

# Chapter 9

## Discontinuities in the Faunal Assemblages and Early Human Populations of Central and Western Europe During the Middle and Late Pleistocene

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**Abstract** The middle and late Pleistocene history of Central and Western Europe includes several intervals of faunal change involving both local extinction and immigration of new species from elsewhere. Substantial faunal turnovers correspond to times of climate change. For many species, Central and Western Europe was a peripheral part of their geographic range and thus an area of temporal occurrence. The evolution of these taxa can be traced to core areas elsewhere. An important question concerns the extent to which human populations were similarly affected by climate change and faunal turnover. The successive groups of humans that populated Central and Western Europe did not necessarily originate in the same core area, and different areas of origin may explain morphological differences distinguishing various human fossils known from the middle Pleistocene of Germany.

**Keywords** Pleistocene faunal exchange • Central Europe • Mauer • Bilzingsleben • Steinheim • Neanderthal

### Introduction

Central Europe north of the Alps is fairly rich in human fossils of middle and late Pleistocene age due to intensive research during the twentieth century. Most of the human remains do not come from proper archaeological excavations and their age is often uncertain. Nevertheless they have played an important role in the history of paleoanthropology. Several finds were formally named and thus represent the types for species or subspecies. Fossils from Central Europe represent different stages of human evolution, and the finds from Mauer, Bilzingsleben, Steinheim, Reilingen, and Weimar-Ehringsdorf have been interpreted as a more or less consistent evolutionary lineage from archaic humans

to pre-Neanderthals, and proto-Neanderthals leading to classical Neanderthals (Hublin 1990; Condemi 1998).

The mammalian fauna of the middle and late Pleistocene in Central Europe shows repeated alternation of an interglacial *Elephas* assemblage and a glacial *Mammuthus* assemblage. These faunal assemblages immigrated, but became extinct locally when ecological conditions were unfavorable. Multiple climatic oscillations mean that the same faunas reoccur and disappear repeatedly (Koenigswald 2006).

This paper raises the question of whether human populations in Central Europe followed a similar pattern of repeated immigration and disappearance. It is assumed that humans expanded their range from southern France or Spain repeatedly (Gamble et al. 2004). But the occurrence of Asian species in the European mammalian fauna during specific interglacial periods suggests the possibility that human populations migrated from other regions to Central Europe during the middle Pleistocene as well.

Detailed faunal lists were given in Koenigswald and Heinrich (1999). For the hominid fossils mostly the original names are used to ensure the correlation of the specimens to the type sites. The stratigraphic scheme given in Fig. 9.1 shall not camouflage the often neglected uncertainties and discrepancies still existing.








### Specific Geographic Conditions in Central and Western Europe

Central and Western Europe was pivotal in the elucidation of Pleistocene history. It was in this region, that the first traces of the great expansion of glaciers during the Pleistocene were recognized (Agassiz 1840; Torell 1875) and, later, that the alternation of glacial and interglacial periods was deduced from successive generations of moraines and boulder clays. In no other part of the world did this very complex sequence of events become as apparent (Geikie 1894; Keilhack 1899; Penck and Brückner 1901–1909).

Similarly, the fossil occurrences of mammals that live today in the Arctic, such as *Rangifer*, *Gulo*, and lemmings

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Geology		small mammal stratigraphy	significant immigrants	important faunal localities	Interglacial conditions	Supposed OIS
<b>Holocene</b>		<i>Arvicola terrestris</i> -faunas				<b>1</b>
<b>Late Pleistocene</b>	Weichselian					
	Eemian	<i>Arvicola cantianus-terrestris</i> faunas	<i>Elephas antiquus</i> <i>Hippopotamus</i> <i>Bubalus</i>	Lehringen Taubach		<b>5e</b>
<b>Middle Pleistocene</b>	Warthe Drente	late <i>Arvicola cantianus</i> faunas	<i>Elephas antiquus</i> <i>Bubalus</i>	W. Ehringsdorf Steinheim/Murr Schöningen Bilzingsleben		<b>?7</b>
	Dömnitz Hosteinian		<i>Elephas antiquus</i>			<b>?9 ?11</b>
	Elsterian	early <i>Arvicola cantianus</i> faunas	<i>Elephas antiquus</i> <i>Hippopotamus</i> <i>Arvicola</i>	Kärlich G Mosbach Mauer		
	Cromerian Complex		<i>Arvicola</i> <i>Mimomys</i> +			
Brunhes		<i>Mimomys savini</i> -faunas		Süssenbron Voigtstedt		
<b>Lower Pleistocene</b>	Matuyama	<i>Mimomys savini</i> -faunas with <i>M. pusillus</i>	<i>Hippopotamus</i>	Untermaßfeld		<b>&gt;19</b>

**Fig. 9.1** Stratigraphic scheme, indicating the supposed position of faunal localities and the various interglacial phases in Central Europe (From Koenigswald 2006)

