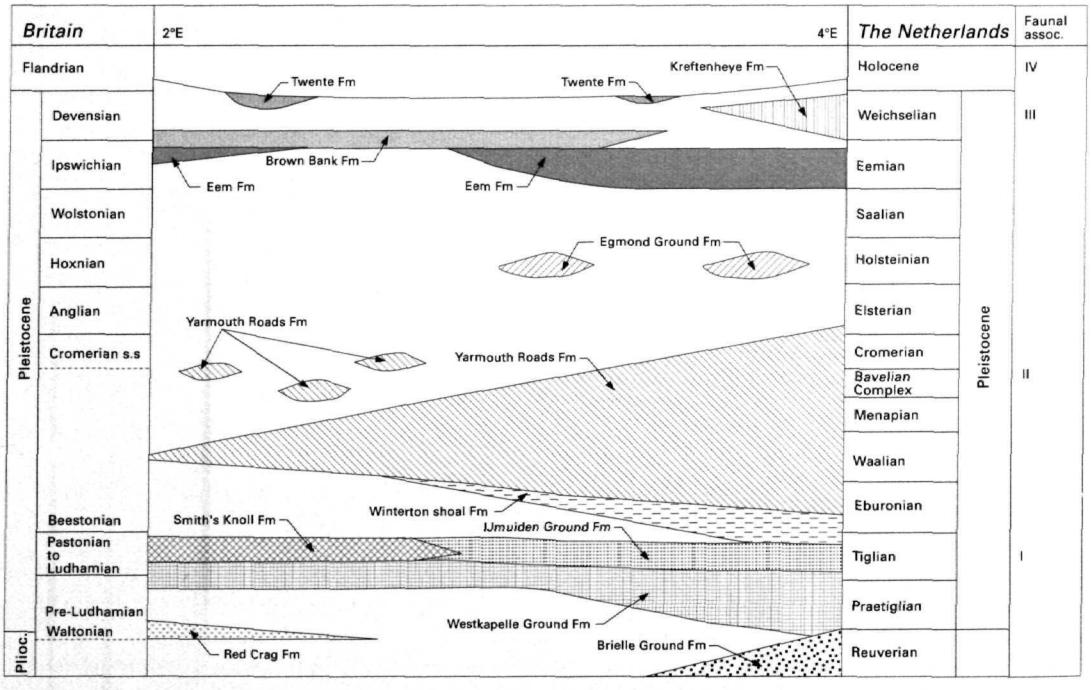


Figure 6

The suggested correlation of sedimentary formations with the Pleistocene and Upper Pliocene stages of Britain and the Netherlands. At the right 4 faunal associations which are found.

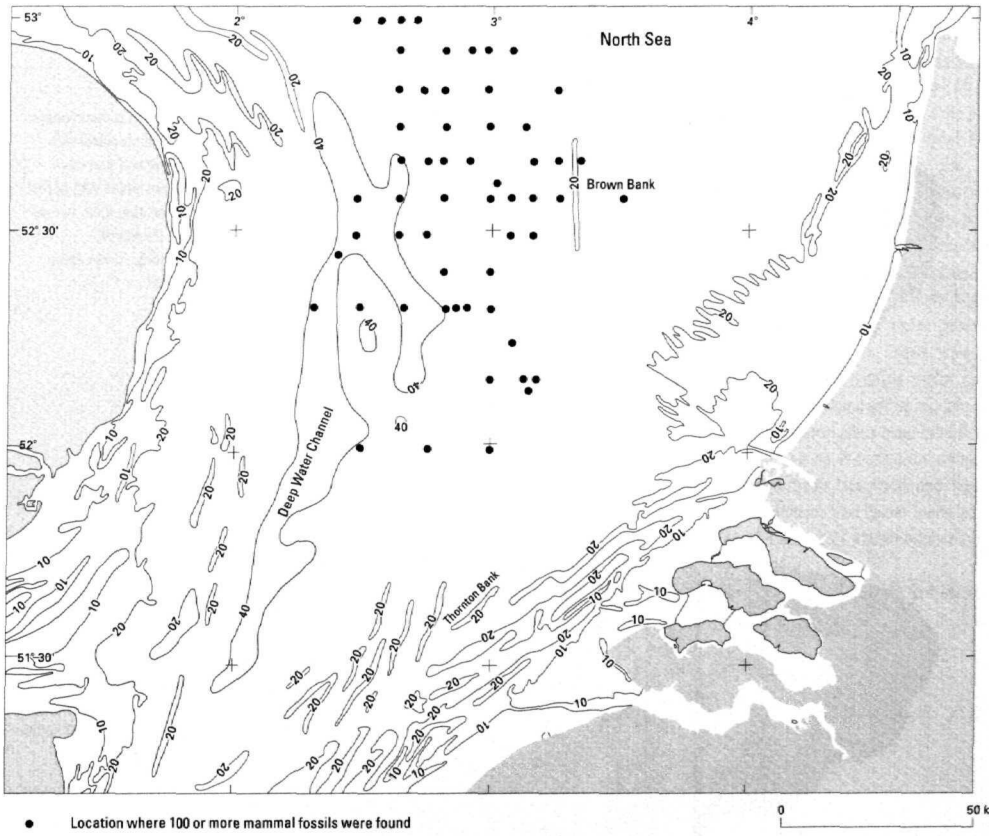
about large amounts of fossils from the Dogger Bank, a huge sand bank in the central part of the North Sea, are unsubstantiated. The Dogger Bank is known to consist of reworked Pleistocene glacial deposits overlain by early Holocene tidal flat deposits (Jeffery et al., 1988).

