Stable isotope ecology of Miocene large mammals from Sandelzhausen, S Germany

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5 figures, 5 tables

Abstract: The enamel carbon, oxygen, and strontium isotope composition of enamel from 53 teeth of large Miocene herbivorous mammals from Sandelzhausen (MN 5, Lower/Middle Miocene) in the North Alpine foreland basin, were analyzed to infer their diet and habitat. The mean enamel $\delta^{13}C$ value of -11.4±1.0‰ for the 9 taxa analyzed (proboscideans, cervids, suids, chalicotheres, equids, rhinocerotids) indicates a pure C_3 plant diet for all mammals. $^{87}Sr/^{86}Sr$ ratios of ~0.710 indicate preferential feeding of the mammals in the northeastern Molasse basin. The sympatric herbivores have different mean $\delta^{13}C$ and $\delta^{18}O$ values which supports niche partitioning and/or use of different habitats within a C_3 plant ecosystem. Especially the three sympatric rhinoceroses *Plesiaceratherium fahlbuschi*, *Lartetotherium sansaniense* and *Prosantorhinus germanicus* partitioned plants and/or habitats. The palaeomerycid *Germanomeryx fahlbuschi* was a canopy folivore in moderately closed environments whereas *Metaschizotherium bavaricum* and *Prosantorhinus germanicus* were browsers in more closed forest environments. The horse *Anchitherium aurelianense* was probably a more variable feeder than assumed from its dental morphology thusfar. The forest hog *Hyotherium soemmeringi* has the highest $\delta^{13}C$ and lowest $\delta^{18}O$ value of all taxa, possibly related to an frugivorous diet. Most taxa were water dependent browsers that record meteoric water $\delta^{18}O$ values of about –5.7±1.1‰ VSMOW. Using a modern-day mean annual air temperature (MAT)–$\delta^{18}O_{H2O}$ relation a MAT of 18.7±1.7°C can be reconstructed for Sandelzhausen. A serially sampled *Gomphotherium subtapiroideum* tusk does not record a clear $\delta^{18}O$ seasonality pattern. Thus most taxa were C_3 browsers in a forested and humid floodplain environment of the Molasse basin under a warm-temperate to subtropical low seasonality climate.

Keywords: carbon isotopes, oxygen isotopes, strontium isotopes, mean annual air temperature, enamel, diet, drinking water, Molasse basin

Introduction

Next to palaeontological evidences such as the dentition, dental wear, stomach contents and coprolithes, the stable carbon and oxygen isotope analysis of fossil tooth enamel has become an important tool in palaeoecology and palaeodietary reconstruction (overviews in KOHN & CERLING 2002; KOCH 2007). These geochemical systems allow an inference of the diet and feeding behaviour and the niche partitioning among taxa within modern and ancient ecosystems (e.g., CERLING ET AL. 1997a, b, 2003a; SPONHEIMER & LEE-THORP 1999a; MACFADDEN ET AL. 1999; KOHN ET AL. 2005) as well as drinking behaviour and water use efficiency of mammals (LONGINELLI 1984; KOHN ET AL. 1996, 1998; LEVIN ET AL. 2006). Furthermore, the vegetation (e.g. abundance of C_3 versus C_4 plants) and habitat conditions (open grasland versus closed woodland or canopy) are recorded in mammalian skeletal remains (e.g., van der Merwe & Medina 1991; CERLING ET AL. 2004; KOHN ET AL. 2005). Tooth enamel is especially suited for such geochemical reconstructions as it tends to preserve the original chemical and isotopic composition over millions of years (LEE-THORP & VAN DER

MERWE, 1987; WANG & CERLING, 1994; KOHN ET AL. 1999), in contrast to that for bone. Most carbon isotope studies to reconstruct the niche partitioning and palaeodiet of mammals have focused on environments distinguishing C_3 browsers and C_4 grazers. However, recent studies also used enamel carbon isotopes in modern and ancient C_3 ecosystems to infer niche partitioning (QUADE ET AL. 1995; DRUCKER ET AL. 2003; CERLING ET AL. 1997a, 2003b, 2004, MACFADDEN & HIGGINS 2004; FERANEC & MACFADDEN 2006; FERANEC 2007; NELSON 2007; ZANAZZI & KOHN, 2008). In Europe C_4 plants were no significant component in the Tertiary, therefore, C_3 plant ecosystems prevailed (BLONDEL ET AL. 1997; CERLING ET AL. 1997b).