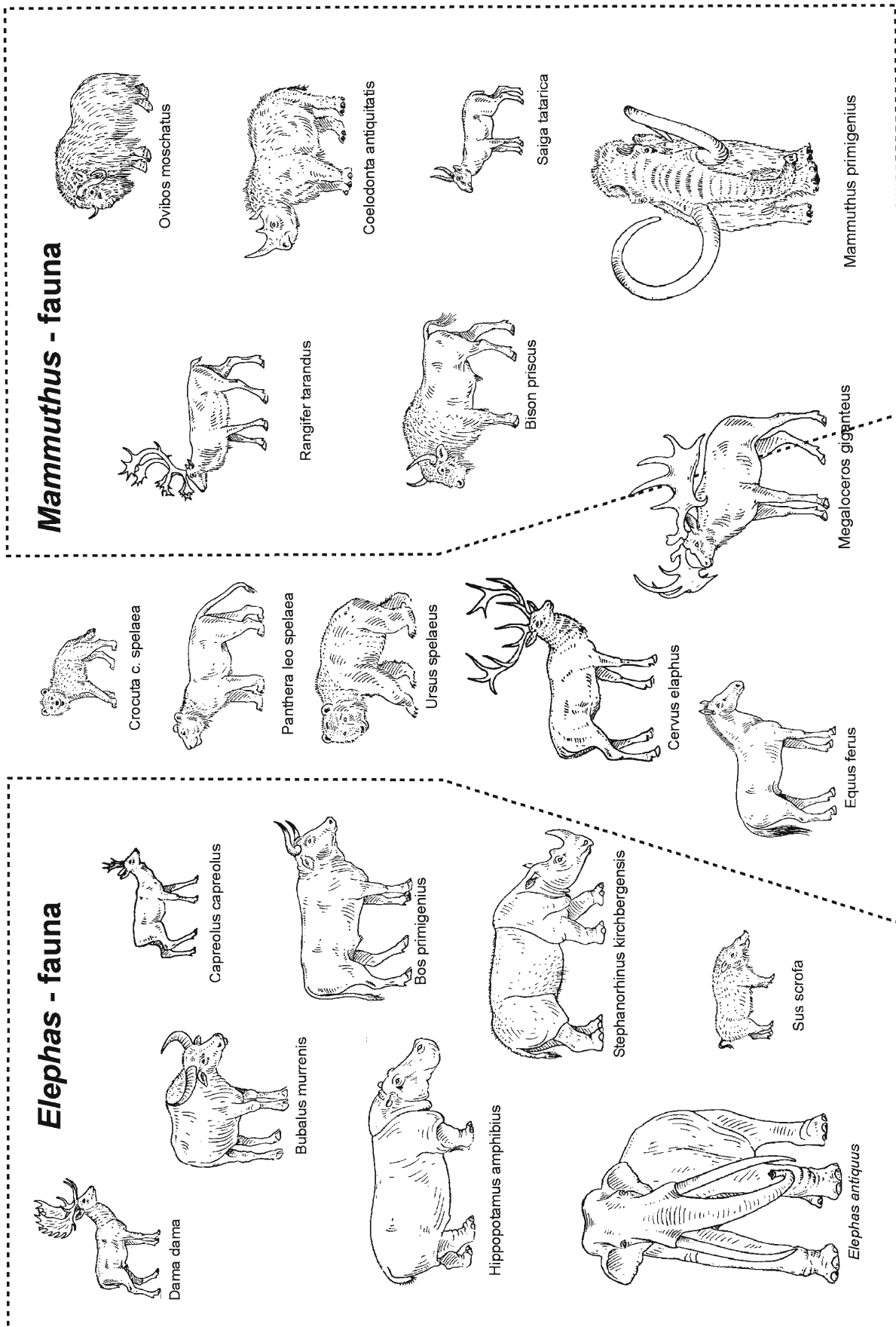
(*Lemmus* and *Dicrostonyx*), was recognized in the fossil record (Nehring 1880, 1890). Koken (1912), for example, when describing the Pleistocene faunas of Paleolithic sites in Germany, differentiated between glacial faunas characterized by *Mammuthus primigenius* and interglacial faunas characterized by *Elephas antiquus*.

In Western and Central Europe, faunas and floras can often be more readily attributed to a glacial or interglacial environment than to a specific age, since very similar faunal and floral assemblages appeared in all the glacial or all the interglacial faunal periods, respectively (Fig. 9.2). In the Pleistocene flora, studied in pollen profiles from lake deposits, the sequence of immigration of the various plant taxa is very characteristic for each interglacial (Litt 1994). In contrast, Pleistocene faunal localities reflect neither the sequence of immigration nor do they always enable successive interglacials to be distinguished.

The geography of Europe, specifically the orientation of the mountain ranges, is responsible for the great difference between glacial and interglacial floras and faunas. The Pyrenees and the Alps are both oriented from west to east and thus they form an ecological barrier between Central Europe and the Mediterranean region. They also buffer minor

climatic oscillations. Any influence from the Arctic is ameliorated in the Mediterranean region, and during times of glaciation minor climatic oscillations did not affect the glacial fauna in the north. Faunal turnovers occurred in Western and Central Europe only between glacial and interglacial periods. Glacials and interglacials differed not only in their mean annual temperatures, but even more so in the magnitude of annual temperature fluctuation and relative humidity. Glacial periods had a strong continental climate, while interglacials were characterized by a strong maritime influence. Changes in humidity were particularly important in catalyzing the drastic faunal changes between *Mammuthus* assemblages and *Elephas* assemblages.

