



Paleoecological and climatic implications of stable isotope results from late Pleistocene bone collagen, Ziegeleigrube Coenen, Germany



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ABSTRACT

Climatic and ecological conditions during Marine Oxygen Isotope Stage (MIS) 3 are complex and the impact of cold spells on the ecosystems in Central Europe still needs to be investigated thoroughly. Ziegeleigrube Coenen (ZC) is a late Pleistocene MIS 3 locality in the Lower Rhine Embayment of Germany, radiocarbon-dated to >34 ^{14}C ka BP. The site yielded a broad spectrum of mammal species. We investigated the carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$) and sulfur ($\delta^{34}\text{S}$) isotope signatures of bone collagen, since these are valuable tools in characterizing ecological niches, environmental conditions and aspects of climate and mobility. By comparison with pre- and post-Last Glacial Maximum (LGM) sites in Central Europe we show that ZC belongs in a cold event of MIS 3 and was climatically more similar to post-LGM sites than to pre-LGM sites. However, the trophic structure resembled that of typical pre-LGM sites in Belgium. This cold event in MIS 3 changed the bottom of the foodweb, but do not seem to have had a direct impact on the occurrence of the mammalian species and their ecological distribution. Apparently the (mega-) faunal community could adapt also to harsher environmental conditions during MIS 3.

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Introduction

The late Pleistocene in Central Europe is characterized by intensive climatic oscillations and corresponding changes in environmental conditions (Dansgaard et al., 1993; Svensson et al., 2008). Even during the period between 50 and 30 ka ago, significant environmental fluctuations have been demonstrated by different approaches (pollen analysis, lake sediments, cave speleothems, among others) (Roucoux et al., 2005; Bohncke et al., 2008; Van Meerbeeck et al., 2011). Despite these changes, assemblages of large mammals in NW and Central Europe are strikingly monotonous, including herbivores such as woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), horse (*Equus* sp.), large bovines (*Bos/Bison*), giant deer (*Megaloceros giganteus*) and reindeer (*Rangifer tarandus*), as well as carnivores such as cave hyena (*Crocuta spelaea*), cave lion (*Panthera spelaea*) and wolf (*Canis lupus*). This faunal assemblage is characteristic of the “mammoth-steppe fauna” and seems to be resilient to a certain degree of climatic changes. One of the most interesting aspects of the Pleistocene is the adaptation of these species to such abiotic processes.

Techniques such as stable isotope analysis of fossil bones or tooth microwear analysis can be due to gain dietary information for these large mammal species and to evaluate their ecological flexibility (e.g., Rivals et al., 2009; Bocherens et al., 2011a; Drucker et al., 2014).

Over the past decades, stable carbon and nitrogen isotope ratio values in bone collagen have been used successfully to decipher dietary preferences and niche partitioning among herbivorous and carnivorous species of the late Pleistocene in Europe (Fizet et al., 1995; Bocherens and Drucker, 2003; Bocherens et al., 2011a). The analysis of sulfur ($\delta^{34}\text{S}$) provides insights about the individual origin and mobility of the specimen (Drucker et al., 2012). The overall goal of the present study is to apply the carbon, nitrogen and sulfur isotope approach to finds from the recently reinvestigated paleontological site of Ziegeleigrube Coenen (Matzerath et al., 2012), and to present these results in the context of mammal ecology and their flexibility within Marine Oxygen Isotope Stage (MIS) 3 and MIS 2 at seven sites in Central Europe.

In order to generate paleoecological information on aspects such as soil activity, herbivore habitat characteristics, niche partitioning of the mammal assemblage and site integrity, it was necessary to compare the faunal spectrum of ZC to assemblages from sites of similar age located in neighboring regions (Fig. 1). Scladina Cave layer 1A (Bocherens et al., 1997) in Belgium was chosen, since it is approximately the same age as ZC and is located ~100 km away. This comparison will provide an example for the ecological variability within assemblages from the

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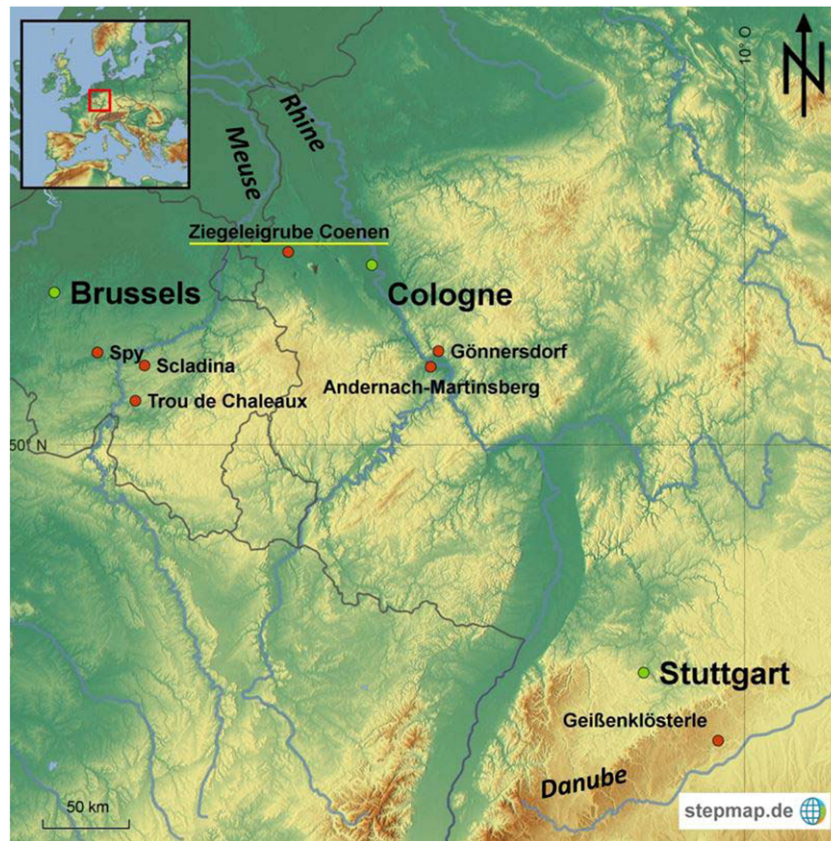


Figure 1. Location of the sites described in the paper (red dots).

late Pleistocene, since most of the terrestrial mammalian species mentioned here are represented at both sites.

The horse (*Equus* sp.) is the most common species at ZC, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values from these horses will be compared to existing isotope data of equids with secure stratigraphical, chronological and environmental contexts at other sites. These sites include the late glacial open-air settlements of Gönnersdorf and Andernach–Martinsberg, located in the Central Rhineland of Germany, and the late-glacial occupation level at the Trou de Chaleaux cave site in Belgium. Additional data are included from pre-LGM occupations at Spy, Scladina (Belgium) and Geißenklösterle (South Western Germany).

Principles of isotopic ecology of late Pleistocene fauna

Plant materials differ in the composition of their carbon, nitrogen and sulfur isotope values due to isotopic fractionation during chemical and physical processes, which depend on abiotic factors such as temperature, water availability, CO_2 -concentration, nitrogen availability, salinity and irradiance and the geological background. The plant isotopic signature is passed on to the animal isotopic signature and then through the whole trophic web up to the top predators (Minagawa and Wada, 1984). Carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$) and sulfur ($\delta^{34}\text{S}$) isotope values in terrestrial mammal bone collagen reflect an average of the isotopic composition of dietary protein consumed during the last few years of an individual's life (DeNiro and Epstein, 1978, 1981; Nehlich and Richards, 2009; Drucker et al., 2012).

