

On the application of fossil mammals to the reconstruction of the palaeoenvironment of northwestern Europe

Thijs VAN KOLFSCHOTEN

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Abstract. The fossil record from the Quaternary deposits of the Northern European Plain shows palaeobotanical as well as palaeozoological associations that differ in various degrees from the extant flora and fauna. The record is interpreted and translated into palaeoenvironmental as well as palaeoclimatological pictures, which are mainly based on a comparison with the extant flora and fauna. The interpretation of Middle and Late Pleistocene mammal assemblages is, however, hampered by taphonomic biases and the fact that mammals have the capacity to adapt to environments and tolerate circumstances other than those under which they live today. Despite these restrictions it is obvious that the accuracy of the reconstruction of a palaeoenvironment increases if mammalian data are incorporated. A lack of mammalian data may result in a local instead of a regional reconstruction. Furthermore, it appears to be problematic to use terms such as interglacial and glacial *sensu stricto* to characterize fossil faunal associations. We should avoid these terms as much as possible and define, in the near future, faunal units that are characteristic of a particular palaeoenvironment in a restricted area. This would increase the applicability of fossil mammals to the reconstruction of the palaeoenvironment.

Key words: Pleistocene, mammals, Northwestern Europe, palaeoenvironment.

Thijs VAN KOLFSCHOTEN, Institute of Prehistory, Leiden University, P.O. Box 9515, 2300 RA Leiden, The Netherlands.

I. INTRODUCTION

The reconstruction of climates and environments in the geological past is often based on geological, palaeobotanical, as well as palaeozoological evidence. The data for such a reconstruction are of regional to very local origin. Palynological data inform us about the regional vegetation, whereas palaeobotanical macro-remains, as well as malacological data, come from the direct surroundings of a locality. Vertebrate remains may be indicative of the local as well as the regional fauna. To produce an accurate reconstruction of the palaeoenvironment, complementary data are indispensable.

Data from different disciplines are not always equally represented, however. Molluscs and smaller mammal remains are often absent in acid, organic deposits and palaeobotanical information can often be absent from fluviatile, loess, or cave deposits.

Vertebrate fossils, in particular, have played a major role in the reconstruction of the climate and local and regional environmental conditions at a number of palaeolithic sites, such as Maastricht-Belvédère (The Netherlands), Miesenheim I, and the East Eifel localities Plaidter Hummerich, Tönchesberg, Schweinskopf-Karmelenberg and Wannen (Germany) where palaeobotanical data are lacking.

This paper deals with the reconstruction of the palaeoenvironment of northwestern Europe, i. e., the western part of the Northern European Plain. This is a confined area with little topographic variation and hence a rather uniform natural flora and fauna. The fossil record from the Quaternary deposits of the Northern European Plain shows palaeobotanical as well as palaeozoological associations that differ in various degrees from the extant flora and fauna.

The fossil record is interpreted and translated into palaeoenvironmental as well as palaeoclimatological pictures, which are mainly based on comparisons with the extant flora and fauna. The vegetation of northwestern Europe and its development during the Middle and Late Pleistocene are summarized in the first part of the paper, followed by a section on the extant mammal fauna. The interpretation of Middle and Late Pleistocene mammal assemblages is discussed in the second part of this paper.

II. THE VEGETATION OF NORTHWESTERN EUROPE

Northwestern Europe, defined here as the area between 10W. and 15E. and 50 and 55N., including Ireland, the United Kingdom, The Netherlands, Belgium, Luxembourg, northern France and the northern part of Germany, shows little topographic variation and hence a rather uniform vegetation. The area is situated in a zonobiome with a temperate-nemoral climate; a climate influenced by the Atlantic Gulf Stream and with a marked but not too prolonged cold season and a more or less evenly distributed annual precipitation. The warm vegetational season lasts 4-6 months, the mild winter 3-4 months. The annual temperature range is comparatively small. This type of climate is especially suited to the deciduous tree species of the temperate climatic zone, which avoid the extreme maritime as well as the extreme continental regions (WALTER 1985). A broadleaf or 'summer green' deciduous forest was the native vegetation of northwestern Europe. The forest was dominated by tall broadleaf trees such as oak (*Quercus*) and ash (*Fraxinus*) and in the cooler and moister areas beech (*Fagus*). Lower layers of small trees and shrubs are weakly developed and in spring a low layer of herbs quickly develops, but this is greatly reduced after the broadleaf trees begin shading the ground (STRAHLER & STRAHLER 1992).

