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The Eemian mammal fauna of central Europe

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Abstract

The knowledge of the Eemian fauna of central Europe is based on the fossil record from a number of sites located in the eastern part of Germany. The faunas with different deer species as well as *Sus scrofa*, *Palaeoloxodon antiquus*, *Stephanorhinus kirchbergensis* and *Glis glis* indicate a forested environment alternating during the climatic optimum of the Eemian s.s. with areas with a more open environment inhabited by species such as *Cricetus cricetus, Equus* sp. (or *Equus taubachensis*), *Equus hydruntinus* and *Stephanorhinus hemitoechus.* Characteristic for the Rhine valley fauna are *Hippopotamus amphibius* and the water buffalo (*Bubalus murrensis*); both species are absent in the eastern German faunas with an Eemian age.

Taking into account the short period of time covered by the Eemian s.s., the amount of data on the Eemian mammalian fauna is remarkably large. There is, however, still an ongoing debate on whether the stratigraphical position of a number of faunas are of Eemian or 'intra-Saalian' age. Furthermore, there are faunal assemblages or stratigraphically isolated finds referred to the Eemian without indisputable evidence. This is particularly the case in the Rhine valley, where most of the so-called Eemian fossils come from dredged assemblages. The picture of the evolution of the Eemian fauna and its geographical variation is consequently still incomplete.

Keywords: central Europe, Eemian, mammalian faunas, Northwestern Europe, Pleistocene

Introduction

Important in the debate on present-day climatic changes are the solid data from earlier interglacials that can be deduced from the fossil botanical and zoological records. The last interglacial in particular is important since the set of data is rich compared to that of earlier interglacials. This is also the case for the mammalian record and – although the mammalian fauna differs in many aspects from the present-day fauna of NW and central Europe – the fossils may contribute to the reconstruction of the environment and its evolution during the earlier part of the Late Pleistocene.

Many faunas have been referred to the last interglacial (which is known in western and central Europe as the Eemian stage, the Riss-Würm interglacial or, in the British Isles, the Ipswichian), the interval following the penultimate (Saalian/Riss/Wolstonian) glacial ice-advance and preceding the last (Weichselian/ Würm/ Devensian) glacial stage. Nowadays, it is known, however, that the Eemian stage – as defined at the type locality near Amersfoort (the Netherlands) – covers only a restricted part of the interval between the two glacial ice-advances. The Eemian in a strict sense is the first warm/temperate episode after the retreat of the Saalian continental icecap; it is broadly the continental equivalent of the marine isotope substage (MIS) 5e (see Turner, 2000 – this issue). Several temperate interstadials separate the Eemian s.s. from the latest (Weichselian) glacial maximum and part of the fossil remains, previously referred to the Eemian, might date

from these interstadials. In the present contribution, the author focuses on the Eemian s.s. and in particular on the mammalian record from this time.

When discussing the Eemian s.s. fossil record, it is important to realise that there are no mammalian remains from the type locality of the Eemian nor from Eemian deposits in the type region, the Amersfoort Basin. Correlations between the type deposits and mammalian faunas are often based on palynological data, absolute dates and/or the stratigraphical position of the levels that yielded the fossil remains. A number of faunal remains have been referred to the Eemian because of the 'interglacial' character of the fauna; solid independent evidence for an Eemian age is, however, sometimes missing. In order to avoid circular reasoning (*Hippopotamus* indicates an Eemian age; Eemian faunas are characterised by the presence of *Hippopotamus*), the author has decided to restrict the analyses of Eemian faunas to those associations that can be correlated with the Eemian s.s. and to define the Eemian fauna in the various regions on the basis of sites with dating evidence independent of the mammalian fauna itself, be it lithostratigraphic or radiometric.

Central Europe (in particular the eastern part of Germany: Fig. 1) is of major interest for the study of Eemian faunas. Localities in this area have yielded the most extensive record. A general picture of the Ee-