In terrestrial ecosystems stable carbon isotopes are powerful tools in distinguishing between C3 or C4 photosynthesis pathway-based foodwebs (Farquhar et al., 1989; Cerling et al., 1998). In boreal and temperate ecosystems, where C4-plants are more or less absent, different values of $\delta^{13}\text{C}$ have been recorded for C3 plants, depending on whether the plants are growing in open or closed habitats. This phenomena is due to the canopy effect (Drucker et al., 2008). A vertical gradient in

the $\delta^{13}\text{C}$ values of forest plants, with higher $\delta^{13}\text{C}$ values at the top of the canopy and lower values at the bottom, is typical of the canopy effect (Dawson et al., 2002; Drucker et al., 2008). However, it should be noted that a significant degree of forest closure is necessary to trigger detectable depletion in the $\delta^{13}\text{C}$ values of understory plants. Furthermore, a minor enrichment in $\delta^{13}\text{C}$ values can be observed through the trophic web. Some authors (Bocherens and Drucker, 2003) suggest a shift of 0.8 to 1.3‰ between herbivores and carnivores.

^{15}N isotope enrichment of around 3–5‰ occurs at every trophic level, providing an instrument to reconstruct different trophic levels within the same ecosystem at a given place and time (DeNiro and Epstein, 1981; Ambrose, 1990; Bocherens and Drucker, 2003). In general $\delta^{15}\text{N}$ values also underlying climatic conditions such as temperature and humidity (Heaton et al., 1986). Soil and plant $\delta^{15}\text{N}$ values systematically decrease with increasing mean annual precipitation (MAP) and decreasing mean annual temperature (MAT) (Amundson et al., 2003). Several studies have shown that some excursion of the baseline $\delta^{15}\text{N}$ values did take place in the late Pleistocene, shifting the whole terrestrial foodweb (e.g., Fizet et al., 1995; Drucker et al., 2003; Richards and Hedges, 2003; Stevens and Hedges, 2004; Fox-Dobbs et al., 2008; Stevens et al., 2008; Bocherens et al., 2014; Stevens et al., 2014).

Sulfur stable isotope values ($\delta^{34}\text{S}$) can be used to distinguish between marine and terrestrial resource exploitation (terrestrial animals usually have $\delta^{34}\text{S}$ values around 5–10‰ while marine organisms have a relatively constant $\delta^{34}\text{S}$ value of 20‰) and as an indicator for freshwater resource consumption (range between -22 and $+22$ ‰) (Peterson and Fry, 1987). In purely terrestrial contexts, they are also useful as indicators of a geographical/geological origin (Drucker et al., 2012; Nehlich, 2015). The majority of the sulfur is taken up through the roots as sulfate, which originates either from the bedrock or is deposited by rain. Plants receive the majority of their sulfur through their roots as sulfate, which is derived from the weathering of local geological formations. Therefore sulfur isotope analysis can be used analogous to,

e.g., strontium isotopes as a geographical/geological indicator (Nehlich, 2015; Richards et al., 2003).

Material

Between 2009 and 2014 the paleontological assemblage from the loess site “Ziegeleigrube Coenen” (ZC), district of Düren, province Nordrhein–Westfalen in Germany, has been undergoing reinvestigation (Matzerath et al., 2012; Matzerath et al., 2014). In this paper we present 29 isotope values from ZC and discuss their ecological and climatic implications in the context of other pre- and post-LGM sites.

The faunal remains from the ZC were collected intermittently during 1964, 1967 and 1969 and consequently the assemblage is not complete (Matzerath et al., 2012). The paleontological remains consist of seven species of megafauna (2013): *Equus* sp., *Bos/Bison*, *Coelodonta antiquitatis*, *Megaloceros giganteus*, *Mammuthus primigenius*, *Crocota spelaea* and *Panthera spelaea* (Table 1). The material was stored and cataloged at the Museum Zitadelle Jülich. Here we use sample numbers according to the inventory numbers of the museum, except that we replaced “1964-” by “ZC-” (Tables 2 and 3). Earlier AMS radiocarbon analysis (Matzerath et al., 2012) placed ZC in MIS 3, with ages falling between 34 and 43 ¹⁴C ka BP. Two additional ages were beyond the limit of the radiocarbon method (Table 2).

Apart from the faunal remains, Hartwig Löhr also described two stone artifacts (now missing) from this site in 1969. With the only other trace of human activity being two bones displaying modifications possibly produced during marrow procurement (horse, *Equus* sp., ZC-101 and large bovid, *Bos/Bison*, ZC-95; Matzerath et al., 2012, 2014) the site cannot be classified unequivocally as “archeological.”

The original find horizon was removed during intense quarrying activities. However, Matzerath et al. (2014) were able to reconstruct the sequence by comparing profile drawings sketched by W. Krieger, H. Löhr and J. Schalich in 1964 and 1969 with a section opened 100 m to the east of the place where the faunal remains have been found in the layer (Matzerath et al., 2014). The sediment in which the faunal remains were embedded was stratified in a sequence of loess deposits some 5.50 m below the surface. The remains had been deposited in the gravel and sand infill of a small channel, some 30 cm deep (Matzerath et al., 2014). Processes of erosion and accumulation characterized the deposit and the channel had probably cut through different sediment units in the course of its formation, resulting in a channel fill comprising mixed materials from maybe more than one stratigraphic layer. This mixing could explain the range in radiocarbon ages, discussed in the Discussion section below.

Methods: bone collagen extraction and isotopic analysis

Bone pieces between 200 mg and 350 mg were cut with a diamond-tipped cutting wheel set on a Dremmel rotating tool. Although care was taken to select untreated specimens, two of the bone samples, ZC-35 and ZC-91, have possibly been conserved with linseed oil (Matzerath et al., 2014). Collagen was extracted from 24 samples by the Biogeology

working group in Tübingen University. Five additional collagen samples were extracted at the Center for Isotope Research, Groningen University, and sent to Tübingen for isotopic analysis. All stable isotope analyses were performed in the Department of Geosciences in Tübingen University following standard methods (Bocherens et al., 2011a,b). The outer bone surfaces of all samples were mechanically abraded, the bone pieces were washed twice in an ultrasonic bath in acetone and several times with distilled water, then dried and powdered to a homogeneous sample with a particle size less than 0.7 mm.

A preliminary determination of the whole bone nitrogen (N) content was performed following Iacumin et al. (1996, 1997) and Bocherens et al. (2005) to characterize the potential collagen preservation. Fresh bone contains around 4% nitrogen (e.g., Bocherens et al., 1991). The collagen extraction protocol was performed following a method modified from Longin (1971) as described by Bocherens et al. (1997). Some 250 mg of the bone powder was decalcified in 1 M HCl during 20 min at around 20°C and filtered through a 5 µm filter. The amount of bone powder depended on the nitrogen content of the bone, which approximately reflects the collagen yield. The residue was soaked in 0.125 M NaOH for 20 h at around 20°C. Afterwards the rinsed residue was heated in a closed container at 100°C for 17 h in a HCl solution with pH 2 until the collagen gelatinized. After filtration through a 5 µm filter, the liquid containing the gelatin was freeze-dried. The yield was calculated and expressed relative to the bone weight in mg g⁻¹ (Bocherens et al., 1997). Elemental analysis (C_{coll}, N_{coll}, S_{coll}) was conducted at the Department of Geosciences at the University of Tübingen using an NC2500 CHN-element analyzer coupled to a Thermo Quest Delta + XL mass spectrometer. The chemical preservation of the collagen is expressed by the C_{coll}/N_{coll} atomic ratio (Table 2). A C:N atomic ratio of between 2.9 and 3.6 (DeNiro, 1985) and a nitrogen percentage of collagen (N_{coll}) above 5% (Ambrose, 1990) are considered to indicate well preserved collagen. The standard for δ¹³C is the internationally defined marine carbonate (V-PDB). The standard for δ¹⁵N is the atmosphere (AIR). Analytical error based on laboratory standards is ± 0.1‰ for δ¹³C values and ± 0.2‰ for δ¹⁵N. Samples were calibrated to δ³⁴S values relative to international standards NBS 123, NBS 127, IAEA-S-1 and IAEA-S-3. The reproducibility is ± 0.4‰ for δ³⁴S measurements, and the error on amount of S measurement is 5%. Only δ³⁴S values of samples for which the atomic C/S_{coll} and N/S_{coll} ratios were in the range of 300 to 900 and 100 to 300, respectively, were retained (Nehlich and Richards, 2009; Bocherens et al., 2011b; Nehlich, 2015). In modern mammals, the collagen sulfur content was found to vary from 0.14 to 0.33% (Bocherens et al., 2011b), which generally fits the theoretical range of 0.14 to 0.29% based on DNA and amino acid sequence (Nehlich and Richards, 2009). This study presents only δ³⁴S values derived from samples with a sulfur content in collagen between 0.13 and 0.24% (Table 3). Comparable methods of collagen extraction were applied to bone samples at all the other sites discussed in this paper.