Because northwestern Europe has been densely populated for centuries, no remnants of a primeval forest have survived. Most existing forests have been modified by practices of tree farming and large forest areas have been completely and permanently removed by farming, urban development, and roads. The deciduous mixed oak forest, the native vegetation of northwestern Europe, is characteristic of the climatic optimum of an

interglacial phase such as the Holocene. JESSEN & MILTHERS (1928) defined an interglacial as a period with a vegetational and hence climatic evolution similar to that of the Holocene. Following this definition we can only use the term interglacial if we recognize a phase with a clear expansion of thermophilous trees. Temperate phases without such a clear expansion are referred to as interstadials.

The interglacials of the Brunhes period can roughly be divided into two types, high and low sea level interglacials (ZAGWIJN 1989). The climate during the high sea level episodes, like the Eemian and the Holsteinian, was oceanic in Western as well as in Central Europe, as indicated by the frequent occurrence of ivy (*Hedera*) and holly (*Ilex*) in pollen sequences in western Russia. The climate was also similar to or warmer than the present one, and climate and vegetation were rather uniform over large areas. This is in contrast to the situation during the low sea level interglacials, when the environmental gradient must have been steeper (ZAGWIJN 1989). The low sea level interglacials have a more continental character, with a distinct north-south and east-west gradient in vegetation and less ecological homogeneity. This steep gradient can be observed in the vegetation of the Early Weichselian interstadials.

Deciduous mixed oak forests covered northwestern Europe only during the middle phase, the climatic optimum, of an interglacial period, i.e. only during about 12% of the past 900 000 years (ZAGWIJN pers. comm. 1993). In its development it is preceded by a herb-dominated vegetation and coniferous forest and it is succeeded by more open coniferous forest which in turn is followed by a herb-dominated vegetation (TURNER & WEST 1968). The glacial maxima of the past 900 000 years have also lasted for about 12% of the total timespan. Although the vegetation during the glacial episodes is poorly known in its details, it is evident that northwestern Europe south of the continental ice mass was covered by a treeless, herb-dominated flora. Data from various disciplines show that the timespan between real interglacial and real glacial phases lasted for about 75% of the total during the past 900 000 years. The winters during these periods were relatively cold and the vegetation of northwestern Europe was dominated by a more or less open boreal coniferous forest and some scattered deciduous forests (ZAGWIJN pers. comm. 1993).

III. THE PRESENT DAY TERRESTRIAL MAMMAL FAUNA OF NORTHWESTERN EUROPE

The present-day terrestrial mammal fauna of northwestern Europe consists of about 80 species, 15 of which (*Oryctolagus cuniculus*, *Sciurus carolinensis*, *Tamias sibiricus*, *Rattus rattus*, *Rattus norvegicus*, *Mus musculus*, *Ondatra zibethicus*, *Myocastor coypus*, *Nyctereutes procyonoides*, *Procyon lotor*, *Hydropotus inermis*, *Muntiacus reevesi*, *Dama dama*, *Cervus nippon* and *Ovis ammon musimon*) do not belong to the native fauna but were introduced by man from areas inside or outside Europe (NIETHAMMER & KRAPP 1978, 1982, 1990; BROEKHUIZEN et al. 1992). A number of additional species (*Canis lupus*, *Ursus arctos*, *Bos primigenius*) can also be regarded as native. They occurred in NW Europe until historical times but persistent human hunting and deforestation have resulted in their extermination. The aurochs, *Bos primigenius*, the ancestor of all domestic

cattle, became entirely extinct. The last auroch in Europe was killed in Poland in 1627 (CORBET & HARRIS 1991).