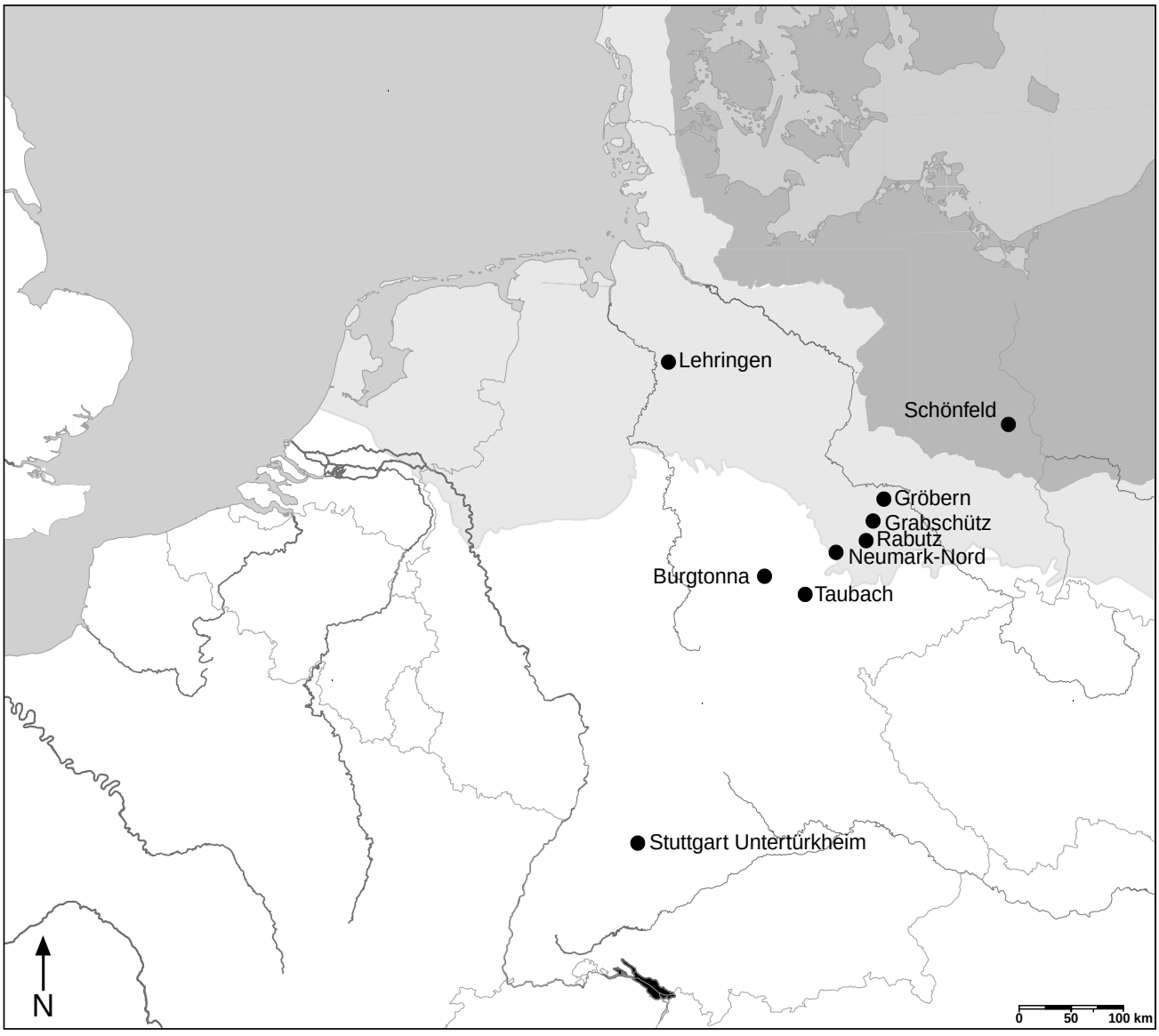

Fig. 1. Location of the sites with a clear stratigraphical setting, where mammalian remains with an Eemian s.s. age have been collected.

mian fauna of central Europe will be presented and the geographical differences will be discussed in the following.

Eemian faunas from central and western Europe

The number of independently well-dated Eemian faunas is restricted; there are only a few rather long successions with a good Eemian mammalian record. A number of these faunal assemblages come from the northern and eastern part of Germany, from a geologically special area. The area had previously been covered by the Saalian ice sheet; after its withdrawal, sedimentation took place at certain places (for example in pingo depressions) upon the Saalian subglacial tills. The sites are located south to southwest of the maximum extent of the Weichselian ice sheet; the sediment accumulations with the mammalian remains have, therefore, not been destroyed by the Weichselian ice. The presence of Saalian tills of the Drenthe I, II and/or Warthe substages provides important stratigraphical markers at the sites in the glaciated area. Outside of the glaciated area, one has to rely on other criteria, such as absolute dates. This is the case in the German travertine sites.

Sites in the glaciated area

Lehringen (Niedersachsen)

Mammalian remains of Eemian age, exposed during quarrying between 1945 and 1950, have been collected from marls near Lehringen. The marls were deposited in a number of small lakes, connected by a small river, the former river Lehrde. The marl deposits are intercalated with peat deposits on top of the Drenthe (= Saalian) till. Palaeobotanical and malacological investigations of the succession exposed at the Lehringen locality indicate that the peat and marl were formed under forested conditions. It is therefore obvious that the succession is incomplete; the beginning as well as the end of the interglacial are absent. Palaeobotanical research indicated furthermore that the so-called Lehringer interglacial is equivalent to the Eemian interglacial.

Von Sickenberg (1969) described the larger mammal remains from the Lehringen site, gathered by an amateur collector. The exact data on the stratigraphical provenance of the remains are lacking; palynological research of sediment from molar cavities or from skull fragments of for example the straight-tusked elephant indicate, however, that the fossils originate from the marls, deposited during the interglacial optimum. The fossil assemblage from Lehringen represents twelve species (Table 1).

Gröbern (Sachsen-Anhalt)

A few hundred kilometres south-east of the Lehringen locality lies the Gröbern site, in the Leipzig lowlands (Fig. 1). Fossil bones from the site have been known since 1986 (Hartung, 1991). In 1987, during the removal of overburden from the lignite pit, a nearly complete skeleton of a straight-tusked elephant was found, together with flint artefacts, in an infilled lake (Erfurt & Mania, 1990). The depression had been formed as a kettle hole in glaciofluvial sands and gravels on top of the Saalian (Drenthe) till; it contains Eemian and early Weichselian limnic sediments (Litt, 1990). The latter shows an alternation of silty muds (deposited during the colder episodes), calcareous muds, gyttja and peat from the warmer episodes. The lacustrine sediments are overlain by Weichselian sands and solifluction material (Eissmann et al., 1988). Palynological research has indicated that the depression contains a complete Eemian and early Weichselian sequence. The latter is characterised by the alternation of three treeless stadials and two interstadials with boreal tree cover (Brørup and Odderade) (Litt, 1990). The palaeobotanical observations are supported by climatic reconstructions based on the coleopteran record from the same sequence (Walking & Coope, 1996).