Results

The isotopic results are summarized in Tables 2 and 3. Collagen was successfully extracted for isotope analysis from all of the ZC bone specimens. The atomic C/N ratios for the extracted collagen ranged from 3.2 to 3.5 and none of the %N in collagen is lower than 11%, indicating that all of the extracted collagen was well-preserved.

The δ¹³C values obtained for the herbivores ranged between -22.1‰ for mammoth (ZC-140) and -20.3‰ for *Bos/Bison* (ZC-45) and woolly rhinoceros (ZC-89). The average δ¹³C values for the herbivores was -21.0‰ (n = 26; s.d. 0.43‰). The δ¹³C values for the carnivores ranged from -20.4‰ for hyena (ZC-91) and -19.1‰ for cave lion (ZC-48). The average δ¹³C values for the carnivores was -19.9‰ (n = 3; s.d. 0.7‰). Cave lion (ZC-48) produced the highest δ¹³C values (-19.1‰) of the whole fauna, while the lowest value was yielded by mammoth with -22.1‰.

Table 1
Faunal remains from Ziegeleigrube Coenen.

Faunal remains	NISP (number of individual specimens)	MNI (minimum number of individuals)
<i>Equus</i> sp.	78	5
<i>Bos/Bison</i>	9	1
<i>Coelodonta antiquitatis</i>	5	1
<i>Megaloceros giganteus</i>	4	1
<i>Mammuthus primigenius</i>	2 (3?)	1
<i>Crocota spelaea</i>	2	2
<i>Panthera spelaea</i>	1	1
Not defined	6	-
Total	107	11

Table 2
Ziegeleigrube Coenen.

Species	Site code	Element	N [%]-bone	%C _{coll}	%N _{coll}	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C:N _{coll}	AMS age (¹⁴ C yr BP) ^a	AMS-code ^a
Coenen <i>Equus</i> sp.	ZC-34	Metatarsus III. right	2.9	41.2	14.4	−21.1	1.9	3.3		
Coenen <i>Equus</i> sp.	ZC-35	Metatarsus III. right	2.7	40.0	14.1	−21.5	2.6	3.3		
Coenen <i>Equus</i> sp.	ZC-38	Metatarsus III. right	1.3	36.0	12.6	−21.3	2.7	3.3		
Coenen <i>Equus</i> sp.	ZC-40	Metatarsus III. right	2.0	38.5	13.6	−21.3	2.5	3.3		
Coenen <i>Equus</i> sp.	ZC-55	Tibia. right	2.3	40.2	14.0	−21.2	1.9	3.3		
Coenen <i>Equus</i> sp.	ZC-63	Tibia. right	2.9	37.5	13.2	−20.9	4.1	3.3		
Coenen <i>Equus</i> sp.	ZC-94	Tibia. right	2.0	38.2	13.2	−21.4	2.3	3.4		
Coenen <i>Equus</i> sp.	ZC-142	Tibia. left	n.a.	43.5	15.1	−21.0	5.8	3.4	42,340 + 500/− 440	GrA-53423
Coenen <i>Equus</i> sp.	ZC-98	Tibia. right	1.6	37.3	13.0	−21.2	1.7	3.3		
Coenen <i>Equus</i> sp.	ZC-119	Tibia. right	2.8	40.6	14.2	−20.9	3.3	3.3		
Coenen <i>Equus</i> sp.	ZC-124	Metatarsus III. right	3.1	40.9	14.3	−21.4	3.1	3.3		
Coenen <i>Equus</i> sp.	ZC-143	Tibia. left	1.1	34.2	11.9	−21.0	5.4	3.3		
Coenen <i>Equus</i> sp.	ZC-101	Radius. right	n.a.	44.2	15.4	−21.3	2.0	3.3	>45,000	GrA-53420
<i>Crocota spelaea</i>	ZC-41	Radius	3.5	38.5	13.7	−20.1	7.2	3.3		
<i>Crocota spelaea</i>	ZC-91	Mandibula	3.7	42.2	15.3	−20.4	8.7	3.2	35,990 + 410/− 390	KIA-44873
<i>Panthera spelaea</i>	ZC-48	Humerus. left	1.5	40.4	14.1	−19.1	8.8	3.3	38,040 + 500/− 470	KIA-44361
Bos/Bison	ZC-95	Radiocubitus. right	n.a.	42.4	14.8	−20.5	5.1	3.3	>45,000	GrA-53421
Bos/Bison	ZC-45	Humerus. right	2.0	40.6	14.2	−20.3	2.8	3.3		
Bos/Bison	ZC-79	Astragalus. left	2.8	40.2	14.1	−21.0	3.6	3.3		
Bos/Bison	ZC-78	Femur. left	2.2	43.5	15.0	−20.5	6.8	3.4	34,190 + 330/− 320	KIA-44874
Bos/Bison	ZC-141	Radius. right	1.6	38.4	13.3	−20.6	3.3	3.4	42,140 + 750/− 680	KIA-44872
<i>Megaloceros giganteus</i>	ZC-86	Pelvis. left	2.7	39.1	13.5	−20.8	3.8	3.4		
<i>Megaloceros giganteus</i>	ZC-69	Mandibula	2.1	37.0	12.8	−20.6	4.7	3.4		
<i>Megaloceros giganteus</i>	ZC-88	Mandibula	n.a.	46.4	16.0	−20.5	4.6	3.4	43,150 + 550/− 470	GrA-53422
<i>Coelodonta antiquitatis</i>	ZC-82	Radius. left	1.9	40.7	14.0	−20.9	2.8	3.4		
<i>Coelodonta antiquitatis</i>	ZC-89	Humerus. right	0.6	33.9	11.6	−20.3	4.2	3.4		
<i>Coelodonta antiquitatis</i>	ZC-92	Tibia. left	0.9	32.9	11.1	−20.6	4.2	3.5		
<i>Coelodonta antiquitatis</i>	ZC-144	Tibia. right	1.9	39.6	13.7	−20.6	2.2	3.4		
<i>Mammuthus primigenius</i>	ZC-140	Long bone	n.a.	43.4	15.3	−22.1	5.9	3.3	41,700 + 490/− 420	GrA-53419

Acronym "Coll": values measured on collagen

Specimen numbers correspond to museum numbers, year 1964 is replaced through ZC: e.g., museum number 1964-34 is here ZC-34.

^a Radiocarbon data are from Matzerath et al. (2012).

The δ¹⁵N values for herbivores ranged between 1.7‰ for horse (ZC-98) and 6.8‰ for *Bos/Bison* (ZC-78) and the average δ¹⁵N were 3.6‰ (n = 26; s.d. 1.4‰). The δ¹⁵N values of the carnivores ranged between a minimum of 7.2‰ (ZC-41) for hyena and a maximum of 8.8‰ (ZC-48) for cave lion. The average δ¹⁵N value for carnivores was 8.3‰ (n = 3; s.d. 0.9‰). At ZC there are no shifts in δ¹⁵N values in correspondence with the radiocarbon age.