Early Pleistocene smaller mammal remains obtained from boreholes [74GS/04 (S 10-68), 81H/61 (R 7-3), 87MK/19 (S 1-112)] are found in sediments deposited during the Eemian and the Holocene. The mammalian fossils confirmed the idea, obtained from malacological studies (Meijer, pers. comm., 1989), that the deposits contain much reworked material with an Early Pleistocene age (Van Kolfschoten, 1989a).

The mammals from the North sea

The fossil mammals recorded from the North Sea represent a number of fauna-associations which differ in age and the recorded species indicate different environments. The remains show a large variation in the degree of mineralization. The specimens can roughly be divided into 'old', heavily mineralized and 'young', less heavily mineralized remains. The oldest specimens recorded from the North Sea are not only heavily mineralized, but are also dark-coloured. This phenomena led to the adoption of the term "Black Bone" fauna, often used in literature (e.g. Hooyer, 1957), to refer to the oldest fauna-association from the Schelde estuarine as well as to the oldest fauna from the North Sea, thus suggesting we are dealing with a single association. However, the dark-coloured fossils are now known to represent different fauna-associations and moreover the fossils are not uniform in colour either. Arguments to stress that the use of the term "Black Bone" fauna should be discontinued were advanced by Drees (1986), a view also shared by the present authors.

The taxa can also be divided into two groups, notably a



● Location where 100 or more mammal fossils were found

Figure 7

The area of investigations and the locations where concentrations of mammal fossils were found (based on unpublished data from J. Mulder, published by Drees, 1986).

group which lives in the marine environment and a group of terrestrial mammals. A number of the marine mammal remains, which are not further considered in this paper, have been described by Erdbrink (1972), Erdbrink & Van Bree (1986; 1990) and Van Bree & Erdbrink (1987). The oldest marine mammal fossils may date from Late Pliocene or Early Pleistocene, the younger ones from the Late Pleistocene or Holocene.

The terrestrial mammals from the North Sea are divided into four fauna-associations (I-IV) which may be regarded as groups of larger mammals with a comparable age although their occurrence is not necessarily regarded as contemporaneous. The Holocene association (IV) is the best represented in the fossil record from the North Sea, although the Late Pleistocene assemblage (III) with *Mammuthus primigenius* is the best known. The oldest heavily mineralized mammalian remains, and referred to species of the so-called "Black Bone" Fauna, do not, however, represent a single fauna-association. The list includes species which are restricted to the Early and Middle Villafranchian as well as species with a Late Villafranchian age. This indicates that we are dealing with at least two different age assemblages. The oldest association (I) is correlated with the Tiglian whereas the younger one (II) is correlated with the later part of the Early Pleistocene. A number of heavily mineralized specimens without diagnostic features are problematic and cannot readily be referred to either fauna association I or II.

I. Early Pleistocene association

Anancus arvernensis

Mammuthus meridionalis

A single specimen of *Anancus arvernensis* has, to date, been described (Mol, 1991). The molar fragment comes from close to the Thornton Bank in the south-east part of the North Sea, west of the Schelde estuary, and from an area where deposits occur of the IJmuiden Ground and the Winterton Shoal formations, both with a fluviatile and deltaic component. These Early Pleistocene sediments are covered by Late Pleistocene and Holocene formations. It is improbable that the specimen of *Anancus arvernens* originates from the Thornton Bank itself which