The vertebrate remains from the site are from the Eemian deposits, from layers referred to the Eemian pollen zones E4a and E4b or from the E4b – E5 transition (Benecke et al., 1990). The vertebrate assemblage is diverse; apart from the mammalian record (Table 1; the Chiroptera *Pippistrellus* sp. is not included in the list) there are at least six different fishes (mainly Cyprinidae), two amphibians and two reptiles represented.

Grabschütz (Sachsen-Anhalt)

Interglacial deposits with mammalian remains are also known from the Grabschütz locality, an opencast lignite mine at Delitzsch, southwest of Gröbern. The geological setting at the site is more or less similar to the one at Gröbern, i.e. interglacial deposits in a basin formed in glacial deposits referred to the Saalian (Drenthe) ice-advance. According to Litt (1990, 1994), the interglacial lacustrine and peat deposits are, based on palynological data, of Eemian age. Silts, solufluction material and loess deposits, all referred to the Weichselian, and a Holocene soil overlie the interglacial deposits (Wansa & Wimmer, 1990). The interglacial deposits have yielded amphibian, reptilian and mammalian remains (Benecke et al., 1990).

Table 1. List of mammalian species represented in the Eemian s.s. assemblages from sites in central Europe.

	Lehringen	Gröbern 1	Grabschütz	Neumark-Nord	Rabutz	Schönfeld	Taubach	Burgtonna	Stuttgart-Untertürkheim
REPTILIA									
Emys orbicularis	x			x	x	x	x	x	
MAMMALIA									
Insectivora									
Erinaceus europaeus						x			x
Talpa europaea			x	x		x	x	x	x
Sorex araneus		sp.	ex gr.		ex gr.	ex gr.	cf.	x	x
Sorex minutus									
Neomys fodiens						x			
Neomys anomalus						cf.			
Crocidura suaveolens						cf.		sp.	sp.
Lagomorpha									
Lepus timidus									
Lepus europaeus			x			cf.		sp.	x
Rodentia									
Glis glis								x	
Cricetus cricetus						sp.	x	x	
Cricetus major								x	
Castor fiber	x					x	x	x	
Clethrionomys glareolus		x	x	x		x	x		
Arvicola terrestris		sp.	sp.	x		x	x		x
Microtus arvalis							x	x	x
Microtus agrestis							x		x
M. arvalis/M. agrestis		sp.	sp.	ex gr.		x			
Microtus subterraneus		x					x		
Microtus oeconomus						x			
Apodemus sylvaticus		sp.	sp.	sp.		sp.	x	x	
Apodemus flavicollis		cf.							
Apodemus maastrichtiensis		cf.	x						
Carnivora									
Canis lupus	x			x	cf.	x	x		x
Vulpes vulpes				x				x	x
Ursus arctos	sp.			x	x		x	x	x
Ursus spelaeus							x		x
Martes martes						x			
Mustela erminea									

Table 1 (continued).

Mustela putorius									x
Meles meles						x	?		x
Lutra Lutra						x	x		
Crocuta crocuta								x	x
Felis lynx							x		
Felis sylvestris								x	x
Panthera panthera pardus							x		
Panthera leo				x	x		x	x	x
Proboscidea									
Palaeoloxodon antiquus	x	x		x	x		x	x	x
Perissodactyla									
Equus sp.	x			x	x		x	x	
Equus hydruntinus	?							x	x
Stephanorhinus kirchbergensis	x	sp.	sp.	x	x		x	x	
Stephanorhinus hemitoechus							x	x	x
Artiodactyla									
Sus scrofa					x		x	x	x
Hippopotamus amphibius									
Megaloceros giganteus	x			x	x		x		x
Dama dama	x	x		x			x	x	
Cervus elaphus	x	x	x		x	x	x	x	x
Alces alces					sp.		x		
Capreolus capreolus	x		x		x	x	x	x	x
Bubalus murrensis									
Bos primigenius	x			x	x		x		x
Bison priscus				sp.	x		x	x	
Bos/Bison			x						x

Neumark-Nord (Sachsen-Anhalt)

A significant interglacial flora and fauna has been collected from lacustrine deposits exposed in the open-cast lignite mine at Neumark-Nord. The lacustrine sediments represent a small lake accumulation formed in the Saalian till deposits that cover the area; they lie on top of Saalian (Drenthe) till and meltwater deposits. The interglacial deposits are topped by a Holocene soil and a periglacial succession that can be subdivided into upper and lower loesses, which are separated by, for instance, an alternation of humic gley deposits. In the lower part of this succession well-developed ice wedges occur. There is no doubt about the age of the upper part of the periglacial sequence: all authors refer this part of the succession to the Weichselian. There is, however, a debate on the age of the lower part of the sequence. Mania (1992) assumed that the lower part was to be correlated with the Saalian (Warthe substage); the lacustrine deposits have an intra-Saalian age in this scenario. Litt (1990) argued for an Eemian age based on palynological data. This discrepancy will be discussed later on.

The mammalian record from Neumark-Nord is remarkable because of its unusually large number of more or less complete skeletons of large mammals (Mania, 1992; Pfeiffer, 1998): *Palaeoloxodon antiquus* (3), *Stephanorhinus kirchbergensis* (1), *Dama dama* (80), *Cervus elaphus* (18) and *Bos primigenius* (1). In addition, there is a collection of smaller vertebrates and isolated remains of, among others, *Emys orbicularis* and carnivores such as *Ursus arctos, Panthera leo* and *Canis lupus*.