Bats, represented in NW Europe by 22 different species (BRINK 1967), are very poorly represented in the fossil record and are therefore excluded from the discussion on the application of mammals to the reconstruction of the palaeoenvironment.

Almost all native species of mammals are adapted to midlatitude deciduous forests, the natural vegetation of northwestern Europe before the influence of man. Only a few species are narrowly specialised in their habitat requirements and restricted to the original type of habitat; most species are very versatile and occur in various habitats. These habitats can be roughly divided into woodland and more open habitats. The woodland habitat varies from boreal coniferous forest or taiga in the north to mixed forest and deciduous forest further south. The forest tundra marks the transition from the boreal forest to the open tundra habitat, whereas the forest steppe forms the transition from the deciduous forest to the dry steppe. Open habitats (such as grasslands) are also widely distributed in northwestern Europe, due to deforestation and grazing. These habitats are more humid than the open, steppic habitats in Eastern Europe and Asia.

A number of native species of mammals are highly adaptable and are today widespread in all types of habitat. *Sorex araneus*, *Sorex coronatus* and *Sorex minutus* are found almost everywhere, provided that low vegetation cover is available. *Talpa europaea*, originally an inhabitant of deciduous woodlands (CORBET & HARRIS 1991), is now present in most habitats (though uncommon in coniferous forests) where the soil is sufficiently deep for burrowing. Carnivores such as *Vulpes vulpes*, *Canis lupus*, *Mustela erminea*, *Mustela nivalis*, *Mustela putorius*, *Meles meles*, *Martes martes* and *Martes foina* are (or were) widely distributed and occupy a variety of habitats that offer both cover and prey. Some of these carnivores (*Mustela erminea*, *Meles meles* and *Martes martes*) can be found in a wide range of habitats but they do have a preference for woodland. *Cervus elaphus* is also highly adaptable and associated with many climatic and vegetational types (CORBET & HARRIS 1991) and the present-day restriction to deciduous and mixed woodlands is not natural (BÜTZLER 1986).

A number of mammal species can be regarded as (semi)aquatic, and as such are closely associated with fresh water and occur in wetlands such as marshes. *Neomys fodiens*, *Neomys anomalus*, *Castor fiber*, *Arvicola terrestris* and *Lutra lutra* are associated with water. *Neomys fodiens* and *Arvicola terrestris* live on vegetated banks of rivers and streams, though the latter is not entirely confined to this type of habitat as the water vole may also occur in areas away from water where it lives below ground, in burrows.

The woodlands of NW Europe also have a specific faunal community with a number of species associated with and more or less restricted to that habitat. Some of these species, e. g., *Erinaceus europaeus*, *Erinaceus concolor*, *Apodemus sylvaticus*, *Clethrionomys glareolus* and *Capreolus capreolus*, mainly occur along the edges of woodlands. They use the woods for cover and the adjacent grassland for feeding. Other species (*Sciurus vulgaris*, *Apodemus flavicollis*, *Glis glis*, *Muscardinus avellanarius*, *Sus scrofa*) prefer the forests. *Ursus arctos*, *Felis catus*, *Lynx lynx*, *Bos primigenius* and *Bison bonasus* are also associated with a wooded habitat (SMIT & VAN WIJNGAARDE 1981; PUCEK 1986;

CORBET & HARRIS 1991). *Bos primigenius* originally inhabited the steppes, whereas both *Cervus elaphus* and *Capreolus capreolus* were previously found in the forest steppe. *Eliomys quercinus* inhabits the coniferous and mixed forests of Central and Eastern Europe. The presence of forests is of secondary importance to the presence of a rocky subsoil, however (STORCH 1978). *Sicista betulina* also occurs in the woodland zone of northern Europe, but its habitat is not restricted to a wooded environment, since it also lives on moors. Its sole requirements are a densely vegetated ground cover and humid conditions (PUCEK 1982).