The reconstructions of palaeodiet and palaeoenvironment for the Middle Miocene vertebrate fossil locality of Sandelzhausen, Bavaria, S Germany, have mainly focussed on geologic, palaeontologic and sedimentologic evidence (e.g. FAHLBUSCH ET AL. 1972, 1974, 1996; SCHMID 2002; MOSER ET AL. this issue a) and dental wear (KAISER & RÖSSNER 2007; SCHULZ ET AL. 2007; SCHULZ & FAHLKE this issue), respectively. In this study we use stable carbon, oxygen, and strontium isotopes of the enamel of different sympatric large herbivorous mammals such as proboscideans, rhinozerotids, equids, cervids and suids to infer their feeding and drinking behaviour as well as habitat and niche partitioning of these taxa at the Sandelzhausen site.

Geological setting

The early Middle Miocene fossil locality of Sandelzhausen, a former gravel pit, is situated 60 km north of Munich in the North Alpine Foreland Basin (Fig. 1). The fossiliferous sediments are part of the limnofluviatile Upper Freshwater Molasse. On the basis of a biostratigraphical correlation using micromammals Sandelzhausen is placed in the European Land Mammal Zone MN 5 (HEISSIG 1997). This corresponds to an early Middle Miocene sedimentation age of ~16 Ma close to the Lower/Middle Miocene boundary (HEISSIG 1997; ABDUL-AZIZ ET AL. 2008; MOSER ET AL. this issue a).
The depositional environment was a low relief, fluvial plain with sedimentary conditions varying between river channels, flood plains and riparian ponds and lakes. The fossil bearing limno-fluvial sediments consist of a 2 to 3 m thick succesion of gravels to marls with variable but decreasing gravel content towards the top of the section (FAHLBUSCH ET AL. 1972, 1974; SCHMID 2002; MOSER ET AL. this issue a). The sediment is partly cemented by pedogenic carbonates and soil formation processes occurred (SCHMID 2002). The sediment was probably deposited within a relatively short interval and no time averaging of the faunal remains is recognized. Deposition took place in two fresh water settings under high ground water level but with different hydrologic regimes: (1) the marly gravel of the lower part in a fluvial floodplain environment with seasonally fluctuating groundwater tables and flood events from a larger river in the vicinity, (2) the marly upper part in a lacustrine setting of a permanent shallow riparian pond with a relatively stable groundwater table and a more stagnant water body (BÖHME 2005 pers. comm.).

The lower half of the sediment section includes a humus-enriched brown colored layer of 10-35 cm thickness containing a 10 cm thick lignitic coaly layer around which most of the fossils are concentrated (FAHLBUSCH ET AL. 1972; MOSER ET AL. this issue a). The mammal teeth analyzed in this study come from both stratigraphic units, below and above this coaly layer. The sekeletal remains were washed in with floods from carcasses or represent remnants of crocodile prey, as indicated by frequent bite marks (HEISSIG 2005 pers. comm.). Therefore, almost only disarticulated skeletal elements such as jaw fragments, teeth or single bones were found. About 50,000 disarticulated vertebrate remains were found, as well as plant and invertebrate fossils, including 69 species of gastropods, bivalves, ostracods (WITT 1998;

FAHLBUSCH 2003; MOSER ET AL. this issue b). Most of the Fauna consists of micro + macro vertebrates including teleost bony fish, amphibians, turtles, lizards, snakes, crocodilians, birds and 66 species of mammals (FAHLBUSCH 2003; MOSER ET AL. this issue a) including rhinocerotids, gomphotherids, suids, equids, palaeomerycids, cervids, lagomerycids, and tragulids. The richness of this terrestrial macro- and micro-vertebrate fauna and the extraordinary systematic diversity with a total of more than 200 taxa makes Sandelzhausen an exceptional site (FAHLBUSCH 2003; MOSER ET AL. this issue a). Remarkable in the vertebrate fossil assemblage is the high percentage of juvenile individuals present for many taxa.