The Pleistocene fauna of the Mediterranean is characterized by successive waves of faunal immigration (Azzaroli et al. 1982; Kotsakis 2006), but not by comparable faunal change between glacial and interglacial periods. In this respect Central and Western Europe differ very much from North America or most other regions of the world. The orientation of the mountain belts is most significant and may be the explanation for the difference. In North America the Rockies and Appalachians are oriented north-south and, in



**Fig. 9.2** The main components of the interglacial *Elephas* fauna and the glacial *Mammuthus* fauna. They occurred alternatively in Central and Western Europe

contrast to Europe, cold winds from the north may reach much farther south. The Great Plains between the two mountain ranges maintained a continental climate. In contrast to the climatic alternation in Europe between continental and maritime conditions, Siberia has always maintained a very dry and continental climate. In Siberia interglacial faunas hardly differ from glacial assemblages in the same area (Sher 2006). The vast area north of the Himalayan belt was continuously continental even as the Pleistocene climate changed. Hence, it is not surprising that faunas of the glacial and interglacial periods in Siberia and North America did not change to the same extent that they did in Western or Central Europe.

### Immigration and Local Extinction are the Pattern of Faunal Exchange in Western and Central Europe

*Mammuthus* assemblages characterizing glacial periods in Western and Central Europe immigrated from the northeast. In contrast, *Elephas* assemblages expanded their range from Mediterranean regions using the major river valleys of the Rhine and the Danube as immigration routes. The faunal exchange was very intensive, since only a few herbivores occurred in both assemblages. Carnivores were generally not as much affected. Following the onset of unfavorable climate conditions in Western and Central Europe, species that could not tolerate the climate disappeared. The term “emigration” is often used for this process, deduced from the idea that clever humans knew how to escape an unfavorable situation. However, for the fauna, such disappearances should more precisely be called a “local extinction” (Koenigswald 2003). The biological reaction to an unfavorable climate is reduction in the number of offspring. If unfavorable conditions last for several generations, this leads to extinction in a local area. Due to this repeating pattern of immigration and local extinction, Western and Central Europe was an area of “temporal occurrence”, or temporary occurrence, for most mammalian species (Koenigswald 2003). There are only a few genera among herbivores that occur in both glacial and interglacial faunas, e.g., *Ursus*, *Cervus*, and *Arvicola*. Nevertheless even in these genera it cannot be excluded that there was some replacement of populations, since subspecies are generally not recognizable in the fossil record. Central Europe and the northern part of Western Europe was a typical area of “temporal occurrence” (Fig. 9.3). Although some taxa like rhinos and elephants are represented by more derived forms in subsequent periods, their evolution seemingly took place in areas where the taxa were present continuously. Such areas are defined as “core areas,” and these are the areas from which the species migrated into Central Europe again.

Only in the core areas was there any evolutionary continuity. Nevertheless, even in the regions of temporal occurrence these newly evolved forms may have reappeared in each subsequent phase.