Most of the woodland inhabitants occur in deciduous woods, mixed-oak forests as well as coniferous forests. Only *Erinaceus europaeus*, *Erinaceus concolor*, *Glis glis*, *Apodemus flavicollis*, *Felis catus*, *Sus scrofa* and *Bison bonasus* are mainly restricted to deciduous and mixed-oak forests.

Open habitats also have some characteristic species. The common hamster, *Cricetus cricetus*, is restricted to an open environment and lives under rather arid conditions. The harvest mouse, *Micromys minutus*, prefers arid conditions to a more humid environment. The root vole, *Microtus oeconomus*, is indicative of humid, open habitats. The short-tailed vole, *Microtus agrestis*, and the common vole, *Microtus arvalis*, are also restricted to open environments. *Microtus arvalis* lives under more arid conditions than *Microtus agrestis* in areas where the species co-occur.

IV. THE GEOGRAPHICAL DISTRIBUTION OF THE SPECIES THAT OCCUR IN NORTHWESTERN EUROPE

The distribution of plant species is, according to WALTER (1985), only indirectly dependent on the physical conditions prevailing in the habitat. These conditions are only of importance in so far as they influence the competitive ability of the various species. The physical environmental factors are of direct importance only at the absolute distribution limit. Plant species are therefore capable of existing far beyond their present-day natural distribution if they are protected from competition from other species (WALTER 1985). The ecological optimum, i. e., the conditions under which a species occurs most abundantly in nature, is therefore not identical with the physiological optimum. This applies also to mammal species and the consequence is that the ecological ranges (i. e., the geographical distributions) of living mammals can only be used to a limited degree for statements regarding physiological conditions in the past. Mammal species can, however, still be indicative of environmental conditions, in spite of these restricting factors. These will be rough indications, mainly based on the geographical distribution of the species. The degree of applicability of the indications depends upon the location of the fossil mammal fauna in relation to the geographical distribution of the living species.

A number of species are polyzonal, inhabiting the Northern European Plain as well as areas to the north and south of it. Such species are, e. g., *Erinaceus europaeus*, *Sorex minutus*, *Sorex araneus*, *Neomys fodiens*, *Talpa europaea*, *Lepus europaeus*, *Sciurus vulgaris*, *Apodemus sylvaticus*, *Clethrionomys glareolus*, *Arvicola terrestris*, *Microtus agrestis*, *Microtus arvalis*, *Vulpes vulpes*, *Mustela erminea*, *Mustela nivalis*, *Putorius*

putorius, *Martes martes*, *Meles meles*, *Lutra lutra*, *Cervus elaphus* and *Capreolus capreolus*. The application of these species to the reconstruction of environmental conditions in northwestern Europe is limited because of the wide zonal range of these species.

A second group of species has its northern limit in or just south of the Northern European Plain. These are, e. g., *Crocidura suaveolens*, *Crocidura russula*, *Crocidura leucodon*, *Eliomys quercinus*, *Glis glis*, *Muscardinus avalanarius*, *Microtus subterraneus*, *Felis catus* and *Sus scrofa*. Their major distribution center is located south and/or southeast of the Northern European Plain. These species can be expected to have migrated from the south/southeast to northwestern Europe after the last glaciation. They are of particular interest because their distribution is at least in part restricted due to climatic conditions (temperature is probably the limiting factor). Based on the present-day distribution of these species, it can be concluded that their presence in the fossil record of northwestern Europe indicates real interglacial conditions and the occurrence of deciduous forests.

Another group of species (*Erinaceus concolor*, *Apodemus flavicollis*, *Apodemus agrarius* and *Cricetus cricetus*) have their major distribution center further to the east/south-east. Humidity is the major factor which discourages further expansion to the west. Their occurrence in the fossil record is therefore indicative of rather arid conditions.