The horse (*Equus* sp.) is of special interest since it is the most common species in ZC (NISP = 78; MNI = 5). Horse δ¹⁵N values ranged from 1.7‰ (ZC-98) to 5.8‰ (ZC-142) with an average of 3‰ and a standard deviation of 1.3‰ (n = 13). Two samples are conspicuously high in value, samples ZC-142 and ZC-143 with δ¹⁵N values of 5.8‰ and 5.4‰, respectively. These samples were actually taken at different places on the same bone/individual. If we exclude this individual (samples ZC-

142 and ZC-143), the average δ¹⁵N horse value is 2.5‰ and the standard deviation is only 0.7‰ (n = 11).

The large variation in the δ¹⁵N values from the hyena samples (ZC-41 and ZC-91) is an unequivocal indication we are dealing here with bones from two animals, since the difference (1.5‰) is too great for variation within one individual. Trophic enrichment from one level to another has also been detected at ZC: carnivorous species are enriched in δ¹³C by about 1.5‰, and in δ¹⁵N by about 4.5‰, in comparison to herbivorous species (Table 2).

We were able to obtain 14 δ³⁴S values from bones representing five horses, two individuals of hyena, one cave lion and two specimens of *Bos/Bison*, giant deer and rhinoceroses respectively, that were consistent with the chemical conditions mentioned above. The values ranged from 1.1‰ for one of the samples from horse (ZC-63) up to 6.6‰ for the cave lion sample (ZC-48). The total values have an average of 3.6‰ and a standard deviation of 1.4‰.

Discussion

Previous radiocarbon ages

AMS radiocarbon analyses were earlier performed on collagen extracted from nine samples from the Ziegeleigrube Coenen site (Matzerath et al., 2012). Those nine uncalibrated ¹⁴C ages are given in Table 2. Analyses were done at two laboratories, in Kiel (KIA) and Groningen (GrA). The ¹⁴C ages likely place ZC in MIS 3, with seven heterogeneous uncalibrated ages between 34,190 + 330/− 320 ¹⁴C yr BP (KIA-44874) and 43,150 + 550/− 470 ¹⁴C yr BP (GrA-53422). Two additional ages were beyond the limit of the radiocarbon method, both being older than 45,000 ¹⁴C yr BP (GrA-53420 and GrA-53421).

Radiocarbon ages in this time-range are commonly imprecise and are also extremely sensitive to even very small amounts of contamination by modern carbon (e.g., Wood et al., 2010). Currently an accurate dating of the site has not been achieved and, for this reason, ZC has

Table 3
Ziegeleigrube Coenen δ³⁴S values.
Source: this work.

Species	Site code	S _{coll} (‰)	C:S _{coll}	N:S _{coll}	δ ³⁴ S _{coll} (‰)
Coenen <i>Equus</i> sp.	ZC-34	0.16	728.9	218.3	3.0
Coenen <i>Equus</i> sp.	ZC-38	0.23	444.0	133.3	4.9
Coenen <i>Equus</i> sp.	ZC-40	0.17	641.4	193.7	2.8
Coenen <i>Equus</i> sp.	ZC-55	0.17	669.7	200.4	3.6
Coenen <i>Equus</i> sp.	ZC-63	0.17	625.0	187.9	1.1
<i>Crocota spelaea</i>	ZC-41	0.22	496.4	150.9	2.7
<i>Crocota spelaea</i>	ZC-91	0.15	797.0	247.8	3.3
<i>Panthera spelaea</i>	ZC-48	0.21	544.8	163.6	6.6
Bos/Bison	ZC-45	0.17	677.2	203.2	3.1
Bos/Bison	ZC-79	0.20	570.0	170.9	4.7
<i>Megaloceros giganteus</i>	ZC-86	0.20	553.2	164.1	4.9
<i>Megaloceros giganteus</i>	ZC-69	0.18	581.9	172.8	3.6
<i>Coelodonta antiquitatis</i>	ZC-82	0.15	768.7	226.5	2.7
<i>Coelodonta antiquitatis</i>	ZC-144	0.13	862.5	256.6	2.8

Acronym "Coll": values measured on collagen.

been included in an ongoing comparison of ^{14}C datings between the laboratories in Kiel (KIA), Groningen (GrA) and Oxford (ORAU).

Since all the younger ages from ZC are from the Kiel laboratory and the quality of the Kiel-collagen has not been controlled in the chemical sense, it seems possible that all the samples may be older than 45 ^{14}C ka BP. This scenario is supported by the limited variation in isotopic values for the species (Fig. 2). On the basis of the radiocarbon ages alone the fauna could not be confidently associated with either a warmer (interstadial) or a cooler (stadial) phase within MIS 3.

Site integrity of Ziegeleigrube Coenen: implications from isotopic results

It is necessary to consider the geographical origin of the different specimens when examining site integrity. A common local origin would indicate homogeneity of the assemblage and, in order to detect this, the sulfur isotopic composition of the collagen was analyzed. A clear separation in sulfur isotopic values would be present if the species derive from different regional/geological backgrounds. This is not the case at ZC, and the sulfur isotopic values are relatively homogenous (sd. 1.4‰) in contrast to studies with values from different sites from the Jura Mountains (Drucker et al., 2012). It is worth mentioning that there is no linear correlation of the nitrogen isotopic values and the sulfur isotopic composition ($R^2 = 0.0992$).

During MIS 3, short-term climatic fluctuations (Heinrich events) (Svensson et al., 2008) may have had a marked impact on the isotopic composition of soils and plants. In fact, previous work has documented shifts in the $\delta^{15}\text{N}$ value of whole ecosystems during this time range, at least in Southwestern France (Bocherens et al., 2014). At ZC there are no shifts in $\delta^{15}\text{N}$ values in correspondence with the radiocarbon dates, which implies a common ecological background for the remains.

Ecological implications

The faunal assemblage of ZC was compared with the fauna from Scladina Cave layer 1A in order to obtain additional details about the ecosystem. The complex 1A has been dated to between 43,150 + 950/– 700 ^{14}C yr BP (GrA-32581) and 37,300 + 370/– 320 ^{14}C yr BP

(GrA-32633) (Bonjean et al., 2009; Pirson et al., 2012) and faunal composition at both sites is very similar (Figs. 2 and 3) (Bocherens et al., 1997).

A comparison of all $\delta^{15}\text{N}$ bone collagen values from ZC and Scladina layer 1A (Bocherens et al., 1997) demonstrated that although the relative isotopic position for each species was similar at both sites, the absolute values are around 3‰ higher for herbivores such as mammoth (*M. primigenius*), horse (*Equus* sp.) and woolly rhinoceros (*C. antiquitatis*) at Scladina (Fig. 2). An exception is the giant deer (*M. giganteus*) which has an average of 4.0‰ at Scladina and 4.4‰ at ZC. A similar trend can be observed for the carnivores. The average $\delta^{15}\text{N}$ value of the two hyenas (*C. spelaea*) from ZC is 1.3‰ lower than the specimens from Scladina. A comparable pattern was observed for the felids, where the ZC sample is around 2.8‰ lower in $\delta^{15}\text{N}$ than the one from Scladina. In combination with the $\delta^{13}\text{C}$ results, this indicates specific niche which is similar for the hyenas and felids at both sites. The ecological niche of hyena and cave lion are clearly separated. This affiliated to different hunting strategies of both species and observed elsewhere (e.g., Bocherens, 2015). If one of these species produced clearly different relative values, this would indicate separate ecological niches or at least a certain level of ecological stress for that particular species (Drucker et al., 2014).