Rabutz (Sachsen-Anhalt)

One of the classical sites with an Eemian fauna is Rabutz, between Halle and Leipzig. The first publication reporting the discovery of mammalian fossils from the clay deposits at Rabutz is from Von Fritsch (1880); he described the upper dentition of a rhinoceros, *Stephanorhinus kirchbergensis*. More fossils (including *Emys orbicularis*) have since been collected during an excavation in 1914; Soergel (1920) has described the collected fossil material. A review of the geological setting, the fossil flora and fauna has been published, together with a description of the Palaeolithic artefacts, by Toepfer (1958).

The Rabutz basin with the clay deposits yielding the mammalian fossils is a trench in the Saalian till plateau (Eissmann, 1990). Eissmann (1990) referred the interglacial clay deposits to the Eemian. There is, however, a debate on whether the clay is covered by colluvial deposits or by a late Saalian till as stated by, among others, Erd (1990). The second option would imply that the faunal remains are of 'intra-Saalian', i.e., pre-Eemian, age.

Schönfeld (Brandenburg)

At the Schönfeld locality (near Cottbus), east of the localities mentioned above, a sequence with Eemian deposits yielded a mammalian assemblage that is correlated palynologically with the Eemian pollen zones E4 – E5 (Heinrich, 1991). The lacustrine Eemian deposits were formed in a deep depression in the Saalian III till. At the southern margin of the basin, a succession covered the late Saalian until the early Weichselian. This sequence yielded palaeobotanical remains as well as molluscs and a large number of vertebrate fossils. The vertebrate fossil assemblage represents fishes, amphibians, reptiles (among them *Emys orbicularis*), birds and twenty species of mammals (Böhme, 1991; Fischer, 1991; Heinrich, 1991).

The debate on the age of the interglacial deposits at Grabschütz, Neumark-Nord and Rabutz

The geological setting at the Grabschutz, Rabutz and Neumark-Nord localities is more or less identical and similar to the one at Gröbern, i.e. interglacial deposits in a basin formed within glacial deposits referred to the Saalian (Drenthe) ice advance. According to Litt (1990, 1994), the interglacial deposits are, as indicated by palynological data, of Eemian age. Mania (1999) excluded an Eemian age, however, and preferred to correlate the Neumark-Nord interglacial deposits with an 'intra-Saalian' warm phase, post-dating the older Drenthe and pre-dating the younger Warthe ice advances. This interglacial had apparently subcontinental, warm climatic conditions, as shown by both the malacological and the palaeobotanical record. Von Koenigswald & Heinrich (1999) also preferred to correlate the faunas from Grabschütz and Neumark-Nord with this 'intra-Saalian' event because of the occurrence of *Apodemus maastrichtiensis* in both faunas; this species is absent in the faunas from Gröbern, Taubach and Burgtonna. The fauna from Rabutz might, according to Von Koenigswald & Heinrich (1999), also date from the 'intra-Saalian' interglacial.

The evidence for an 'intra-Saalian' interglacial separating the Drenthe and Warthe substages is, however, still very poor and contradictory (Litt & Turner, 1993). Undeniable interglacial deposits sandwiched between the Drenthe and Warthe tills have never been demonstrated so far and a sequence with the 'intra-Saalian' (post-dating the Drenthe substage) and Eemian interglacial deposits in superposition is as yet also unknown up to now (see also Turner, 2000 – this issue).

Travertine sites

In the unglaciated area not far from the German sites mentioned above, a few localities are present where vertebrate remains with an assumed Eemian age have been recovered from travertine sequences. The exact chronostratigraphical position of the faunal record is, however, not always clear. A direct link with the Saalian Drenthe I and II and Warthe substages, as observed at the sites mentioned above, is missing at these travertine sites. Other methods, for example radiometric dating, must therefore be applied. A second problem is that these assemblages are often from old collections: fossils collected during the exploitation of the travertine many years ago. Detailed information about the exact provenance of many specimens is missing and one can try only to reconstruct their original stratigraphical position by combining present knowledge of the exposures with information from the old literature. This is the case for the German sites in Thuringia (Thüringen) near Weimar and in Baden-Württemberg (near Stuttgart), where travertine deposits of Eemian age were or still are exposed.

Well known are the travertine deposits near Weimar. Three geographically isolated Pleistocene travertine occurrences, in which the sites Taubach, Weimar-Ehringsdorf and Weimar-Belvédère Allee (=Weimar Stadt) are located, yielded mammalian fossils. The fauna from Taubach is one of the classical Eemian faunas. The mammalian fauna from Weimar-Belvédère Allee, also referred to the Eemian, partly resembles the fauna from Taubach; the faunal assemblage from Weimar-Belvédère Allee is a mixed assemblage, however, and the exact stratigraphical origin of several specimens, including the remains of *Mammuthus primigenius, Stephanorhinus hemitoechus* and *Rangifer tarandus*, is unknown. Furthermore, independent age indications for the travertine deposits are missing. The fauna has therefore not been integrated into the analyses.