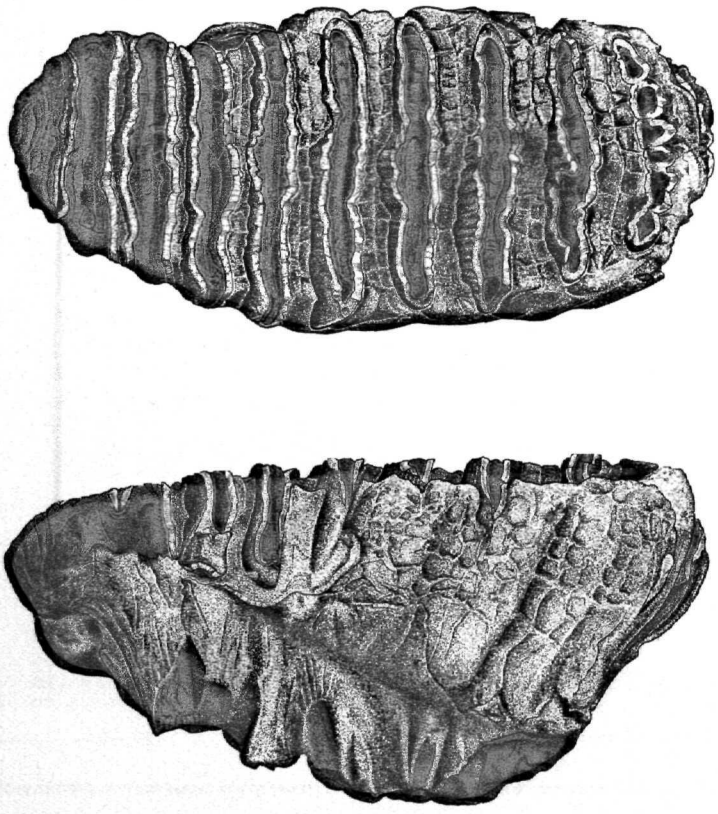


Figure 8
Mammuthus meridionalis: M2 dext.; occlusal view (above) and side view (below), about 70% of the natural size. (Coll. Van der Bok, Ouddorp). (Drawing: H. van Essen, Dieren).

consists of Holocene sand of the Bligh Bank Formation, overlying Eocene clay.

Several rather primitive molars of *Mammuthus meridionalis* (Figure 8) have been collected from the North Sea (see e.g. Hooijer, 1984a). The evolutionary stage of a number of these molars is comparable to that of the *Mammuthus* molars from the Schelde estuary. The molars from Dorst (Van Kolfschoten, 1990) dated to the Bavelian Complex are more advanced (H. van Essen, pers. comm., 1993). The occurrence of the early Villafranchian *Cervus perrieri* Croizet & Jobert is mentioned by Hooijer (1984b). The heavily mineralized antler base shows close similarities with the lower part of the antler of *Cervus perrieri*. Since the specimen is too fragmentary to be certain of specific identification it is omitted from the list.

Anancus arvernensis is know from faunas which are dated to both early and middle Villafranchian (Azzaroli et al. 1983) and which includes both the Reuverian and the Praetiglian (Torre et al., 1992). The species is absent from the Late Villafranchian fauna of Tegelen. An *Anancus* molar obtained from Tegelen-Maalbeek was dated early Eburonian III (Zagwijn, 1963) and supposed to be younger than the fauna from Tegelen. However, investigations of new exposures and material from the Tegelen-Maalbeek pit indicate that the molar was collected from deposits which predates the Tiglian TC5 deposits which yielded the famous Tegelen fauna (Westerhoff pers. comm). *Mammuthus meridionalis* is found in faunas which are dated Middle and Late Villafranchian and which covers the Early Pleistocene as well as the earlier part of the Middle Pleistocene.

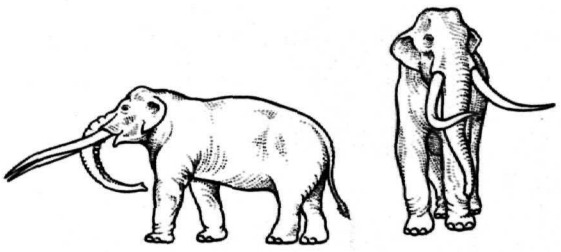
Both *Anancus arvernensis* and *Mammuthus meridionalis* (Figure 9) have also been found in the Schelde estuary (mainly in the Oosterschelde). The heavily mineralized terrestrial fossils from the Oosterschelde are considered to be Middle Villafranchian and are thought to be slightly older than the Late Villafranchian fauna from Tegelen which is dated Tiglian TC5 (Van Kolfschoten & Van der Meulen, 1986). The Tiglian terrestrial fauna-association from the Schelde estuary has been correlated with the faunas from the Upper Shell Bed of the Norwich Crag (Thorpe/Norwich, Easton Bavents) and from the Campine, Belgium (Kunst, 1937; Van Kolfschoten & Van der Meulen, 1986). However, both *Anancus arvernensis* and *Mammuthus meridionalis* have also been collected from the Red Crag Nodule Bed formation of Pliocene age which indicates that the remains from the North Sea might even be older than those from the Schelde estuary.

II. Late Early Pleistocene/early Middle Pleistocene terrestrial association

Mammuthus meridionalis (advanced type)
Mammuthus trogontherii
Equus bressanus
Dicerorhinus etruscus brachycephalus
Hippopotamus antiquus
Cervalces latifrons
Cervidae gen. indet.
Bison sp.