Within the mammoth steppe ecosystem during the pre-LGM period in Europe regular patterns are seen in fauna $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Bocherens et al., 1997; Bocherens, 2003; Bocherens et al., 2011a; Yeakel et al., 2013; Bocherens, 2015; Bocherens et al., 2015). Among the herbivores, woolly mammoth yielded the highest $\delta^{15}\text{N}$ values and relatively low $\delta^{13}\text{C}$ values. Bovids, horses and rhinoceroses have relatively similar values and, in most cases, could not be clearly distinguished individually by their stable carbon and nitrogen collagen isotope ratios. In contrast, reindeer can easily be identified by isotopic analyses due to their high $\delta^{13}\text{C}$ values, which at other sites had been attributed to lichen consumption (Bocherens, 2003; Drucker et al., 2003). So far the isotopic composition for all the ZC species reflects a typical mammoth–steppe ecosystem.

Climatic and chronological implications

In the mammoth steppe ecosystem of Central Western Europe the main limiting factor for the plants is the mean annual temperature

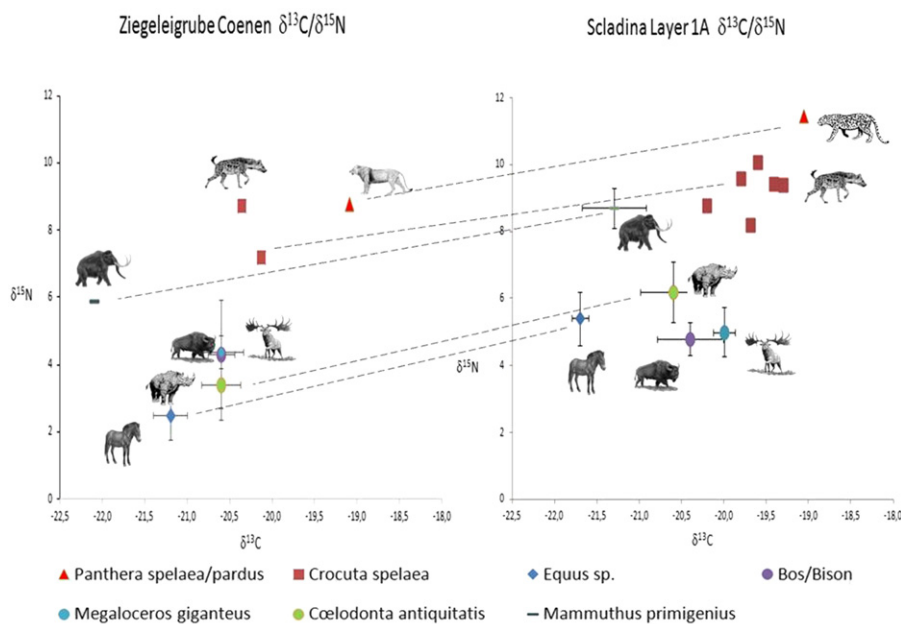


Figure 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ graphs of Ziegeleigrube Coenen and Scladina Layer 1A and comparison of $\delta^{15}\text{N}$ values from both sites. Herbivores are represented by average values with standard deviation, carnivores are represented by single individuals.

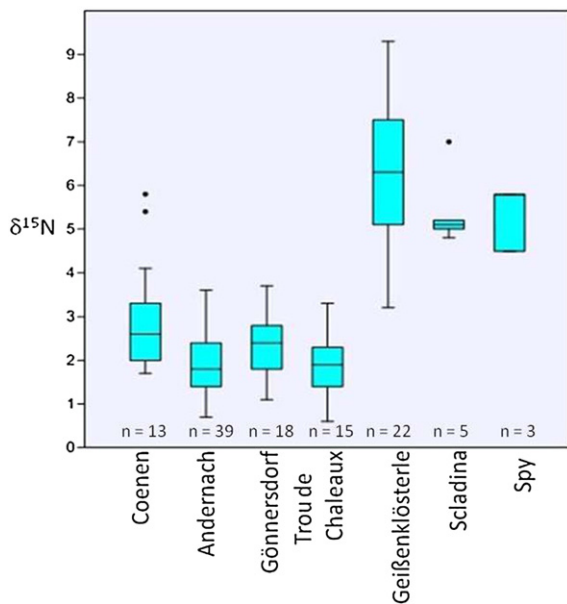


Figure 3. $\delta^{15}\text{N}$ values of horse collagen from pre- and post-LGM sites discussed in the text: pre-LGM: Ziegeleigrube Coenen (the two dots are specimens from the same bone), Geißenklösterle, Scladina and Spy; post-LGM: Andernach–Martinsberg, Gönnersdorf, Trou de Chaleaux. $\delta^{15}\text{N}$ values include standard error of horse collagen (whisker length indicates 95% interval).

(MAT). MAT is an essential factor, since in frozen soils the growth of plants/nitrogen fixation and the turnover rate of nutrients are extremely reduced. The $\delta^{15}\text{N}$ values of plants are determined by the source of nitrogen they access, its chemical form and, in particular, influence of mycorrhizae (Hobbie and Hogberg, 2012). Mycorrhizae and micro-organisms make organic nitrogen available for plants. Leguminous plants are an exception to this since they fix nitrogen from the atmosphere with microbe-symbionts. A decrease in available nutrients throughout the glacial period intensifies the impact of the developments of the mycorrhiza and results in a depletion in soil/plant $\delta^{15}\text{N}$ (Stevens and Hedges, 2004). Soil activity in (semi-) permafrost ecosystems is limited in comparison to that observed under warmer conditions, and it is recognized that soil $\delta^{15}\text{N}$ values increased with increasing mean annual temperature (Brenner et al., 2001). On the contrary, decreasing temperatures in a (semi-) glacial context, with low soil activity due to the occurrence of permafrost, can be related to decreasing $\delta^{15}\text{N}$ values of herbivore collagen over time and space (Heaton et al., 1986; Ambrose, 1991; Drucker et al., 2003). Consequently the lower $\delta^{15}\text{N}$ collagen values from the late Pleistocene site ZC represent a cooler habitat with harsher conditions than those found at other pre-LGM sites such as Scladina layer 1A or Geißenklösterle and Spy (Table 4). At this stage of research it is not possible to quantify the differences but further investigation, in particular the $\delta^{18}\text{O}$ values from bones, could provide some hints about relative temperature changes in this context.

We focused on horse $\delta^{15}\text{N}$ values in order to examine and understand the ecological characteristics of different sites dating to MIS 3 and 2. Horses are an exclusively herbivorous species and, in general, any differences in $\delta^{15}\text{N}$ values in horse bone, correspond to differences in the isotopic values of the plants in their diet (Rodière et al., 1996) and the metabolic processes. We assume that there were no significant differences in the metabolic processes of horses during the Pleistocene and consequently changes in the $\delta^{15}\text{N}$ values correspond to differences in values of the horse diet.

The inter-site comparison shows two groups defined by their mean values (Fig. 3). The first group has relatively low $\delta^{15}\text{N}$ values, including ZC (mean: 2.5‰ if samples ZC-142, 143 are excluded), Andernach (mean: 1.9‰), Gönnersdorf (mean: 2.3‰) (Stevens et al., 2009b) and Trou de Chaleaux mean: 1.9‰ (Table 5) (Stevens et al., 2009a). These

sites are post LGM in age with the exception of ZC, which is clearly pre-LGM. ZC yielded values which correspond to those observed at the younger Late Glacial sites. This pattern indicates similar environmental conditions or at least a comparable degree of soil activity. Stevens et al. (2009b) argued that we may be dealing with a pre-interstadial period with stadial–interstadial warmer conditions, at least in Gönnersdorf and Andernach–Martinsberg (Stevens et al., 2009b). They place the onset of the occupation at these sites prior to the warming of Greenland Interstadial GI 1e (Stevens et al., 2009b). We assume a similar situation in Trou de Chaleux (Fig. 3).