Species such as *Castor fiber*, *Microtus oeconomus*, and *Sicista betulina* are distributed mainly in the north/north-east of northwestern Europe. Their occurrence in the fossil record may, on the basis of the present-day circumstances under which these species live, be indicative of cooler conditions.

V. THE FOSSIL RECORD

The Late Pleistocene and Early Holocene fossil record of northwestern Europe includes another 35-40 species of mammals apart from the native ones listed above. Many of these 'exotic' species still exist and inhabit either the continental (partly forested) steppe zones south or east-southeast of the Northern European Plain (*Ochotonapusilla*, *Hystrix cristata*, *Marmota* sp., *Citellus citellus*, *Allactaga major*, *Sicista subtilis*, *Cricetulus migratorius*, *Lagurus lagurus* and *Saiga tatarica*) or the boreal forest zone and the arctic tundra north/northeast of the area discussed in this paper (*Sorex minutissimus*, *Dicrostonyx torquatus*, *Lemmus lemmus*, *Lemmus schisticolor*, *Clethrionomys rutilus*, *Alopex lagopus*, *Gulo gulo*, *Alces alces*, *Rangifer tarandus* and *Ovibos moschatus*). The presence in northwestern Europe of species of the former group indicates arid, continental climatic conditions, whereas the occurrence of species of the latter group indicates cool, 'glacial' conditions. The tundra vole, *Microtus gregalis*, has a patchy distribution and inhabits a steppe as well as a tundra biotope. This also applies to the ground squirrel, *Spermophilus* (*Urocitellus*) *undulatus*.

The Late Pleistocene desmans of northwestern Europe are very similar to, and probably conspecific with, the living (semi)aquatic *Desmana moschata*, which now occurs in Ukraine and Russia. Their occurrence in the fossil record points to an aquatic environment. The fallow deer, *Dama dama*, inhabited northwestern Europe during several warm phases of the Middle and Late Pleistocene but did not migrate into the area during the Holocene.

The species was reintroduced to northwestern Europe from southeastern Europe or Asia Minor about 800 years ago (CORBET & HARRIS 1991). *Dama dama* is characteristic of mature woodland; it prefers deciduous or mixed woodland with an established undergrowth, although it sometimes colonizes coniferous plantations (provided these contain some open areas). The chamois, *Rupicapra rupicapra*, and the ibex, *Capra hircus*, are nowadays mainly restricted to mountainous areas. The fossil record, however, indicates that both species also occurred on the Northern European Plain during the Late Glacial. The extant chamois inhabits the forest zone (deciduous, coniferous and mixed forest) whereas the ibex lives on less vegetated steep cliffs but also occurs in coniferous woodland (CORBET & HARRIS 1991).

Very exotic for northwestern Europe are species such as *Hippopotamus amphibius incognitus* and *Bubalus murrensis*, which are related to the extant *Hippopotamus amphibius* and *Bubalus mindorensis*, *Bubalus arnee* and *Bubalus bubalus* respectively. Today, the extant species normally live under tropical and subtropical conditions, but we have to be aware that their occurrence in the fossil record does not necessarily imply similar conditions for northwestern Europe (STUART & GIBBARD 1986; KOENIGSWALD 1988). In historic times the hippopotamus was distributed throughout Africa, from the Cape to the upper Nile River, wherever suitable bodies of water occurred (OWEN-SMITH 1988). They generally spend the daytime largely submerged in water, thereby avoiding heat stress. Although they spend much time in water, the musculature of the fore and hind legs does not show any adaptation to this specific environment, but is adapted to terrestrial locomotion, and the foreleg, which supports around 75 % of the bodyweight, is equipped with a number of tendons that can act as a passive standing mechanism (MACDONALD et al. 1985; KOLFSCHOTEN unpublished). Their musculature might be adapted to a life on land, but other physiological factors seem to restrict their distribution to areas with open water, i. e., areas without long periods of frost. This also applies to *Bubalus* (KOENIGSWALD 1988).