The *Mammuthus meridionalis* remains from the North Sea are very variable in size, hypsodonty, lamellar frequency and thickness of the enamel. Mr. J.A. van Essen, who has made a thorough study of the elephant remains from the North Sea as well as from England and the Netherlands concluded that the collection of *Mammuthus meridionalis* molars from the North Sea can be divided in two groups. The more advanced molars, which are referred to as fauna-association II have (in comparison to molars referred to as fauna-association I, and described above), a relatively higher number of plates, thicker enamel and are in general more robust and hypsodont (J.A. van Essen, pers. comm. 1993). Fauna association II contains molar specimens (apart from the advanced *Mammuthus meridionalis*), which are referred to as *Mammuthus trogontherii*. A fragment of a molar referred to as *Mammuthus armeniacus* (=*M. trogontherii*) has been described and figured by Hooijer (1984a). In addition, Van Essen (pers. comm., 1993) has attributed a number of *Mammuthus* molars to *Mammuthus trogontherii*.
Both *Mammuthus meridionalis* and *Mammuthus trogon-*

Figure 9
The larger mammals of fauna-association I from the North Sea. The figures are from Thenius (1962).



Anancus arvernensis ***Mammuthus meridionalis***

therii are part of the mammoth lineage which ends with *Mammuthus primigenius*. *Mammuthus meridionalis* is assumed to be the ancestor of *Mammuthus trogontherii* and the *meridionalis/ trogontherii* boundary has been dated at 0.7-0.6 Ma BP (Lister, 1993). However, more recent discoveries indicate that *Mammuthus trogontherii* was present before the Brunhes/Matuyama boundary, i.e. before 0.78 Ma BP whereas *Mammuthus meridionalis* is still present in Middle Pleistocene faunas such as Voigtstedt. This therefore indicates an overlap in the stratigraphical range of both species; one which covers the late Early and early Middle Pleistocene (Van Kolfschoten & Turner, in press; Lister, 1993).

Heavily mineralized postcranial horse remains are also recorded from the North Sea. Hooijer (1984a) describes a very large calcaneum which is referred to as *Equus bressanus* (=*Equus* cf. *robustus* of Kortenbout van der Sluijs, 1970-1971).

The dimensions of the distal portion of a humerus of a rhinoceros equate closely with those of humeri referred to as *Dicerorhinus etruscus brachycephalus* and described by Guerin in 1980 (Van Kolfschoten, 1989b).

At least four incomplete bones of a *Hippopotamus* have been collected from the North Sea and include two distal parts of a humerus, an almost complete unciform and a proximal part of a femur. The morphology of the specimens including the very large dimensions of one of the humerus fragments and in particular that of the femur indicate *Hippopotamus antiquus* (=*Hippopotamus major*) (Van Kolfschoten & Vervoort-Kerkhoff, 1985). *Cervalces latifrons* is represented by two proximal antler beam fragments with a characteristic morphology. The dimensions correspond with those of *Cervalces latifrons* antlers from Süssenborn, Germany (Kahlke, 1969). A few antler fragments are heavily mineralized but they are hard to identify and are therefore referred to Cervidae gen. indet. Erdbrink (1983b) describes a metacarpal III/IV which he refers to *Dama dama clactoniana*, a fallow deer known from the early Middle Pleistocene. However, the metacarpal exhibits characteristics which indicate that it is probably a metacarpal bone from the reindeer *Rangifer tarandus* (Van Kolfschoten & Zijlstra, 1992). The presence of a large bovid is indicated by a very heavily mineralized large metacarpus which exhibits the characteristics of a metacarpus of a *Bison*.

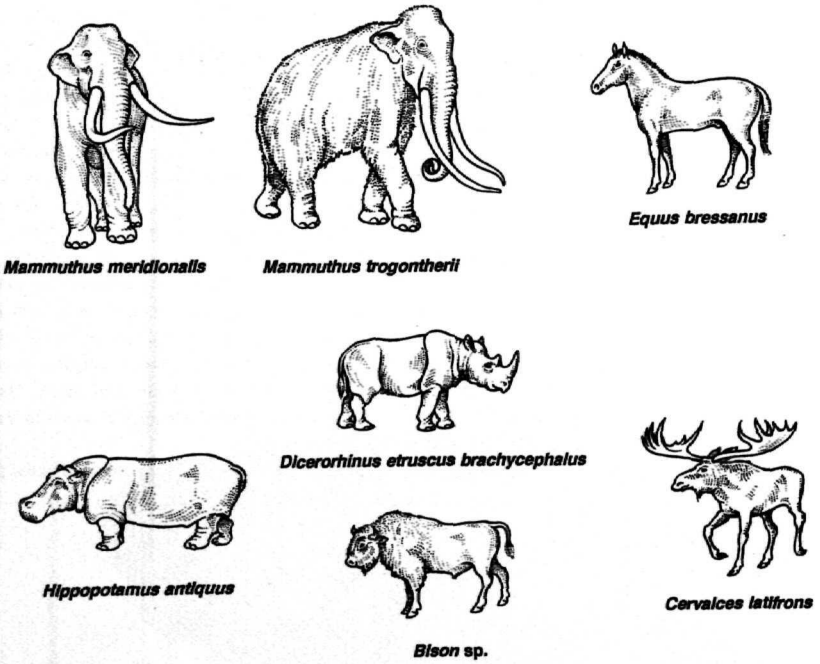


Figure 10
The larger mammals of fauna-association II from the North Sea. The figures are from Thenius (1962).