Some general trends in $\delta^{15}\text{N}$ horse collagen values can be observed at least in Central Europe. There is a dramatic rise of $\delta^{15}\text{N}$ values from around 13,500 ^{14}C yr BP or even earlier, until around 10,000 ^{14}C yr BP. Values are very low between 13,500 ^{14}C yr BP and 12,000 ^{14}C yr BP and increased to around 4–5‰ by 10,000 ^{14}C yr BP (Stevens and Hedges, 2004). This phenomenon can be correlated with a recovery of soil activity and soil features. Strictly speaking, a gradual shift from ecto- and ericoid mycorrhiza to arbuscular mycorrhizae. In addition, the predominant form of nitrogen changes from organic to inorganic and whereas phosphorous is abundant, availability of nitrogen is limited. All these factors are connected with increasing temperatures after the Last Glacial Maximum. It is important to mention that a general depletion of $\delta^{15}\text{N}$ during and after the Younger Dryas cannot be recognized (Stevens and Hedges, 2004; Drucker et al., 2011). Lower temperatures and all their consequences for plant and soil activity during and after the LGM had a much stronger impact on the ecosystem in Europe rather than e.g., conditions occurring during the Younger Dryas. It is however important to keep in mind that the $\delta^{15}\text{N}$ variation does not directly track temperature fluctuations.

The second group consists of sites with a relatively higher nitrogen horse collagen isotopic composition. All of the sites pre-date the LGM, Scladina Layer 1A has a mean $\delta^{15}\text{N}$ value of 5.4‰ (Bocherens et al., 1997), Spy 5.1‰ (Bocherens et al., 2013) and Geißenklösterle 6.4‰ (Bocherens et al., 2011a) (Fig. 3). The sites are relatively close in age. It appears that the herbivorous megafauna at all of the pre-LGM Ardenne and Swabian Jura sites dating to around 40,000 to 24,000 ^{14}C yr BP occupied comparable ecological niches in terms of their diet (comparable pattern) according to $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in bone collagen (Bocherens et al., 2011a). It is interesting that ZC yielded relatively low $\delta^{15}\text{N}$ values. As mentioned above the nitrogen isotopic values can hint at chronological classifications according to some general trends in Europe (Richards and Hedges, 2003; Stevens and Hedges, 2004; Drucker et al., 2011). We can exclude that ZC is very close in age to the other pre-LGM sites, otherwise we would expect comparable $\delta^{15}\text{N}$ values and the same ecological frame. We consider that either the environment or at least the soil activity with all its associated consequences, e.g., lower $\delta^{15}\text{N}$ values in a colder phase and higher in a warmer context, was not the same as in the other pre-LGM sites. Local differences caused by different types of bedrocks can be excluded; this is strongly supported by the homogeneous sulfur isotopic values.

Consequently the ecological information derived from the stable isotope data suggest a stadial date, which argues for a MIS 3/Heinrich 5 date (Cacho et al., 1999; Sánchez Goñi et al., 2008; Svensson et al., 2008). The scattered radiocarbon data are consistent with the MIS 3 assignment. If this chronological association is correct, it would mean that the Heinrich 5 event must have been cold enough to have an impact on the biogeochemical cycle of nitrogen in soils, as reflected by the decrease of $\delta^{15}\text{N}$ values at the base of the ecosystem. However, it must have been less severe than the LGM, during which time Western Germany was more-or-less totally deserted by humans and large mammals. Moreover, the Heinrich 5 event would not have been harsh enough to disrupt the trophic structure of the ecosystem, either for the herbivores or their predators. This conclusion is particularly important in understanding the fluctuations of prehistoric human populations, in this case Neanderthals, in response to the climatic shifts during MIS 3.

Table 4

Pre-Last Glacial Maximum sites: Scladina, Geißenklösterle and Spy.

Sources: 1 = Bocherens et al. (1997). 2 = Bocherens et al. (2011a). 3 = Stevens and Hedges (2004). 4 = Conard and Bolus (2008). 5 = Germonpré et al. (2014).

Species	Site code	Element	%C _{coll}	%N _{coll}	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C:N _{coll}	Source	AMS age (¹⁴ C yr BP)	AMS-code
<i>Site: Scladina</i>										
<i>Crocota spelaea</i>	SC1800	Phalanx I	42.9	15.6	−20.2	8.8	3.2	1		
<i>Crocota spelaea</i>	SC1900	Phalanx I	42.6	15.6	−19.6	10.1	3.2	1		
<i>Crocota spelaea</i>	SC2000	Phalanx I	42.8	15.7	−19.7	8.2	3.2	1		
<i>Crocota spelaea</i>	SC2100	Phalanx I	42.9	15.6	−19.4	9.5	3.2	1		
<i>Crocota spelaea</i>	SC1700	Mandible	39.9	14.6	−19.8	9.6	3.2	1		
<i>Crocota spelaea</i>	SC2200	Maxillary	42.0	15.4	−19.3	9.4	3.2	1		
<i>Panthera pardus</i>	SC30700		40.5	14.1	−19.1	11.5	3.4	2		
<i>Mammuthus primigenius</i>	SC600	Tooth	42.6	15.5	−20.9	8.4	3.2	1		
<i>Mammuthus primigenius</i>	SC700	Tooth	41.5	15.2	−21.5	9.4	3.2	1		
<i>Mammuthus primigenius</i>	SC800	Tooth	41.3	15.1	−21.6	8.3	3.2	1		
<i>Cœlodonta antiquitatis</i>	SC900	Lower P2 (R)	42.6	15.5	−20.9	5.5	3.2	1		
<i>Cœlodonta antiquitatis</i>	SC1000	Lower P2 (R)	42.1	15.4	−20.3	6.9	3.2	1		
<i>Cœlodonta antiquitatis</i>	SC1100	Lower P2 (R)	42.2	15.2	−20.0	6.4	3.2	1		
<i>Cœlodonta antiquitatis</i>	SC1200	Lower P2 (R)	41.2	15.0	−21.1	5.3	3.2	1		
<i>Cœlodonta antiquitatis</i>	SC1300	Lower P2 (R)	41.8	15.2	−20.4	7.5	3.2	1		
<i>Cœlodonta antiquitatis</i>	SC1400	Lower P2 (R)	43.1	15.7	−20.6	5.5	3.2	1		
<i>Equus ferus</i>	SC3900	Upper tooth (R)	42.5	15.6	−21.7	5.2	3.2	1		
<i>Equus ferus</i>	SC4100	Upper tooth (R)	42.6	15.8	−21.7	5.1	3.1	1		
<i>Equus ferus</i>	SC4200	Upper tooth (R)	42.8	15.8	−21.9	5.0	3.2	1		
<i>Equus ferus</i>	SC4300	Upper tooth (R)	39.9	14.5	−21.5	4.8	3.2	1		
<i>Equus ferus</i>	SC4400	Upper tooth (R)	40.9	15.0	−21.6	7.0	3.2	1		
<i>Bison priscus</i>	SC29000	Lower M3 (R)	32.6	11.5	−20.8	4.4	3.3	2		
<i>Bison priscus</i>	SC29100	Lower P4 (L)	32.1	12.8	−19.8	5.6	2.9	2		
<i>Bos</i> or <i>Bison</i>	SC4500	Lower P (R)	41.7	15.2	−20.5	4.8	3.2	1		
<i>Bos</i> or <i>Bison</i>	SC4700	Lower P3 (R)	42.7	15.7	−20.5	4.3	3.2	1		
<i>Bos</i> or <i>Bison</i>	SC4800	Lower M1 (R)	41.2	15.3	−19.9	5.3	3.1	1		
<i>Bos</i> or <i>Bison</i>	SC4900	Lower P3 (R)	40.8	15.0	−20.7	4.4	3.2	1		
<i>Bos primigenius</i>	SC28800	Lower M3 (L)	33.9	12.7	−20.7	4.9	3.1	1		
<i>Bos primigenius</i>	SC28900	Lower P4 (L)	35.0	13.6	−20.3	4.5	3.0	2		
<i>Megaloceros giganteus</i>	SC2300	Tarsal bone	41.6	15.2	−20.2	4.0	3.2	1		
<i>Megaloceros giganteus</i>	SC2500	Upper tooth	43.7	15.9	−20.2	5.0	3.2	1		
<i>Megaloceros giganteus</i>	SC29800	Lower P4 (R)	40.9	13.5	−19.7	5.9	3.5	2		
<i>Site: Geißenklösterle</i>										
<i>Equus</i> sp.	EQ-GK 313	Radius	39.2	14.1	−19.8	4.1	3.2	2		
<i>Equus</i> sp.	EQ-GK 314	Tibia	43.2	15.7	−20.7	8.7	3.2	2		
<i>Equus</i> sp.	EQ-GK 316	Humerus	41.5	14.6	−20.6	7.3	3.3	2		
<i>Equus</i> sp.	EQ-GK 317	Femur	36.3	13.5	−20.7	5.5	3.1	2		
<i>Equus</i> sp.	EQ-GK 318	Tibia	42.8	14.3	−21.8	3.4	3.5	2		
<i>Equus</i> sp.	EQ-GK 319	Tibia	42.2	14.8	−21.4	4.2	3.3	2		
<i>Equus</i> sp.	EQ-GK 321	Tibia	37.8	13.9	−20.1	8.5	3.1	2		
<i>Equus</i> sp.	EQ-GK 322	Tibia	36.3	13.7	−20.8	6.3	3.1	2		
<i>Equus</i> sp.	EQ-GK 323	Tibia	36.1	13.6	−20.7	6.1	3.1	2		
<i>Equus</i> sp.	EQ-GK 325	Tibia	41.6	14.4	−20.8	7.1	3.3	2		
<i>Equus</i> sp.	EQ-GK 326	Humerus	42.9	15.3	−21.0	6.1	3.2	2		
<i>Equus</i> sp.	EQ-GK 327	Tibia	41.6	15.0	−20.9	5.9	3.2	2		
<i>Equus</i> sp.	EQ-GK 329	Tibia	40.7	15.5	−20.8	6.9	3.0	2		
<i>Equus</i> sp.	EQ-GK 330	Tibia	28.6	10.9	−21.6	6.9	3.0	2		
<i>Equus</i> sp.	EQ-GK 331	Tibia	43.8	16.2	−20.6	6.1	3.1	2		
<i>Equus</i> sp.	OxA-4857	–	–	–	−20.0	9.2	3.0	3	27,500 ± 550	OxA-4857
<i>Equus</i> sp.	OxA-5227	–	–	–	−20.7	9.3	3.2	3	28,050 ± 550	OxA-5227
<i>Equus</i> sp.	OxA-5707	–	–	–	−20.6	7.5	3.1	3	33,200 ± 800	OxA-5707
<i>Equus</i> sp.	OxA-4856	–	–	–	−20.6	5.1	3.2	3	30,950 ± 800	OxA-4856
<i>Equus</i> sp.	TUB-77	Femur	39.3	14.6	−21.1	3.2	3.1	4	36,490 + 350/− 340	KIA-17303
<i>Equus</i> sp.	TUB-78	Humerus	39.7	14.2	−21.2	8.5	3.3	4	31,870 + 260/− 250	KIA-8958
<i>Equus</i> sp.	TUB-79	Radius	41.4	14.9	−21.8	4.7	3.2	4	36,700 + 450/− 430	KIA-17299
<i>Site: Spy</i>										
<i>Equus</i> sp.	Spy 14038 Ulg	–	44.3	14.0	−21.4	5.8	3.2	1 + 5	34,580 + 330/− 290	GrA-37932
<i>Equus</i> sp.	IV2E 4207	–	35.6	14.2	−20.5	4.5	2.5	1 + 5	32,810 + 250/− 230	GrA-44576