The present-day restrictions seem also to apply to the Pleistocene *Hippopotamus*, as can be deduced from the associated palynological information. The Ipswichian (= Eemian) *Hippopotamus* records from Britain are associated with pollenzones IpIIb (mixed oak forest) and IpIII (temperate forest with hornbeam) (STUART & GIBBARD 1986). The presence of holly (*Ilex*) in the pollen spectra associated with *Hippopotamus* remains indicates warm winters with mean January temperatures of 0°C (ZAGWIJN, pers. comm. 1993). The Eemian Interglacial has been characterized as strongly oceanic in Western as well as in Central Europe. This is indicated, for example, by the frequent occurrence of ivy (*Hedera*) and holly in Eemian pollen sequences in western Russia, much further east than their present distribution (ZAGWIJN 1992). This is most probably the result of a very high sea level, which resulted in a direct connection between the Baltic Sea and the Arctic Ocean (GERASIMOV & VELICHKO 1982). This connection allows the 'warm' North Atlantic Gulf Stream, which has a dominant influence on the climatic conditions of northwestern Europe, to shift further east, resulting in specific warm-temperate climatic conditions. These conditions appear to be favourable for *Hippopotamus* and *Bubalus*. It is, however, not clear why *Hippopotamus* did not appear during the Holsteinian, a period with climatic conditions similar to those of the Eemian.

Some of the species of mammals present in northwestern Europe during the Late Pleistocene have become extinct. Not only the woolly mammoth, *Mammuthus primigenius*, the straight-tusked elephant, *Elephas antiquus*, the woolly rhinoceros, *Coelodonta antiquitatis*, and the giant deer, *Megaloceros giganteus*, but also the large carnivores *Panthera leo spelaea*, *Crocota crocota spelaea* and *Ursus spelaeus* and the large herbivores *Dicerorhinus kirchbergensis*, *Dicerorhinus hemitoechus* and *Equus hydruntinus* were unable to survive the rapid environmental changes of the Late Pleistocene and Early Holocene and the influence of Palaeolithic man. The environmental conditions to which these species were adapted have been deduced from a variety of evidence, e. g., associated faunal and floral data, the hypsodonty of the molars, the morphology of the skull or the remains of stomach contents (information which can be used to decide whether we are dealing with browsers or grazers).

The extinct large carnivores are known from 'glacial' as well as 'interglacial' faunas; they probably lived in a variety of habitats. *Elephas antiquus* and *Dicerorhinus kirchbergensis* are, based on the types of arguments presented above, associated with a more wooded environment, whereas species such as *Mammuthus primigenius* and *Coelodonta antiquitatis* are indicative of the "Mammoth Steppe", an open, very rich and diverse habitat with certain seasonal characteristics (for a detailed description see GUTHRIE 1982, 1990, 1995). Horses (*Equus* sp.), *Dicerorhinus hemitoechus* and *Equus hydruntinus* also inhabited the 'glacial' "Mammoth Steppe" but they occurred in northwestern Europe in areas with an open, steppic vegetation during 'interglacial' phases as well. A steppic environment is, however, not the only natural environment of horses. They are today mainly restricted to open grasslands because of human impact, but the presence of horses in the fossil record also indicates the presence of shrubs (WALTER 1985).

VI. THE INTERPRETATION OF THE FOSSIL RECORD

Taphonomic restrictions

When we interpret a fossil assemblage, we must first of all be aware of taphonomic biases. The fossil record is very often not a reflection of the original fauna of the region. Remains of smaller mammals are, in most cases, transported to the locality by birds of prey, and the composition of these faunas will therefore be affected by the diet of these birds. The fauna of a palaeolithic site, particularly the larger mammal fauna, may be affected by the activities of humans. Hyaenas are also known to accumulate bones and their selection results in an abnormal composition of the mammal fauna. Furthermore, phenomena such as hydrodynamic sorting and hibernation act on the composition of the fossil faunal assemblage.