Even more problematic – and heavily debated for many years – is the age of the sequence exposed at Weimar-Ehringsdorf. The geological setting of the travertine deposits at Weimar-Ehringsdorf is roughly comparable to that of the sequence at Taubach; both travertine successions were deposited on gravels of the Ilm river and have an assumed Saalian age. The sequence at Weimar-Ehringsdorf differs, however, in some aspects. The so-called 'Pariser Horizon' is missing in the Taubach sequence but more important are the differences in the malacological assemblages from both sequences; the *Helicigona banathica* association, known from Eemian deposits at Taubach and Burgtonna, is missing in Weimar-Ehringsdorf. Mania (pers. comm., 2000) therefore postulates a pre-Eemian age for the main travertine section at Weimar-Ehringsdorf. Heinrich (1982) also assumed a pre-Eemian, i.e. late Middle Pleistocene age, for the fauna from Weimar-Ehringsdorf because of the evolutionary stage of the watervole *Arvicola terrestris.* It is, however, not clear whether the Lower and Upper Travertine, separated by the Pariser horizon, date from a single warm/temperate episode or clearly differ in age. The Lower Travertine might date from the Middle Pleistocene, whereas the Upper Travertine and the Pariser Horizon might date from the Late Pleistocene. The situation at Weimar-Ehringsdorf might be even more complex, due to karstic fissure infillings in which younger (Eemian?) sediments (including fossil remains) penetrated into the older travertine deposits (Mania, 1997). Other authors have questioned this concept (Kahlke, pers. comm., 2000).

It is obvious that the situation at Weimar-Ehringsdorf is far from clear. Therefore only the fauna from Taubach is included in the analyses; the faunas from Weimar-Belvédère Allee and Weimar-Ehringsdorf are ignored. The Eemian assemblage from Burgtonna, a site at about 50 km west of Weimar where Late Pleistocene (Eemian and Weichselian) faunas have been collected, is also included. Far beyond the area, in southern Germany near Stuttgart, is another travertine site called Stuttgart-Untertürkheim, which has yielded an extensive assemblage of Eemian vertebrate remains.

Taubach (Thüringen)

During the second half of the 19th century, intensive extraction of travertine took place at the village of Taubach, about 3 km southeast of Weimar. The majority of the palaeontological and archaeological finds, including two hominid teeth, were collected between 1870 and 1900 (Kahlke, 1994). The geological setting of the Pleistocene deposits at Taubach is rather complex and differs over short distances (Steiner, 1976). The general, simplified Pleistocene section shows Saalian gravels of the Ilm river at the base, covered by more fine-grained flood-deposited loams. On top of these deposits occurs an alternation of thin plates of compact travertine and less compact sandy travertine layers, some of which are rich in molluscs. Halfway up the section an up to 1.5 m thick compact travertine bed (the so-called 'Werkstein Travertine') is present, with on top the lower humic travertine sands, a level that yielded flint artefacts and larger mammal bone fragments as well as a small number of smaller mammals. The layer with artefacts is covered by more massive travertine layers, the upper humic travertine sands and, again, an alternation of thin plates of compact travertine and less consolidated sandy travertine layers rich in molluscs.

The stratigraphical origin of the major larger mammal assemblage, collected during the end of the 19th century, is not clear. Steiner (1976) assumed that the so-called 'Knochensand', which yielded the larger mammal fossils, should be correlated with the lower part of the sequence, the section between the flood-deposited loams at the base and the Werkstein Travertine. The malacological record from the sequence exposed at Taubach does not show hiatuses; the record is comparable to that from the Eemian travertine sections at Burgtonna.

The correlation between the mammalian fauna and the Eemian interglacial was initially based on the distinct interglacial character of the fauna and its lithostratigraphical position. Absolute dates confirmed the earlier assumptions. The travertine deposits at Taubach have been radiometrically dated to 116 ± 19 ka (Brunnacker et al., 1983). The fauna from Taubach is very divers; the fossil assemblage is, however, dominated by *Ursus arctos* (number of specimens, n, = 1557), *Stephanorhinus kirchbergensis* (n = 1224), *Bison priscus* (n = 532), *Castor fiber* (n = 323), *Cervus elaphus* (n = 207) (Bratlund, 1999). All other species are less frequent. The presence of *Stephanorhinus hemitoechus* in the main fauna from Taubach, listed in Von Koenigswald & Heinrich (1999), for example, is not certain; this species is represented by an isolated molar, the provenance of which is unknown (Kahlke, 1977). Taphonomical processes (in particular the activity of hominids) affected the composition of the faunal assemblage, as can be deduced from the age profiles of the dominant species and the cut-mark frequencies (Bratlund, 1999).

Burgtonna (Thüringen)

The travertine deposits at Burgtonna overlie Saalian fluvial terrace deposits; they are, in turn, overlain by Weichselian loess. The travertine complex has a thickness of about 15 m and is composed of several, rather well stratified layers. The travertine succession is very rich in molluscs: 140 species have been recorded (Mania, 1973). The mollusc fauna from the upper part of the travertine succession is characterised by the occurrence of *Helicigona banatica,* indicating warm and humid climatic conditions. The floral remains (also well represented in the travertine deposits) indicate a mixed oak forest with thermophilous Mediterranean and Atlantic species. Fishes, a herpetofauna, including *Emys orbicularis* (Böhme, 1989) and birds as well as a diverse mammalian fauna, have been collected from these travertine deposits. The mammalian fauna assemblage presented by Kahlke (1978) is dominated by *Cervus elaphus* (n = 108); *Bison priscus* is also well represented (n = 22). The other species occur with less than twenty specimens.