acronym "Coll": values measured on collagen.

Conclusion

The fauna from the Ziegeleigrube Coenen (ZC) is potentially significant for understanding the paleoecological context of northwestern Europe during a critical period of human evolution in Europe, before and around the time of Neanderthal replacement by anatomically modern humans (Conard and Bolus, 2008; Flas, 2011; Higham, 2011; Higham et al., 2012, 2014; Pirson et al., 2012). It seems that cooling events in MIS 3 like Heinrich events had not significantly impacted the megafaunal

composition in parts of Central Europe. Hence, these regions could provide the preferred prey of Neanderthals during such cold spells. In contrast to the many cave sites from this period, ZC is one of the few late Pleistocene sites in an open air loess context. Due to the extraordinary preservation of the ZC remains, this site yielded a considerable spectrum of Pleistocene faunal material comprising several carnivores and herbivores. The chemical bone preservation is good and, consequently, the collagen content and preservation was acceptable for extraction and could be processed successfully. Applying radiocarbon and isotopic

Table 5

Post-Last Glacial Maximum sites: Andernach, Gönnersdorf and Trou de Chaleux.

Source: 1 = Stevens et al. (2009b), 2 = Stevens et al. (2009a).

Species	Site code	Element	%C _{coll}	%N _{coll}	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C:N _{coll}	Source	AMS age (¹⁴ C yr BP)	AMS-code
<i>Site: Andernach</i>										
<i>Equus</i> sp.	A/AND/B/35	–	38.8	13.8	–20.1	2.4	3.3	1		
<i>Equus</i> sp.	A/AND/B/43	–	39.9	14.3	–21.1	1.1	3.3	1		
<i>Equus</i> sp.	A/AND/B/24	–	37.7	13.3	–21.0	3.6	3.3	1		
<i>Equus</i> sp.	A/AND/B/40	–	35.2	12.5	–21.0	2.0	3.3	1		
<i>Equus</i> sp.	A/AND/B/44	–	39.6	14.1	–21.3	0.9	3.3	1		
<i>Equus</i> sp.	A/AND/B/1	–	38.7	13.8	–20.9	2.0	3.3	1		
<i>Equus</i> sp.	A/AND/B/2	–	35.2	12.6	–21.2	1.7	3.3	1		
<i>Equus</i> sp.	A/AND/B/4	–	32.6	11.6	–20.9	1.3	3.3	1		
<i>Equus</i> sp.	A/AND/B/6	–	30.1	10.8	–20.7	1.6	3.2	1		
<i>Equus</i> sp.	A/AND/B/14	–	37.4	12.8	–21.1	1.3	3.4	1		
<i>Equus</i> sp.	A/AND/B/15	–	36.4	13.3	–21.1	3.5	3.2	1		
<i>Equus</i> sp.	A/AND/B/16	–	37.7	13.2	–21.2	2.1	3.3	1		
<i>Equus</i> sp.	A/AND/B/17	–	33.5	12.1	–21.1	1.3	3.2	1		
<i>Equus</i> sp.	A/AND/B/18	–	39.2	14.0	–20.8	1.7	3.3	1		
<i>Equus</i> sp.	A/AND/B/19	–	33.9	12.1	–20.7	0.7	3.3	1		
<i>Equus</i> sp.	A/AND/B/20	–	34.5	12.3	–21.0	2.0	3.3	1		
<i>Equus</i> sp.	A/AND/B/21	–	38.7	14.7	–21.0	1.3	3.1	1		
<i>Equus</i> sp.	A/AND/B/22	–	35.2	12.6	–20.7	1.7	3.3	1		
<i>Equus</i> sp.	A/AND/B/23	–	41.0	14.4	–21.1	2.8	3.3	1		
<i>Equus</i> sp.	A/AND/B/26	–	28.1	10.1	–20.9	2.8	3.3	1		
<i>Equus</i> sp.	A/AND/B/27	–	38.9	13.5	–21.2	1.6	3.4	1		
<i>Equus</i> sp.	A/AND/B/28	–	37.0	13.1	–21.2	2.3	3.3	1		
<i>Equus</i> sp.	A/AND/B/29	–	44.0	15.4	–21.0	1.4	3.3	1		
<i>Equus</i> sp.	A/AND/B/30	–	37.3	13.2	–20.5	2.4	3.3	1		
<i>Equus</i> sp.	A/AND/B/31	–	34.6	12.5	–21.2	3.2	3.2	1		
<i>Equus</i> sp.	A/AND/B/32	–	30.4	11.2	–21.3	2.1	3.2	1		
<i>Equus</i> sp.	A/AND/B/33	–	34.3	12.2	–20.9	2.6	3.3	1		
<i>Equus</i> sp.	A/AND/B/34	–	37.6	13.4	–21.2	1.1	3.3	1		
<i>Equus</i> sp.	A/AND/B/36	–	36.5	12.7	–21.1	1.2	3.3	1		
<i>Equus</i> sp.	A/AND/B/37	–	38.8	13.9	–20.8	1.5	3.3	1		
<i>Equus</i> sp.	A/AND/B/38	–	39.4	14.0	–21.2	1.8	3.3	1		
<i>Equus</i> sp.	A/AND/B/39	–	38.7	13.9	–21.2	2.0	3.3	1		
<i>Equus</i> sp.	A/AND/B/41	–	40.3	14.1	–21.4	1.8	3.3	1		
<i>Equus</i> sp.	A/AND/B/42	–	41.5	14.9	–21.3	2.7	3.3	1		
<i>Equus</i> sp.	A/AND/B/45	–	37.1	13.8	–21.2	1.9	3.1	1		
<i>Equus</i> sp.	A/AND/B/46	–	32.4	11.2	–21.7	1.9	3.4	1		
<i>Equus</i> sp.	A/AND/B/47	–	34.9	12.6	–20.6	1.8	3.2	1		
<i>Equus</i> sp.	A/AND/B/48	–	37.7	13.3	–20.9	1.4	3.3	1		
<i>Equus</i> sp.	A/AND/B/49	–	38.7	13.8	–20.4	2.5	3.3	1		
<i>Rangifer tarandus</i> N = 11	max δ ¹³ C – 19.2 min δ ¹³ C – 21.2	max δ ¹⁵ N 2.8 min δ ¹⁵ N 1.4			av – 19.8	av 2.1		1		