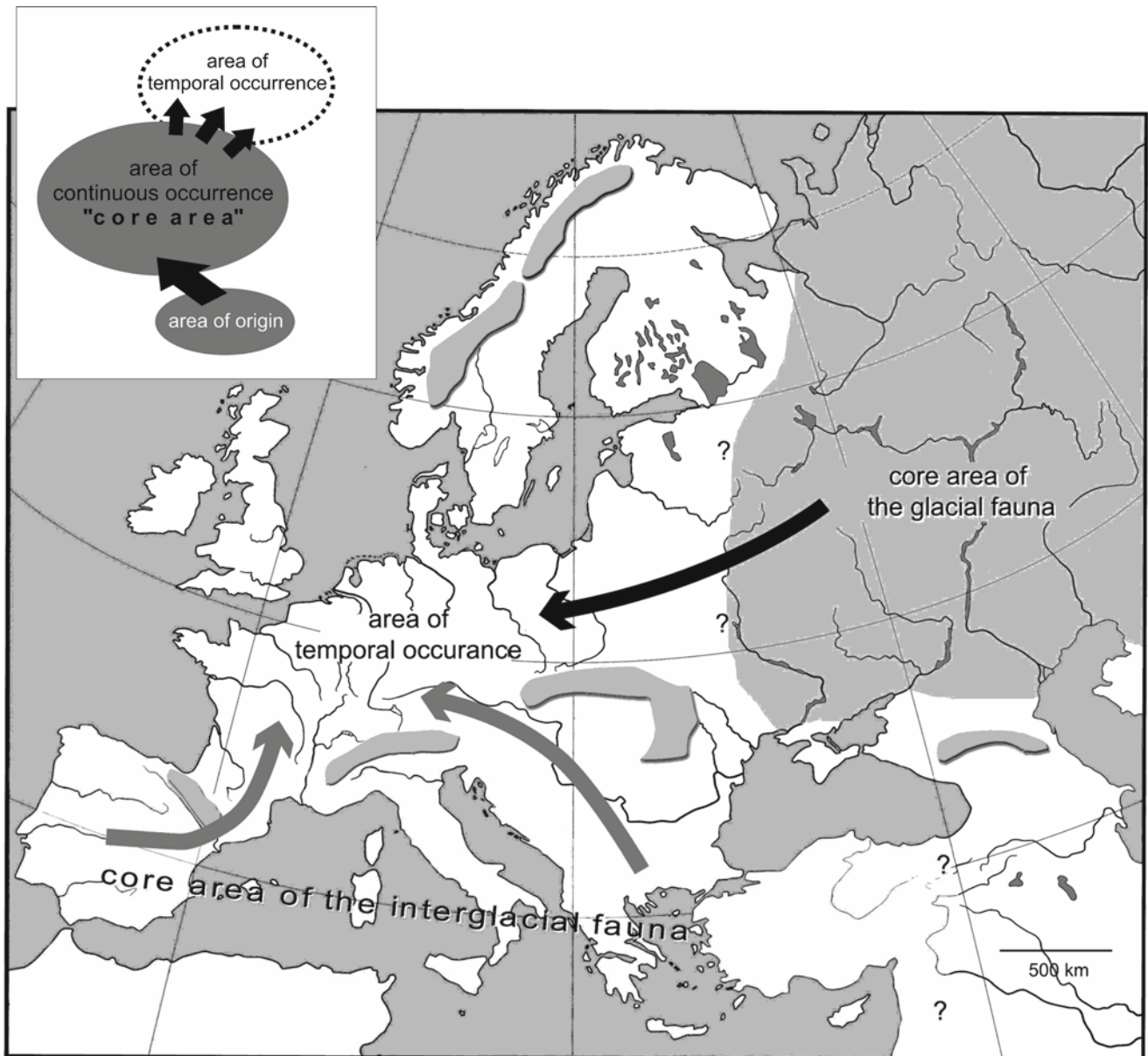
The extent to which human populations were involved in a similar pattern of repeated migration, like the mammalian fauna, remains an open question. Certainly human populations expanded their territories when conditions were favorable, but whether human populations suffered local extinctions, or rather were able to escape to more favorable areas can be questioned. In Central Europe a simple southward migration might have been stopped by the Alps. The disappearance of Vikings in Greenland is an historical example of local extinction of a once flourishing human population due to climatic changes.

In the early part of the middle Pleistocene, humans occurred in Central Europe only during interglacial periods, and thus with each warming a new immigration is probable. Only during the (late?) Saalian Complex did pre-Neanderthals coexist in Central Europe in the biome with *Mammuthus* fauna. During the Eemian, humans hunted game of the *Elephas* assemblage, while during the Weichselian humans, this time in the form of the classical Neanderthals, again lived alongside the *Mammuthus* assemblage. The fossil record shows the presence of humans during this interval of glacial-interglacial-glacial conditions, but not enough is known to indicate whether these populations were continuously present in areas north of the Alps, or whether different populations alternated in the region.

### Biostratigraphy of the Middle and Late Pleistocene in Central Europe

The multiple faunal exchanges in Western and Central Europe are characterized by a repeated immigration of taxa. Thus it is difficult to do any stratigraphy using first and last occurrence records or datums (FAD, LAD). The presence of taxa was not continuous, and some taxa were irregular in their reoccurrence. The time span of the middle and late Pleistocene was too short, compared to the Tertiary, for major evolutionary changes, and continuous evolution of certain forms can be expected only in the core areas.

The rodent *Arvicola*, a vole, is one of the few taxa present in Western and Central Europe throughout the middle and late Pleistocene, and it shows evolutionary changes that can be used as stratigraphic markers (Koenigswald and Heinrich 1999). A biostratigraphic framework based on *Mimomys* and *Arvicola* voles is summarized here. One species in particular, *Mimomys savini*, characterizes mammalian faunas at the beginning of the middle Pleistocene, which are found at Voigtstedt and Süssenborn in Thuringia, and the Upper



**Fig. 9.3** Central and Western Europe as an area of temporal occurrence for both, the glacial *Mammuthus* fauna and the interglacial *Elephas* fauna

Freshwater Bed of the Cromer Forest Bed Series in East Anglia. In this way, the *Mimomys savini* faunas correlate with part of the Cromerian complex.