The uppermost part of the travertine sequence has yielded a small fauna with, among others, a porcupine, *Hystrix* cf. *vinogradovi* (Maul, 1994). The level is correlated with a late interglacial phase. In the Early Weichselian sequence, two levels with mammalian remains have been recorded; the lowermost is characterised by the occurrence of *Spermophilus citelloides*, the upper level by the presence of *Lagurus lagurus*.

The Eemian age of the main travertine deposits at Burgtonna is primarily based on the interglacial character of the floral and faunal assemblages from the deposits and the evolutionary stage of mammalian species (such as *Arvicola terrestris*). The correlation is supported by radiometric dates of 104–111 ± 7 ka (Brunnacker et al., 1983).

Stuttgart-Untertürkheim (Baden-Württemberg)

Several travertine outcrops occur in the area near Stuttgart. The outcrop at Stuttgart Bad Cannstatt, at the left bank of the Neckar valley, is known for its Middle Pleistocene fauna. The travertine of Stuttgart-Untertürkheim, on the right bank of the Neckar valley, has yielded a Late Pleistocene fauna correlated with the Eemian stage. The reader is referred for more detailed information to Wenzel (1996) and others.

The travertine sequence at Stuttgart-Untertürkheim is divided in a consolidated Lower Travertine and an unconsolidated Upper Travertine by a dark-coloured, humic layer, the so-called 'Steppennagerschicht'. The vertebrate fauna from the latter level is rich in species; the presence of, among others, *Ochotona pussila, Lagurus lagurus, Alactaga major, Mammuthus primigenius, Coelodonta antiquitatis* and *Rangifer tarandus* indicate a 'mammoth steppe' biotope for this level. Wenzel (1996) correlated the Steppennagerschicht with the early Weichselian Herning stadial; he correlated the Upper Travertine with the Brørup interstadial.

Only the Lower Travertine is of Eemian age; the fauna listed in Table 1 originates from the Lower Travertine deposits. The Lower Travertine fauna is rich in carnivores; dominant in the assemblage are the remains assigned to *Felis* sp. (n = 46) (Wenzel, 1996) (= *Felis sylvestris* as listed by Von Koenigswald & Heinrich, 1999). Species that are also well represented in the fauna are *Cervus elaphus* (n = 18), *Panthera leo spelaea* (n = 13) and *Vulpus vulpus* (n = 8). The Lower Travertine has also yielded a floral record; it indicates interglacial conditions (Schweigert, 1991).

The assumed Eemian age of the Lower Travertine is supported by the results of U-series dating (Grün et al., 1982). The three samples from the Lower Travertine gave ages of 133 +21/–17 ka, 106 +6/–6 ka

and 105 +9/–7 ka, respectively, whereas sample 4, taken from the base of the Upper Travertine (20 cm above the Steppennagerschicht) gave an age of 105 +4/–4 ka.

The Rhine valley and other sites

Distributed over northwestern and central Europe there are several other localities where fossil remains with an assumed Eemian age have been collected. A number of these sites are located in the valleys of the Rhine and its tributaries such as the IJssel (the Netherlands) where, at numerous places, sediments have been dredged up. Large numbers of fossils, in particular mammalian remains were also dredges. The bulk of the dredged sediments date from the Late Pleistocene and Holocene; hence, the majority of the mammalian remains are of Late Pleistocene or Holocene age. The mammalian record from these sites is composed of a combination of remains from domesticated animals and extinct species such as the woolly mammoth. These mixed assemblages are known from many gravel pits (Groß-Rohrheim, Eich and Leeheim) in the upper Rhine valley west of Heidelberg (Germany) and from pits along the IJssel near Zwolle (the Netherlands). The mammalian record from these sites shows the presence of species indicative of glacial conditions (such as *Mammathus primigenius, Coelodonta antiquitatis, Rangifer tarandus*), as well as species that inhabited the area under warmer/temperate conditions (such as *Palaeoloxodon antiquus, Stephanorhinus kirchbergensis, Hippopotamus amphibius, Bubalus murrensis)*. The former species are assigned to the Weichselian, whereas the latter group of species is dated as Eemian.

Although it is obvious from additional (palaeobotanical and geological) research that part of the dredged sediments and hence, most probably also part of the fossil remains, date from the Eemian, it is still unclear which part of the assemblage should be referred to the Eemian. Because of the ecological demands of the hippopotamus, *Hippopotamus amphibius*, and the water buffalo, *Bubalus murrensis*, which both cannot tolerate periods of severe or long-lasting frost, one may assume that both species date from the Eemian (Von Koenigswald, 1988; Van Kolfschoten, 1995). This is, however, less obvious for other species of the warm/temperate group. One cannot exclude that the remains of, for example, *Palaeoloxodon antiquus* and *Stephanorhinus kirchbergensis* exclusively date from the Eemian s.s. and not from the temperate Early Weichselian interstadials.