It is difficult to determine whether the fauna-association (Figure 10) represents a single fauna or is composed of a number of species which did not live contemporaneously. An argument in favour of the second option is the occurrence of both *Mammuthus meridionalis* and *Mammuthus trogontherii*. If the assumption is accepted that the two species which have an overlap in their stratigraphical range, preferred different habitats, the conclusion is that both species did not occur contemporaneously. However, they might have roughly the same age and both date from the late Early Pleistocene or early Middle Pleistocene.

Fauna-association II shows similarities with fauna-association I from the Maasvlakte, an association with corresponding species such as: *Mammuthus meridionalis, Dicerorhinus etruscus brachycephalus, Hippopotamus antiquus* and *Cervalces latifrons* (Van Kolfschoten & Vervoort-Kerkhoff, 1986; Vervoort-Kerkhoff & Van Kolfschoten, 1988). The Maasvlakte fossils, however, are not collected from in situ deposits and their stratigraphical position is also uncertain. However, it is thought that the Maasvlakte I association most probably dates from the later part of the Early Pleistocene or the earliest part of the Middle Pleistocene due to the presence of *Mimomys savini*, a small *Mimomys* and the absence of *Microtus* (*Allophaiomys*). Smaller mammal faunas with these characteristics date from the Bavelian Complex as well as from the early Cromerian interglacials. Whether *Hippopotamus antiquus* occurred in northwest Europe during the Bavel Interglacial, the Leerdam Interglacial and the early Cromerian Interglacials is not established. *Hippopotamus antiquus* is very well represented in the fauna from Meiningen-Untermassfeld in Germany, and correlated with the Bavel Interglacial (Kahlke, 1987). This indicates that at least some of the fossils from fauna-association II from the North Sea may date from the late Early Pleistocene and more precisely from the Bavel Interglacial.To summarize it is established that the fauna-association II dates from a period to which faunas such as those from Bavel, Dorst, Oosterhout, Westerhoven and Zuurland (at -27 to -37 m NAP) belong. The species listed above have also been recorded from the West Runton Freshwater Bed in East Anglia with an early Middle Pleistocene age. Other remains of these species collected along the coast of East Anglia, are however, not accurately recorded. They may be older than the West

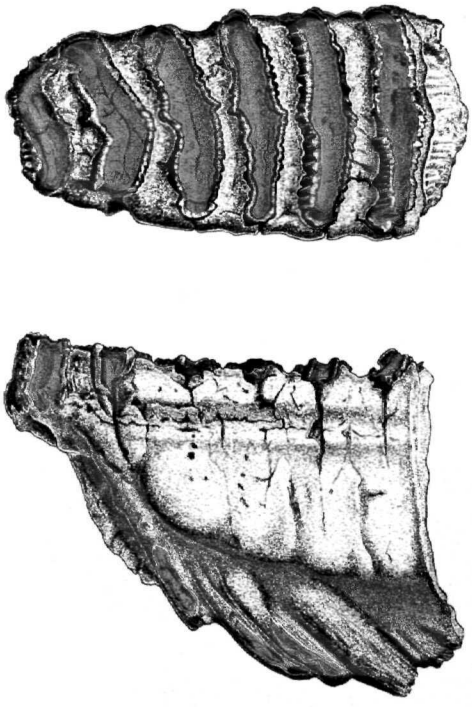


Figure 11
Elephas antiquus: M3 sin. from the North Sea; occlusal view (above) and side view (below), 50% of the natural size .Coll. H. van Essen, Dieren; coll. nr.: 138) (Drawing: H. van Essen, Dieren).

Runton Freshwater Bed fauna. They may date from the stratigraphical gap between the Pastonian faunas correlated with the Tiglian (TC5-6) and the early Cromerian faunas from West Runton (see Gibbard et al., 1991).

III. Late Pleistocene terrestrial association

Elephas antiquus
Canis lupus
Crocuta crocuta
Panthera leo
Ursus arctos
Ursus spelaeus
Mammuthus primigenius
Equus caballus
Equus hydruntinus
Coelodonta antiquitatis
Rangifer tarandus
Megaloceros giganteus
Bison priscus
Ovibos moschatus

A small number of molar fragments, referred to *Elephas antiquus* (Figure 11) have been collected from the bottom of the North Sea by Dutch as well as by British fishermen. The remains most probably date from the Eemian or are associated with one of the warmer episodes of the early Weichselian.