During the Cromerian, *Mimomys savini* was replaced by *Arvicola cantianus* (Koenigswald 1973). This species was recently cited as *Arvicola mosbachensis*, a younger synonym (Maul et al. 2000). *Mimomys* differs in having rooted molars, while those of *Arvicola* are rootless. *Arvicola* most likely evolved from *Mimomys*, however, not in Central Europe but in the south, where it might have been present somewhat earlier. Stratigraphically, *Arvicola cantianus* occurs in Central Europe in the late Cromerian. Although *Arvicola* first appears with interglacial *Elephas antiquus*, this vole remains in

Central Europe even after the onset of cold climate conditions, and after the *Mammuthus* fauna immigrated. These faunas, known as “early *Arvicola cantianus* faunas,” are thought to have antedated the Elsterian. They show a greater diversity of insectivores and rodents than faunas after the Elsterian. Typical sites with early *Arvicola cantianus* faunas are Mauer, Mosbach II, and Kärlich G.

After the Elsterian, *Arvicola cantianus* remained an index fossil, but the diversity of other small mammals became reduced. “Late *Arvicola cantianus* faunas,” which range from the Elsterian to the Holsteinian and the Saalian complexes, occur in both glacial and interglacial phases. Within this time period, a change can be observed in the enamel thickness

of molar teeth of *Arvicola*, which is quantified as SDQ (for *Schmelzband-Differenzierungs-Quotient*; Heinrich 1982). This evolutionary trend can be used to some degree as a stratigraphic indicator. It is still not possible to correlate all faunal levels with the OIS [Oxygen isotope stages] because the position of the Elsterian is still unclear. According to Sarnthein et al. (1986) and Parfitt et al. (2005), the Anglian (=Elsterian) represents OIS 12 and Schreve (2001) correlates the Hoxnian with OIS 11 based on the supposed sequence of faunas and terraces in England. Stringer and Hublin (1999) discuss the Hoxnian as OIS 9 and the post-Anglian “Swancombe stage” as OIS 11. In Central Europe the Holsteinian is defined as the first post-Elsterian interglacial. The type locality of the Holsteinian was dated carefully and correlated with OIS 9 (Geyh and Müller 2005, 2006 but Scourse 2006; Nitychoruka et al. 2006). The possibility that two post-Elsterian interglacials show the same pollen signal was rejected by the geological evidences from the type region.

The stratigraphic positions of interglacials before or within the Saalian complex is problematic due to differing interpretations of the geology in the Elbe-Saale region. Mania and Thomae (2006) postulate four interglacial phases in the Holstein Complex before the Drenthe (first Saalian ice advance), and two additional ones before the Warthe (second Saalian ice advance). Litt et al. (2005) accept one interglacial phase, or at the most two interglacial phases, after the Holsteinian and before the Drenthe, but none between Drenthe and Warthe. Thus he correlates Drenthe and Warthe with OIS 6 (Litt 2006). The *Elephas* assemblages at the relevant sites are nearly identical. It is possible that the occurrence of *Bos primigenius* in Steinheim/Murr and at Schöningen indicates an age younger than Bilzingsleben II.

Faunas of the Eemian (OIS 5e) and the early Weichselian reflect a transition from *Arvicola cantianus* to *Arvicola terrestris*. *Arvicola terrestris* then continues from the Weichselian into the Holocene (OIS 1). The large mammals of the *Mammuthus* assemblage are thus very similar to those of the Saalian.

## Ecology and Biostratigraphy of German Localities with Human Remains

### Middle Pleistocene

Most sites of the middle and late Pleistocene in Germany that have yielded remains of archaic humans, pre-Neanderthals or classical Neanderthals, have also produced mammalian faunas that enable a solid assessment of the ecology and also facilitate biostratigraphic correlation.

The site of Mauer near Heidelberg, where the famous mandible, the holotype of *Homo heidelbergensis* was collected,

yielded a typical interglacial fauna (Schötensack 1908). The *Elephas* assemblage includes *Hippopotamus antiquus*, indicating a strong maritime influence with mild winters. Presence of both early *Arvicola cantianus* and *Stephanorhinus hundsheimensis* in this fauna shows that it preceded the Elsterian biostratigraphically.

The paleoecology of Bilzingsleben II was similar. Here remains of the robust “*Homo erectus bilzingslebenensis*” were found. The vegetation indicates full interglacial conditions, and the fauna represents a typical *Elephas* assemblage (Mania et al. 1997). However, compared with the early *Arvicola cantianus* faunas preceding the Elsterian, the diversity of small mammal faunas is reduced, especially that of insectivores and rodents. Thus Bilzingsleben II is regarded as an early stage of late *Arvicola cantianus* faunal zone (Koenigswald and Heinrich 1999). Geologically the site is located on Elsterian till and thus it is most likely Holsteinian in age. Expansion of the Elsterian ice sheet makes it unlikely that human populations survived in Central Europe. The small corridor between the Scandinavian ice shield and the mountain glaciers of the Alps was only a few hundred kilometers wide. It was most probably not favorable for big game, and it was definitely not favorable for the *Elephas* fauna. The interglacial fauna totally disappeared from Central Europe during the Elsterian, and then immigrated from the Mediterranean again when the climate ameliorated. Thus, most probably, the human population also re-immigrated with the interglacial fauna.