<i>Site: Gönnersdorf</i>										
<i>Equus</i> sp.	A/GON/B/18	–	39.7	14.1	–21.0	1.1	3.3	1		
<i>Equus</i> sp.	A/GON/B/12	–	38.9	13.6	–20.6	3.1	3.3	1		
<i>Equus</i> sp.	A/GON/B/7	–	35.0	12.6	–21.0	1.1	3.3	1		
<i>Equus</i> sp.	A/GON/B/8	–	38.3	13.0	–21.0	1.9	3.4	1		
<i>Equus</i> sp.	A/GON/B/11	–	34.1	12.0	–20.6	1.9	3.3	1		
<i>Equus</i> sp.	A/GON/B/13	–	41.9	14.7	–20.3	2.0	3.3	1		
<i>Equus</i> sp.	A/GON/B/14	–	37.0	12.3	–21.4	2.1	3.5	1		
<i>Equus</i> sp.	A/GON/B/16	–	31.1	10.2	–21.3	1.7	3.5	1		
<i>Equus</i> sp.	A/GON/B/17	–	36.1	12.7	–20.4	2.9	3.3	1		
<i>Equus</i> sp.	A/GON/B/20	–	38.4	13.8	–20.4	2.4	3.2	1		
<i>Equus</i> sp.	A/GON/B/21	–	38.9	13.2	–20.7	2.5	3.4	1		
<i>Equus</i> sp.	A/GON/B/22	–	35.9	12.3	–20.5	3.1	3.4	1		
<i>Equus</i> sp.	A/GON/B/23	–	43.0	15.2	–21.0	2.7	3.3	1		
<i>Equus</i> sp.	A/GON/B/24	–	38.1	13.8	–20.7	1.8	3.2	1		
<i>Equus</i> sp.	A/GON/B/25	–	39.1	13.5	–20.9	2.7	3.4	1		
<i>Equus</i> sp.	A/GON/B/27	–	31.1	11.0	–20.9	3.7	3.3	1		
<i>Equus</i> sp.	A/GON/B/28	–	39.0	13.6	–21.0	2.8	3.4	1		
<i>Equus</i> sp.	A/GON/B/29	–	37.5	13.2	–20.6	1.5	3.3	1		
<i>Rangifer tarandus</i> N = 22	max δ ¹³ C – 19.0 min δ ¹³ C – 20.2	max δ ¹⁵ N 3.0 min δ ¹⁵ N 0.6			av – 19.7	av 1.7		1		
<i>Site: Trou de Chaleux</i>										
<i>Equus</i> sp.	A/CX/B/28	–	19.7	6.3	–21	2.4	3.6	2		
<i>Equus</i> sp.	A/CX/B/29	–	38	13.5	–20.9	1.4	3.3	2		
<i>Equus</i> sp.	A/CX/B/30	–	42.4	15.2	–20.7	2.2	3.3	2		
<i>Equus</i> sp.	A/CX/B/31	–	36.6	12.6	–20.8	2.3	3.4	2		
<i>Equus</i> sp.	A/CX/B/32	–	38.5	13.7	–20.9	3.3	3.3	2		
<i>Equus</i> sp.	A/CX/B/33	–	39.3	14.1	–20.6	1.9	3.3	2		
<i>Equus</i> sp.	A/CX/B/34	–	42.5	15.3	–20.8	1.9	3.2	2		
<i>Equus</i> sp.	A/CX/B/35	–	40.4	14.4	–21	1.6	3.3	2		
<i>Equus</i> sp.	A/CX/B/36	–	42.6	15.4	–21.1	2.1	3.2	2		

(continued on next page)

Table 5 (continued)

Species	Site code	Element	%C _{coll}	%N _{coll}	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C:N _{coll}	Source	AMS age (¹⁴ C yr BP)	AMS-code
Site: Trou de Chaleux										
<i>Equus</i> sp.	A/CX/B/37	–	50.2	17.8	–20.9	1.9	3.3	2		
<i>Equus</i> sp.	A/CX/B/40	–	36.5	13.1	–20.9	1.3	3.2	2		
<i>Equus</i> sp.	A/CX/B/42	–	21.1	7.7	–21	0.6	3.2	2		
<i>Equus</i> sp.	A/CX/B/43	–	19.1	6.8	–21.1	2.3	3.3	2		
<i>Equus</i> sp.	A/CX/B/45	–	39.7	14.2	–20.7	1.3	3.3	2	12,880 ± 100	OxA-3633
<i>Equus</i> sp.	A/CX/B/46	–	43.6	15.9	–21.1	2.1	3.3	2	12,790 ± 100	OxA-3632

Acronym "Coll": values measured on collagen.

tracking to the large mammal bones, we established the integrity and authenticity of the assemblage more in detail, even though the finds were recovered under poor conditions, without systematic documentation and excavation. It was possible to identify a coherent food web and a relatively homogenous ecological affiliation for all of the species.

The δ¹⁵N and δ¹³C values of the mammalian species reflect the typical niche partitioning observed in the mammoth steppe ecosystem (e.g., Bocherens et al., 1997; Bocherens, 2003; Bocherens et al., 2011a; Yeakel et al., 2013). There are no indications of any ecological stress. The δ¹⁵N isotope composition of horse collagen from the sites considered in this paper can be clearly distinguished into relatively high δ¹⁵N values from the pre-LGM sites and relatively low δ¹⁵N values from post-LGM sites. The δ¹⁵N values of horse at the site ZC are clearly closer to those from post-LGM sites mentioned in the paper, indicating environmental conditions during phases of MIS 3 which were similar to those prevailing during the post-LGM sites. We could ascertain that the ecological framework is consistently different from the one represented at other pre-LGM sites mentioned here, while the faunal composition is the same. It is the δ¹⁵N baseline of the ecosystem that is responsible for the lower values.

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