The taphonomic aspects mentioned above restrict the applicability of fossil mammals to the reconstruction of climate and environment. The proportional representation of a species is less important than its actual presence and should therefore be handled with care. This applies to many assemblages, but especially to assemblages of smaller mammals. The diet of birds of prey differs between species but also varies seasonally within

species (ANDREWS 1990). Changes in the abundance of smaller mammal species (cf. CORDY 1991) are, therefore, not necessarily a reflection of climatic development.

Adaptation

The applicability of fossil mammals to the reconstruction of the palaeoenvironment is also hampered by the fact that mammals have the capacity to adapt to various environments and to tolerate other circumstances than those under which they live today. The fossil record shows that some Arvicolidae, for example, evolved rapidly during the Pleistocene. This evolution is most probably not restricted to changes in the morphology; the morphological changes might be the result of adaptations to a different environment. There may even be adaptations to a different environment that are not reflected in morphological changes. A famous example is provided by the Norway lemming, *Lemmus lemmus*, which today inhabits a limited, (sub)arctic biotope, whereas its Early and Middle Pleistocene relatives, which hardly show any morphological differences from the living species, lived under temperate conditions in a more wooded environment (KOENIGSWALD 1970; KO-WALSKI 1995).

There is no consensus in the literature regarding whether the decrease in size of herbivorous mammals of the Late Pleistocene, such as *Bison bison*, *Cervus elaphus*, *Rangifer tarandus*, *Mammuthus primigenius* and *Equus* spp. (GUTHRIE 1985; FORSTEN 1993), should be regarded as interspecific evolution, i. e., as adaptation to environmental change. The same applies to differences that can be observed in some smaller mammals. The Late Glacial *Sorex macrognatus* is larger than its relatives in the *Sorex araneus* group, which occurred in northwestern Europe during the Eemian Interglacial and Early Holocene (STORCH 1973). The Late Pleistocene *Arvicola* from Brillenhöhle (STORCH 1973) and from a calcareous cave near Berndorf (HUTTERER & KOENIGSWALD 1993) show a number of specific characteristics (e. g., the shape of the incisors and the nasal bones, variation in morphology of the molars). One of these characteristics, the pro-odontism of the incisors, is indicative of a more terrestrial and burrowing mode of life. These characteristics may be the result of relatively rapid interspecific adaptation. If mammal species are really able to adapt to different environments this easily, we must be cautious when presenting a detailed reconstruction of the palaeoenvironment on the basis of fossil mammals only. But we must also be careful before using the term contamination to explain an uncommon faunal association, such as for instance those from the German localities Brillenhöhle layer IV, where *Glis glis* occurs together with *Dicrostonyx* and *Lemmus* (STORCH 1973), and Plaidter-Hummerich layer D1, where *Glis glis* and *Dicrostonyx* co-occur (KOLFSCHOTEN & ROTH in press).

VII. CONCLUDING REMARKS

Our knowledge of the palaeoenvironment is to a large extent based on palaeobotanical data and to a lesser degree on palaeozoological data. Palaeobotanical and malacological remains are much more numerous than vertebrate remains, and the lithological units from which the samples are taken are much smaller. These data are therefore potentially much more detailed. Continental stratigraphy is furthermore mainly based on palaeobotanical

evidence and terms such as 'interglacial' have a palaeobotanical definition. Terms such as a high sea level and low sea level interglacial, which originate in oxygen isotope studies, can furthermore at present only be related to palaeobotanical data. We, who study the Quaternary mammalian fauna use the terms glacial and interglacial. If we find *Mammuthus primigenius* we assume that we are dealing with glacial conditions, whereas the discovery of *Hippopotamus amphibius incognitus* indicates interglacial conditions. But which species are indicative of real interglacials, of intervals such as Oxygen Isotope stage 5e? Does the mammal fauna of the oceanic high sea level interglacials, with a mainly north-south gradient in the vegetation, differ from the more continental low sea level interglacials, with a north-south as well as an east-west gradient? The mammal faunas of the different types of interglacials certainly differ but in which respect? Which faunal elements are indicative of real glacial conditions and which species inhabited northwestern Europe during the intervals between glacial and interglacial optima, i. e., during about 75 % of the timespan between 900 000 years ago and the present day? Which faunal associations are characteristic of interstadial phases? All these are questions we would like to answer in spite of the taphonomic bias of the fossil assemblages and the capacity of mammals to adapt to different environments.