Two other sites bearing human remains and related to late *Arvicola cantianus* faunas are Steinheim/Murr and Weimar-Ehringsdorf, which represent interglacial conditions preceding the Eemian. The river deposits of Steinheim/Murr, where the delicate cranium of “*Homo steinheimensis*” was excavated, produced a very diverse interglacial *Elephas antiquus* assemblage. The interglacial fauna from Steinheim/Murr was traditionally referred to the Holsteinian (Adam 1954 a, b, 1966, 2003), but this was based on a now-rejected stratigraphic scheme that included only two interglacial periods (Holsteinian and Eemian) after the Elsterian. Steinheim/Murr is definitively older than Eemian and might belong to OIS 7. Thus between Bilzingsleben II and Steinheim, a cold phase is most probable, during which the *Elephas* faunal assemblage disappeared from Central Europe and was replaced by a *Mammuthus* fauna, which is present at a lower level at Steinheim/Murr.

The interglacial layer at Steinheim/Murr is of special interest because it seems that two bovids, *Bos primigenius* and *Bubalus murrensis* (Berckhemer, 1927), occur at this level for the first time in Central Europe (Fig. 9.4). Ecologically *Bubalus* indicates a warm climate with mild winters, i.e. a maritime influence. The origin of *Bubalus* is of great significance. It is an Asian genus and the closest relative of *Bubalus murrensis* in the extant fauna is *Bubalus arnee* from India. However, in



**Fig. 9.4** Fossils of the *Elephas* fauna. *Bubalus murrensis*, the Indian water buffalo, is an exotic immigrant from Asia. (a): Human cranium from the middle Pleistocene interglacial of Steinheim/Murr. (b): Partial cranium of *Bubalus murrensis* (the water buffalo, an exotic immigrant from Asia) from the same level as the carmium of “*Homo steinheimensis*”. (c) and (d): Two cranial parts of *Bubalus murrensis* from a later reoccurrence during the Eemian, found in sand deposits in the northern Rhineebene near Darmstadt. The triangular shape of the horn cores and the flattened front side are characteristic (c: Wolfskehlen [Felsbergmuseum, Beedenkirchen] and d: Geinsheim [Coll. F. Menger, Groß-Rohrheim]). (a): From Adam et al. 1995; b: photo by Hans Lumpe Stuttgart, c and d: photos by Georg Oleschinski, Bonn)

terms of morphology, Chinese species of *Bubalus* from the late middle Pleistocene are very close to *Bubalus murrensis* (Young 1936; Koenigswald 1986). Unfortunately the fossil record of *Bubalus* is very limited, and the full history of its dispersal is still unknown, but the presence of *Bubalus* shows that Asian immigrants are definitively present in the *Elephas* fauna of Steinheim II.

The *Homo* cranium from Steinheim is much more gracile than that of Bilzingsleben. Besides the discussed assumption that the cranium represents a female from same population as Bilzingsleben, it cannot be excluded that “*Homo steinheimensis*” immigrated at a younger interglacial together with Asian mammals. This might open the question of whether middle Pleistocene hominids always immigrated from the same core area, most probably from the southwest, or if morphological differences may indicate different areas of origin, including possibly an independent immigration from the east. Thus it seems problematic and premature to include “*Homo steinheimensis*” in *Homo heidelbergensis* (Johanson 1998). Such a synonymy may obscure obvious differences that have been known for a long time (Gieseler 1974; Ziegler 2006).

Weimar-Ehringsdorf is a travertine deposit of predominantly interglacial character (Kahlke 1974, 1975). Human remains and a rich *Elephas antiquus* fauna were excavated from the lower travertine, which is of particular interest here. This site was traditionally regarded as Eemian, but several lines of evidence indicate that the Weimar-Ehringsdorf fauna represents an older interglacial period. Some authors assume it represents an interglacial period within the Saalian complex, but according to Litt et al. (2005) there is no evidence for a full interglacial within the Saalian. Thus, most probably, Weimar-Ehringsdorf antedates the Saalian ice advances (Drenthe and Warthe). *Arvicola* is at an evolutionary stage that is intermediate between *Arvicola* from Bilzingsleben and *Arvicola* from typical Eemian sites such as Taubach and Burgtonna. Biostratigraphic correlation between these different interglacial sites is difficult because the typical *Elephas antiquus* assemblages of the late middle Pleistocene and Eemian are very similar. In the lower travertine, which produced the human remains, two Asian immigrants (*Cyanoonyx antiqua*, an otter, and *Ursus thibetanus*, a small bear) are remarkable (Heinrich and Fejfar 1988; Koenigswald and Heinrich 1999).

### The Saalian

Prior to the Saalian Complex in Central Europe, human remains or artifacts were found in interglacial environments only. But during Saalian time (OIS 6–8), the first indication was found that humans lived in Central Europe during cold periods as well.

Acheulean hand axes from Markleeberg are often cited as the oldest evidence that humans lived under glacial conditions in Central Europe (Baumann et al. 1983). The gravels at this site are thought to represent glacial conditions in the early Saalian complex. However, no faunal remains have been found directly associated with the tools. The Körbisdorf gravels at Markleeberg, which represent the main terrace of the early Saalian Complex, yielded the famous skeleton of *Mammuthus primigenius* from Pfännerhall (Töpfer 1957). But at other sites, the gravels produce significant amounts of wood remains, suggesting that they may represent other climatic conditions and not just typical glacial conditions. Thus, there is no clear-cut evidence regarding the ecology of these deposits.