Erdbrink (1985) describes cranial as well as postcranial

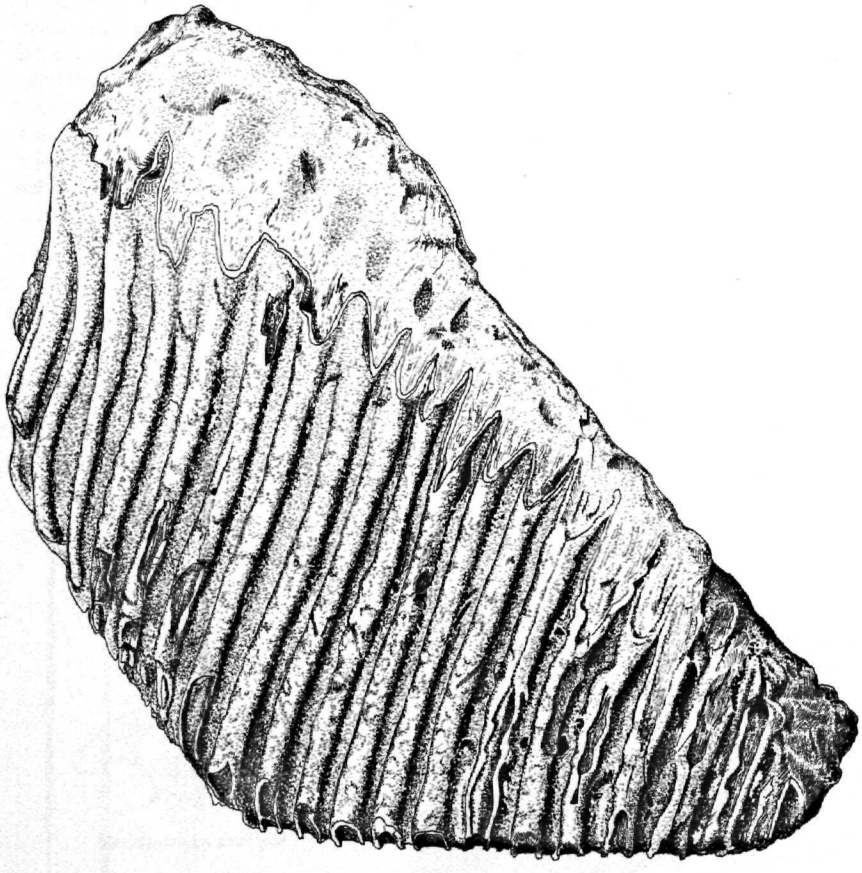


Figure 12
Mammuthus primigenius, dimunitive form: M3 dext. from the North Sea; Side view, about 90% of the natural size. (Coll. H. van Essen, Dieren; coll. nr.: 109; see also Van Essen, 1986) (Drawing: H. van Essen, Dieren).

material which belong to larger members of the genus *Canis* and because of their large size the specimens are referred to *Canis lupus lupus*. They probably originate from Early Weichselian deposits. However, an older date for the more heavily mineralized specimens, referred to *Canis* cf. *lupus* spp., can not be excluded (Erdbrink, 1985). *Panthera leo*: a fragment of a mandibula referred to *Panthera leo spelaea* (Erdbrink, 1981) and postcranial remains (Erdbrink, 1983b and c). The cave Hyaena, *Crocuta crocuta spelaea*, is represented by postcranial bones (Erdbrink, 1983b, c and d). Cranial, as well as postcranial, bear remains are known from the region just to the west of the Brown Ridge; these remains are referred to the brown bear *Ursus arctos* by Erdbrink (1967, 1982a, 1983b) because of their relative small size in comparison to the dimensions of the cave bear *U. spelaeus*. The cave bear is also represented in collections from the North Sea (Erdbrink, 1967, 1983b). The bear remains, according to Erdbrink, date from the Late Pleistocene and the Early Holocene.

The woolly mammoth *Mammuthus primigenius* is very well represented. Thousands of remains of younger, as well as older, individuals have been collected to date. The molars show advanced characters i.e. high crowned, thin enamel and a high lamellar frequence which indicative of Late Glacial (Weichselian) remains. Some of the specimen are remarkably small. They represent the so-called dimunitive forms (Figure 12) of mammoths with a