Interglacial faunas from northwestern Europe

According to the original definition of JESSEN & MILTHERS (1928) we can only use the term interglacial if we can recognize a phase with a clear expansion of thermophilous trees in Northwestern Europe. Only those mammal species that are related to such an expansion are indicative of interglacial conditions. However, most of the woodland inhabitants occur in deciduous woods, mixed-oak forests, as well as coniferous forests, and species such as *Glis glis*, which is nowadays mainly restricted to deciduous and mixed-oak forests, occurs (as mentioned above) in faunal assemblages together with *Dicrostonyx*. The capacity to adapt to other environments also applies to other mammal species, such as *Erinaceus europaeus*, *Erinaceus concolor*, *Apodemus flavicollis*, *Felis catus*, *Sus scrofa* and *Bison bonasus*, which are nowadays mainly restricted to deciduous and mixed-oak forests. It cannot be excluded that these species occurred in northwestern Europe during temperate phases referred to as interstadials, without a clear expansion of thermophilous trees. The species indicate the presence of forests and hence, (warm) temperate conditions. There are no mammal species, apart from *Hippopotamus* and *Bubalus*, which require very specific conditions (as described above), which exclusively occur in northwestern Europe during interglacial phases. Hence, no single mammalian species, apart from *Hippopotamus* and *Bubalus*, convincingly indicates that we are dealing with an interglacial fauna. Only a combination of arguments can lead to that conclusion and it is obvious that, with the present state of knowledge, it is impossible to distinguish high sea level from low sea level interglacial faunas.

Glacial faunas from northwestern Europe

Characterization of glacial faunas seems to be much easier. If *Mammuthus primigenius* and *Coelodonta antiquitatis* are present, we are dealing with glacial conditions. However, there appears to be a problem in distinguishing faunas from glacial maxima, which lasted for about 12% of the total timespan, from those faunas which date from episodes between

real interglacials and glacial maxima (75% of the total timespan). The problems are partly due to the lack of knowledge of the vegetation during these 75%. ZAGWIJN (pers. comm. 1993) assumes a dominance of more or less open boreal coniferous forest and some scattered deciduous forests, whereas GUTHRIE prefers the hypothesis of a more open 'Mammoth Steppe' dominating the vegetation of northwestern Europe during this period. If ZAGWIJN's hypothesis is correct, we would expect to find many faunas with boreal elements and most of the 'mammoth faunas' would then date from glacial episodes. The occurrence of, e. g., *Sorex minutissimus*, characteristic of boreal conditions, in the fossil record of Great Britain, northern France and southern Germany indeed indicates an expansion of boreal forests. There are, however, many fossil faunas with a dominance of herbivores characteristic of the 'Mammoth Steppe', which supports GUTHRIE's hypothesis. The discrepancy between ZAGWIJN's 'boreal coniferous forest' hypothesis and the occurrence of many 'mammoth steppe' faunas may be explained by the fact that palaeobotanists base their ideas mainly on data from wetland environments in the vicinity of the locality whereas palaeozoologists use information from larger areas. If this explanation should prove correct, it implies that the accuracy of the reconstruction of a palaeoenvironment increases if mammalian data are incorporated. A lack of mammalian data may result in a local instead of a regional reconstruction. Furthermore, it appears to be problematic to use terms such as interglacial and glacial *sensu stricto* to characterize fossil faunal associations. We should avoid these terms as much as possible and define, in the near future, faunal units which are characteristic of a particular palaeoenvironment in a restricted area. This would increase the applicability of fossil mammals to the reconstruction of the palaeoenvironment.

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