The loess from Ochtendung has produced very good evidence that pre-Neanderthals were contemporary with a typical *Mammuthus primigenius* fauna. Human artifacts were excavated in association with *Rangifer*, *Coelodonta*, and *Mammuthus* remains (Bosinski et al. 1995). Nearby, at a site with similar conditions, a fragmentary human calvarium was discovered (Berg et al. 2000). Age dating is very good, since the sites are situated on top of small volcanic cones that erupted about 200,000 years ago. These sites are regarded as being about 170 ka and thus correspond to a late phase of the Saalian complex, most probably OIS 6. The Ochtendung calvarium represents the earliest well-dated evidence of humans coexisting with a *Mammuthus* assemblage in Central Europe.

### The Eemian

During the interglacial conditions of the Eemian, humans hunted the various mammals that made up the *Elephas* assemblage. Human remains are rare. The travertine of Taubach near Weimar (Kahlke 1977) is definitively younger than Weimar-Ehringsdorf and correlates with the Eemian. It produced a human molar. Two other sites, Gröbern near Leipzig (Mania et al. 1990), and Lehringen near Verden/Aller (Thieme and Veil 1985; Houben 2003) are to be mentioned here, although they did not yield human remains. Both sites are lake deposits with an extensive pollen record, and thus stratigraphic correlation to the Eemian is secure. These sites are significant because of the discovery of skeletons of *Elephas antiquus* together with artifacts. The elephant carcasses were butchered near the shore, but this does not necessarily imply that humans killed these animals (Koenigswald 2002).

In ecological reconstructions, late Pleistocene deposits of the Rhine River are of great interest, as they have produced both a *Mammuthus* fauna and the typical *Elephas antiquus* assemblage. Years of observations have shown that the glacial fauna comes from the upper part of the section, while thick trunks of black oak (*Quercus* sp.) characterize the lower



section with faunal remains from the last interglacial. In addition to typical taxa of the interglacial fauna, *Bubalus murrensis* and *Hippopotamus amphibius* occur in several Rhine sand pits (Koenigswald 1988, 2006). Their excellent preservation and frequency preclude the possibility of redeposition from older sediments. Correlation to the last interglacial is plausible, first because of the geological situation, and also because *Hippopotamus* occurs frequently on the British Isles during the Ispwichean, but not during the preceding interglacial period.

The occurrence of *Bubalus* and *Hippopotamus* in Rhine sand pits is very significant for reconstruction of the paleoecology (Fig. 9.4). According to the fossil flora, the mean annual temperature was only 2° or 3° higher than today. Thus, *Hippopotamus* and *Bubalus*, which live in subtropical regions today, do not indicate a paleoclimate that was much warmer than that of the present day. Extant animals can tolerate lower temperatures but stay in the water to escape from cold winds. This means mild winters but cooler summers. Thus a strong maritime influence on the climate can be postulated for the Rhine area for at least part of the Eemian. This maritime influence certainly tapered off towards the east; at least *Hippopotamus* did not occur farther to the east during the Eemian.

In one of the sandpits of the Rhine River at Reilingen, a human calvarium was discovered during commercial quarrying. Morphologically the calvarium has been attributed to very different evolutionary stages (Czarnetzki 1989; Adam 1989; Condemi 1996; Ziegler & Dean 1998). The Reilingen sandpit has produced both glacial and interglacial faunal elements including *Hippopotamus*. Since high groundwater levels continuously obscure the stratigraphic section, precise stratigraphic attribution of faunal remains is difficult. Löscher (1989) argued for an Eemian age, while Ziegler and Dean (1998) consider an older age.

## The Weichselian

It is assumed that the *Mammuthus primigenius* fauna immigrated into Central Europe at the beginning of the Weichselian and replaced the interglacial *Elephas antiquus* fauna. However, the palynological record shows several climatic oscillations at the beginning of the Weichselian. Unfortunately, the faunal record is not complete enough to identify exactly when the *Mammuthus primigenius* fauna did appear, nor does it reveal the sequence in which various species appeared. Different mammals undoubtedly expanded their ranges at slightly different times, according to their specific ecological requirements, but this has not been detected yet in the fossil record. The Weichselian *Mammuthus primigenius* fauna is very similar to that of the late Saalian, and while large mammals

cannot be used to differentiate between the two time intervals, the evolutionary stage of *Arvicola* may be helpful since most Weichselian sites show the typical *Arvicola terrestris*.

The *Mammuthus* faunal assemblage has no ecological equivalent in the extant mammalian fauna. Thus ecological reasons are most probably responsible for the extinction of many of the large mammals. The surviving species occupy quite different biotopes. One group lives in an arctic environment, mostly in the open tundra with lemmings, caribou, and muskoxen. Another group lives in Central Asia under very continental conditions: the Saiga antelope and various rodents are included here. However, neither the tundra nor the Central Asian mountain regions can be used as a model for glacial conditions in Central Europe.