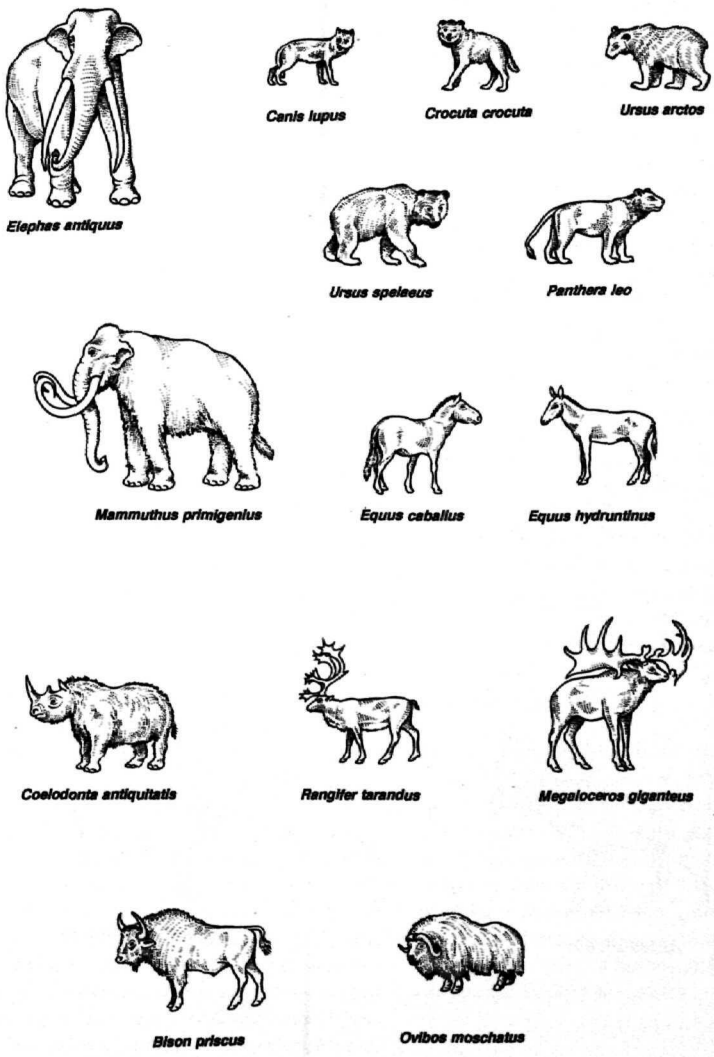


Figure 13
The larger mammals of fauna-association III from the North Sea. The figures are from Thenius (1962).

reduced size which were present at the end of the Weichselian (Mol & Van Essen, 1992).

The equid remains from the North Sea are referred to at least two species. Two very slender metapodials and a first phalanx are referred to *Equus hydruntinus* by Hooijer (1985) while a more robust specimen is referred to *Equus caballus*. The *Equus caballus* material is, however, very variable in dimensions (Ligtermoet & Drees, 1986) and reflects most probably the size reduction known to occur in caballoid horses since the Late Pleistocene (Forsten, 1993). Other species which inhabited northwest Europe during the last glacial, such as *Coelodonta antiquitatis, Rangifer tarandus, Megaloceros giganteus* and *Bison priscus*, are also well represented in the fossil record from the North Sea. The musk ox *Ovibos moschatus*, however, is rare. Two metacarpals and the tip of a right horn-core of *Ovibos moschatus* have been recovered from the bottom of the North Sea to the west of the Brown Ridge (Erdbrink, 1983a).
Remains of the species listed above (Figure 13) are also found in many sand and gravel pits along the rivers Rhine, Maas, Waal and IJssel. The fossils have been dredged up with sands and gravels of the Kreftenheye Formation. The late glacial fauna-assemblages from rich localities such as Lathum on the river IJssel north of Arnhem, are very similar in composition and are possibly of a similar age.

All the above species, with the exception of *Equus hydruntinus* are known from a large number of Late Pleistocene localities in the British Isles (Stuart, 1982).

IV. Holocene terrestrial association
Castor fiber
Lutra lutra
Sus scrofa
Capreolus capreolus
Cervus elaphus
Alces alces
Bos primigenius
Homo sapiens

A number of species listed in the Late Glacial fauna-association (III) such as *Ursus arctos, Canis lupus* and *Equus caballus* are also known to occur in the (early) Holocene of northwest Europe. The collection of mammal remains from the North Sea also contains (sub)recent material of domesticated animals such as cattle *Bos taurus*, pigs *Sus scrofa*, sheep *Ovis aries* and goats *Capra hircus*.

A small proportion of the bones from the North Sea have been used by man. Antler fragments of red deer and postcranial bones of, for example, aurochs are transformed into various implements such as shaft-hole picks, socketed axes and points (Louwe Kooijmans, 1970-71; Erdbrink, 1982b; 1991). The radiocarbon ages are roughly