Another problem with the fossil assemblages from the sites along the Rhine is the fact that many of these assemblages also contain remains of Middle or even Early Pleistocene age. The sections in the Rhine valley show huge hiatuses in several places between Late Pleistocene sediments and those beneath. One cannot, therefore, exclude that part of the fossil record (including warm/temperate indicators) does not date from the Eemian interglacial. It is not accepted therefore to date the remains of the giant beaver, *Trogontherium cuvieri,* the small rhinoceros, *Stephanorhinus* sp. (= *Stephanorhinus* cf. *megarhinus* in Von Koenigswald, 1988), and *Alces latifrons* as Late Pleistocene or even Eemian, as suggested by Von Koenigswald & Menger (1997), Pfeiffer (1999) and Von Koenigswald & Heinrich (1999). The giant beaver and the small rhinoceros are, when collected from a clear stratigraphical context, only known from the Middle or Early Pleistocene. *Alces latifrons* is also known from several Middle Pleistocene localities (Bilshausen, Mosbach, Voigtstedt, to name a few), but its stratigraphical range might be larger if the assignment of the antler fragments from Taubach to *Alces latifrons postremus* is correct. This does not imply that the *A. latifrons* remains from the Rhine valley also date from the Late Pleistocene. They have been heavily mineralised, more than the remains from the same assemblage that were assigned to *Alces alces* by Pfeiffer (1999). This supports the assumption that the remains of *Alces latifrons* might also pre-date the Eemian.

It is obvious that it is not so easy to unravel the mixed, dredged assemblages from localities in the Rhine valley and to divide the list of species represented in the assemblages into stratigraphically natural units, and to filter the purely Eemian faunal elements. This also applies to other mixed assemblages, for instance those from the Maasvlakte near Rotterdam and the Eastern Scheldt estuary where part of the mammalian fossils might have an Eemian age.

There are also a number of localities in northwestern and central Europe where mammalian remains of assumed Eemian age have been collected from clear stratigraphical contexts. One of these sites is Scladina Cave near Sclayn (Belgium), where a level with, among other species, *Canis lupus, Vulpes vulpes, Alopex lagopus, Panthera (Leo) spelaea, Crocuta crocuta spelaea, Ursus arctos* (the dominant species), *Ursus spelaeus, Equus* sp., *Dama dama* and *Homo neanderthalensis* has been assigned to the last interglacial. The absolute dates confirm the early Late Pleistocene age, the dates varying from 100 ka to 127 +46/–32 ka (Bocherens et al., 1999). Palynological correlations suggest, however, that the level corresponds with the Early Weichselian Saint-Germain II interstadial (marine isotope substage 5a) (Bastin, 1992).

The localities Tönchesberg (Van Kolfschoten &

Roth, 1995) and Wallertheim (Conard et al., 1995) has also yielded fossil remains that have been dated as Eemian. It is obvious that part of the sequence dates from the Late Pleistocene, but the Eemian age of specific levels is, however, mainly based on the 'best fit' method. The mollusc associations from Wallertheim show similarities with the associations from the upper part of the last-interglacial sequence at Burgtonna, indicating that the lowermost mammalian find-layer at Wallertheim dates from the later part of the Eemian (Mania, unpubl.). The amount of data supporting the Eemian s.s. age is, however, restricted and an early Weichselian age cannot be entirely excluded. This leaves these faunas less applicable for the unambiguous determination of the Eemian mammalian fauna from central and western Europe.

Another locality with a mammalian fauna dated as Eemian is Steinheim an der Murr (Von Bloos et al., 1991; Von Koenigswald & Heinrich, 1999). The smaller vertebrate fauna comes from slope deposits and badger borrows. The fauna, mainly with voles but also – although rare – *Apodemus, Cricetus* and *Spermophilus citelloides*, does not indicate full interglacial conditions and points as a whole (including gastropods) to early Weichselian interstadial climatic conditions (Von Bloos et al., 1991). An Eemian age for the fauna has, however, been put forward because of the evolutionary stage of the *Arvicola* molars, despite the fact that the remains come from deposits stratigraphically above the 'Eemian' soil. According to Heinrich (in Von Bloos et al., 1991), the enamel differentiation of the molars from Steinheim is less advanced than that of the molars from the Stuttgart-Untertürkheim Eemian fauna. The differences are small: statistically too small to overrule the lithostratigraphical and ecological data. Furthermore, the evolution of the watervole, *Arvicola*, is not so straightforward (Van Kolfschoten, 1990). Because of the discrepancies in the age indications, it has also been decided not to include the Steinheim fauna in the analyses.

Discussion

Current knowledge of the Eemian mammalian fauna from the western and central part of continental Europe is based on the sites listed above: Lehringen, Gröbern, Grabschütz, Neumark-Nord, Rabutz, Schönfeld, Taubach, Burgtonna and Stuttgart-Untertürkheim. The correlation of these faunas with the Eemian, based on the lithostratigraphical position of the deposits (overlying Saalian till) or radiometric data, seems to be well-established. There is, however, as mentioned above, still an ongoing discussion about the age of a number of these faunas. Von Koenigswald & Heinrich (1999), among others, grouped faunas from Rhenen-Leccius de Ridder and Maastricht-Belvédère (the Netherlands) and Hunas, Weimar-Erhringsdorf (Germany) and assumed a pre-Eemian 'intra-Saalian' age for them. The faunas are characterised by the occurrence of *Arvicola terrestris* molars with an evolutionary stage roughly intermediate between that of the Middle Pleistocene *Arvicola terrestris cantianus* from the Reinsdorf interglacial deposits at Schöningen for example and the modern central European *Arvicola terrestris* populations. Von Koenigswald & Heinrich (1999) excluded an Eemian age for the faunas from Neumark-Nord and Grabschütz because of the occurrence of *Apodemus maastrichtiensis*. The first question, however, is whether all these 'intra-Saalian' faunas date from the same warm/temperate event.