The classical Neanderthal of the Weichselian in Central Europe coexisted with a *Mammuthus* assemblage and thus lived under glacial conditions. However, on this point, one has to realize that the *Mammuthus* assemblage represents a cold steppe environment and not necessarily the extreme conditions present during the maximal extent of the glaciers. During the last glacial maximum, it is known that the number of large mammals and the number of humans were greatly reduced, or both were possibly even absent. Thus the presence of human remains or artifacts preserved with remains of a *Mammuthus* assemblage does not prove that people occupied an area throughout an entire glacial period.

In the early and middle Weichselian, sites with Mousterian cultural remains, the culture related to the Neanderthal population, are well represented in Central Europe. Many of these sites produced a rich contemporaneous *Mammuthus primigenius* fauna. However, human remains are not very common.

In northern Germany, the fragmentary human carnium from Salzgitter-Lebenstedt was found together with a typical *Mammuthus primigenius* assemblage including *Rangifer tarandus* (Kleinschmidt 1953; Gaudzinski 1998). From the lake deposits of Königsau a complex stratigraphy of the early Weichselian with Mousterian artifacts was described (Mania and Toepfer 1973).

In southern Germany, several caves contain occupation sites with a Mousterian culture, which show the full diversity of the *Mammuthus primigenius* fauna. Typical sites include various caves near Blaubeuren, such as Sirgenstein (Koken 1912), or in the valley of the Lone near Ulm, such as Bockstein (Lehmann 1969), and Hohlenstein-Stadel (Gamble 1999). The latter produced a shaft of a human femur (Kunter and Wahl 1992). In the Weinberghöhlen near Neuburg/Donau, Mousterian levels (I-G'), as well as the later ones, provide the *Mammuthus primigenius* fauna (Koenigswald et al. 1974). Very important is the Sesselfelsgrötte in Franconia, which produced the fetus of a Neanderthal baby and two milk teeth (Rathgeber 2006). The fauna is not yet fully studied, but it is again a typical *Mammuthus* fauna. *Mammuthus* faunas lived

under glacial conditions, most likely with some permafrost, but most probably not during phases when Scandinavian and Alpine glaciers were at their maximal extent.

The cave site Hunas in Franconia yielded a human tooth attributed to *Homo neanderthalensis* (Alt et al. 2005). According to recent dates, the relevant level of cave sediments is from the early Weichselian (Rosendahl et al. 2006) and not older as supposed by previous authors (Heller 1983).

Minor climatic changes, such as interstadials, do not seem to change the *Mammuthus primigenius* assemblage very much. The occurrence of *Ovibos moschatus* might indicate restricted periods of especially dry and cold conditions, but such finds are not known from Mousterian layers. The lack of exact dating of fossils older than 50,000 years precludes any meaningful consideration of whether Neanderthals lived in the area continuously, during the cold stages of OIS 4, or not.

The fauna does not indicate any significant ecological change at the time when modern humans arrived in Central Europe. The *Mammuthus primigenius* fauna remained unaltered until the beginning of the last glacial maximum (LGM), as shown at the various Aurignacian and Gravettian sites. After the LGM (last glacial maximum), the glacial fauna is characterized once more by a highly continental climate, but the diversity of the fauna is significantly reduced. Thus, changes in the fauna happened distinctly later than the arrival of modern humans.

## Conclusions

In Central and Western Europe, the major climatic changes that took place during the middle and late Pleistocene led to repeated immigration of a *Mammuthus* assemblage and an *Elephas* assemblage. The immigration of these faunas occurred in alternations, and transitional stages are virtually unknown. It is more likely that each faunal assemblage underwent local extinction when a changed environment favored the other.

During most of the middle Pleistocene, humans occurred in Central Europe only during interglacial periods, and they seem to have immigrated, along with the interglacial *Elephas antiquus* fauna, from Mediterranean regions. Thus, based on the faunal record and ecological analysis, the series of human remains from Mauer, Bilzingsleben, Steinheim, Weimar-Ehringsdorf, and Neanderthal do not represent genetic continuity through continuous settlement but multiple re-immigrations.

Human immigrants did not necessarily originate from the same area each time, e.g., southern France or Spain, where continuous human occupation was probable. Immigration of humans from the southeast cannot be excluded during some interglacials, especially when eastern faunal elements occur too, as at Steinheim/Murr.

Even when humans were able to live under glacial conditions with a *Mammuthus* fauna, since the Saalian, it is not certain whether areas north of the Alps were continuously occupied. During the time of maximal extension of the Scandinavian and Alpine ice sheets, life north of the Alps was probably difficult, for fauna and for humans.

Despite its fairly rich fossil record, Central Europe probably played only a marginal role in the evolution of the Neanderthal lineage during the middle Pleistocene. The faunal history is very complex in this area, due to major changes in a sometimes harsh environment, and this led to repeated faunal replacements.

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