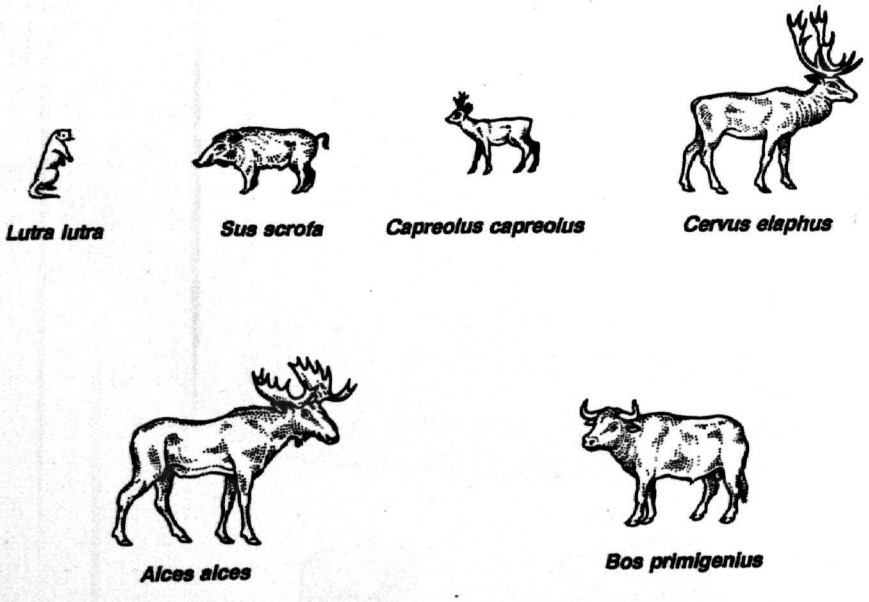


Figure 14
The larger mammals of fauna-association IV from the North Sea. The figures are from Thenius (1962).

between 9300 and 8000 BP, indicate that most of the Mesolithic bone and antler implements have a Preboreal or Boreal age.
The early Holocene association (IV) (Figure 14) originates from the Elbow Formation which occurs in the eastern part of the Flemish Bight area in the southern North Sea.

Conclusions

The four fauna-associations from the southern part of the North Sea represent terrestrial faunas which inhabited the area between Great Britain and the European continent during different episodes of the Quaternary. The occurrence of fossils of terrestrial mammals (Fauna-association I) indicates that the area, or at least part of it, was dry land during a phase of the Tiglian predating the Tiglian C5 and to which the fauna from Tegelen is referred. The terrestrial mammal remains referred to the Bavelian Complex or the early Cromerian (Fauna-association II) indicate a second terrestrial phase. The third is referred to the late Eemian and early Weichselian, while the last one (Fauna-association IV) is early Holocene.
The sediments recorded from the southern part of the North Sea basin broadly reflect this picture. The geological data indicate that during the middle and late Tiglian the deltas of the rivers Rhine and Meuse had filled most of the southern part of the Flemish Bight (Zagwijn, 1979). The coast line crossed the area from Zeeland in the Netherlands to East Anglia in Great Britain. The coast line shifted in a northern direction; during the early Cromerian the southern part of the entire Flemish Bight area was dry. The uppermost sediments on the seismic records show a structureless or chaotic configuration with locally small-scale channels suggesting that the area was occupied by a delta. During the late Eemian brackish marine clay was deposited in this area during the sea level lowering associated with the onset of the Weichselian glaciation. Freshwater clay was subsequently deposited on the marine clay during the early Weichselian. At the end of the Weichselian and during the early Holocene fresh water marshes developed in this area and a blanket of peat was formed. After about 8000 BP the Holocene sea level rise drowned the area and tidal flats covered the entire southern North Sea.

It is obvious that the fauna-assemblages described above do not reflect the entire mammal fauna. Not only are the smaller mammals lacking, but the list of larger mammals is, except for the Holocene fauna-assemblage (IV) very incomplete. This is particularly the case with the oldest association (I) with only two species. There is little doubt that carnivores, equids, cervids and bovids were also part of the fauna but to date they have not been collected or recognized. Fauna-association II is more diverse than I but nevertheless considered still incomplete. Most remarkable is the absence of large carnivores. Fauna-association III, attributed to the Late Glacial, is very similar in composition to Late Glacial associations known from the continent. The North Sea associations seem to represent a fairly good reflection of the entire larger mammal fauna which occurred in northwest Europe during the Late Glacial. However, a number of larger mammals which also inhabit the Mammoth Steppe, the dominant Late Glacial environment, such as the Saiga antilope *Saiga tatarica* and the Ibex *Capra ibex* are lacking. They are recorded from mainland as well as British localities but their remains are, however, always rare.

The fossil record from the North Sea is enormous and is a rich source of considerable potential scientific value. It is obvious that the faunal remains date from different episodes of the Quaternary. The lack of exact stratigraphical information to some extent reduces the scientific value of the mammal fossils, but not to a level whereby the material is solely of interest and value to collectors. If the fossil record is studied in detail and other geological information is taken into account, much can be contributed to the knowledge of the faunal evolution in northwest Europe, more particularly the North Sea area during the Quaternary. The huge number of remains gives, furthermore, the opportunity to study individual variations. The scientific value of this data would be helped much by radiocarbon dating, a method which might be particularly applicable for remains referred to the fauna-associations III and IV. However, to use this method for large quantities of bone samples is expensive. Reliable and cheaper methods would substantially increase the scientific value of these Late Pleistocene and Holocene remains.
There are no reliable physical methods, as yet, to date the older remains associated with fauna-associations I and II. For the interpretation and the stratigraphical correlation of these remains we have to rely on our existing knowledge of the Pleistocene fossil record and on the stratigraphical record of the southern part of the North Sea basin and combine our data with the results of conventional dating methods e.g. palynological analysis.

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