The term 'intra-Saalian' is confusing. Mania (1997) used the term 'intra-Saalian' to indicate a warm/temperate interval post-dating the Drenthe tills and pre-dating the Warthe tills. In his concept, the Saalian begins with the Saalian I (Drenthe) ice advance; he referred to the interval between the Elsterian and the Saalian I as 'Holsteinian Complex' (Mania, 1997). Other authors, however, use the term 'Saalian' to indicate the time between the Holsteinian s.s. and the Eemian. 'Intra-Saalian' might, in this concept, also mean post-Holsteinian and pre-Saale I. The faunas from Rhenen-Leccius de Ridder and Wageningen-Fransche Kamp (Van Kolfschoten, 1990) also have an 'intra-Saalian' age, according to this concept; the sediments in which they were found have been pushed by the Saalian (Drenthe) ice sheet and hence pre-date the Drenthe glaciation. These faunas must be older than the fauna from Neumark-Nord, for example, collected from deposits on top of the Drenthe till. It is therefore assumed that the 'intra-Saalian' faunas are not contemporaneous and should be divided into a group of pre-Drenthe I faunas (e.g., Rhenen-Leccius de Ridder, Maastricht-Belvédère, Wageningen-Fransche Kamp, Hunas, Weimar-Erhringsdorf) and a group of 'Eemian' faunas (e.g., Neumark-Nord, Rabutz and Grabschütz). Theoretically these faunas could date from Mania's pre-Eemian, pre-Warthian 'intra-Saalian' interglacial, but there is no convincing evidence for such a warm/temperate phase (Turner, 2000 – this issue). Weighing all arguments the author assumes that they are Eemian faunas; a conclusion that implies that *Apodemus maastrichtiensis* was also extant during the Eemian stage.

Referring Neumark-Nord, Rabutz and Grabschütz to the Eemian does not imply that the author neglects the arguments proposed by Mania (1997) and Mai (1990 a,b,c). These authors point to differences be-

tween the mollusc associations and flora from these localities and the mollusc and flora data from the 'classical' Eemian sites Taubach and Burgtonna. Differences in associations do, however, not explicitly imply dating to different interglacial phases, i.e. intervals separated from each other in time by a glacial phase. One option might be that there were different episodes within the same interglacial or with geographical variation. Hardly anything is known currently about the faunal changes during the Eemian. Sequences with a good record of molluscs are known from, among other places, Burgtonna (Mania, 1973), but mammalian sequences from the Eemian showing the mammalian changes within the Eemian interglacial are so far poorly known. At Neumark-Nord, Gröbern and Grabschütz several fossiliferous layers were exposed, representing different episodes within the Eemian. A detailed picture of the faunal evolution is missing, however. We only have a general picture of the Eemian fauna of north-western and central Europe, based on the record from the localities mentioned above. The faunas date from the climatic optimum of the Eemian interglacial (Speleers, unpubl.).

Environmental conclusions

The ecological demands of the European pond tortoise, *Emys orbicularis,* the hippopotamus, *Hippopotamus amphibius,* and the water buffalo, *Bubalus murrensis*, present in the Eemian fauna, indicate a climate with relatively high summer temperatures (mean July temperature > 18 °C) and the absence of periods of severe or long-lasting winter frost (Van Kolfschoten, 1995). The mammalian fauna of central Europe – with several deer species as well as the wild boar (*Sus scrofa*), the straight-tusked elephant (*Palaeoloxodon antiquus*), the browser, *Stephanorhinus kirchbergensis*, and the dormouse, *Glis glis* – also indicate the presence of a forested environment. These species occurred together with species indicative of more open environment, such as *Cricetus cricetus*, *Equus* sp. (or *Equus taubachensis*), *Equus hydruntinus* and *Stephanorhinus hemitoechus.* In summary it can be stated that the mammalian record of Central Europe indicates a mosaic environment with an alternation of forested and more open vegetation: a picture that contradicts that of the palaeo-environmental reconstructions based on the palaeobotanical record (Roebroeks et al., 1992). Palaeobotanists assume an oceanic climate in western and central Europe during the climatic optimum, with uniform deciduous forest vegetation (Zagwijn, 1989). Local conditions might explain the discrepancy. The climate in the Toringian basin and the surrounding areas is, nowadays as well as in the past, more than the areas to the west or to the north of the basin influenced by the presence of mountains in the west/southwest of the basin (Kahlke, 1990). This might explain the presence of steppe dwellers in the faunas from the eastern part of Germany. There are, however, also steppe dwellers (*Stephanorhinus hemitoechus, Equus hydruntinus*) in the fauna from Stuttgart-Untertürkheim, indicating a mosaic environment in the area.

General conclusions

In summary, the knowledge of the mammalian fauna from the Eemian interglacial is based on a restricted number of faunas and is still far from complete. A detailed picture of the faunal evolution is unavailable. Only a general picture of the Eemian fauna of north-western and central Europe can be reconstructed based on the record of the climatic optimum of the Eemian interglacial. Taking into account that the interglacial represented only a very short episode in the earth history, the number of rather well-dated Eemian faunas is, however, remarkably large. The fauna is well-documented for the eastern part of Germany but the Eemian s.s. fossil record is poor in other areas. Despite this, geographical differences in faunal composition are apparent; *Hippopotamus* occurred in the Rhine valley together with the water buffalo (*Bubalus murrensis*); both species are absent in central Germany. In the future, investigations should be focused more on the faunal evolution within the Eemian. The results of these investigations will contribute to the debate on the stratigraphical position of the poorly dated faunas and to a better understanding of environmental changes, in the past as well as in the future.

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