The invertebrate fauna of gastropods, ostracods, and rare bivalves are typical for shallow, temperate to subtropical fresh water conditions in the aquatic depositional environment (MOSER ET AL. this issue b; WITT 1998). Landsnail taxa are indicative of humid habitats close to the edge of the water body. Plant remains, however, are scarse or poorly preserved. Only gyrogonites of stoneworts and some fruits of *Celtis* and leaflets of *Gleditsia* were found (FAHLBUSCH ET AL. 1972; GREGOR 1982). The vegetation in the vicinity of Sandelzhausen can thus only be reconstructed on the basis of fossil plant remains from other, nearby Miocene deposits. Such studies support y year-round, seasonally humid, warm-temperate to subtropical climate climate conditions, with evergreen to decidous forests and woodlands (GREGOR 1982; SCHWEIGERT 1992; JECHOREK & KOVAR-EDER 2004).

The environment can be characterized as a humid, periodically flooded riverplain of a braided river system with temporary ponds and lakes, and soil and pedogenic carbonate formation (SCHMID 2002) with a more or less closed forestcover. A certain habitat variability between more forested and more open gravel-sandbar dominated environment can be expected as documented in the vertebrate faunas (e.g., BÖHME 2005 pers. comm.). An annual precipitation of 705±220 mm and a MAT of >17.4°C for the Sandelzhausen setting were estimated from a vertebrate based transfer functions (BÖHME ET AL. 2006, pers comm.).

Carbon isotopes

The carbon isotope composition ($^{13}C/^{12}C$) of fossil vertebrates is informative for both paleodietary and palaeohabitat reconstructions of fossil vertebrates because of differences in carbon isotope compositions of plants, which are transferred to body tissues of the fauna feeding on them (DENIRO & EPSTEIN 1978). The differences in plant carbon isotope compositions are mostly due to different photosynthetic pathways used for carbon assimilation (O´LEARY 1988; FARQUHAR ET AL. 1989). Most terrestrial plants assimilate atmospheric CO_2 with either the C_3 or C_4 photosynthetic pathway. C_3 plants, which include almost all trees and shrubs, and only those grasses favored by cool, wet growing seasons, utilize the enzyme ribulose bisphosphate carboxylase-oxygenase (Rubisco) to fix CO_2, forming a three-carbon sugar. C_4 plants, which include mostly grasses and sedges growing in warm, dry habitats, use a different enzyme to fix CO_2, the phosphoenolpyruvate (PEP) carboxylase, resulting in a four-carbon acid (FARQUHAR ET AL. 1989). Both photosynthetic pathways fractionate the light ^{12}C carbon isotopes to a different degree (FARQUHAR ET AL. 1989). Therefore, the C_3 and C_4 photosynthetic pathway yield different, non-overlapping $^{13}C/^{12}C$ ratios in plant tissues. Modern C_3 plants have a mean $\delta^{13}C$ value of –27‰ and a total range between −22‰ and −36‰, while modern C_4 plants have a mean $\delta^{13}C$ value of –13‰ and range between −10‰ and − 15‰ (DEINES 1980; O´LEARY 1988). CAM plants which include succulents (Cactaceae) exhibit a wide range of $\delta^{13}C$ values that can overlap between those of C_3 and C_4 plants (DEINES 1980; FARQUHAR ET AL. 1989). CAM plants represent only a minor fraction of the overall plant biomass though, and are not considered to be an important food resource for herbivores. However, environmental factors can also influence

the carbon isotope composition of plants (EHLERINGER ET AL. 1986, 1987; EHLERINGER & MONSON 1993).

The non-overlapping $\delta^{13}C$ values of C_3 and C_4 plants (mostly C_4 grasses) are often used in palaeoecological and palaeodietary studies to distinguish browsers from grazers in ecosytems where both types of plants are present (e.g. CERLING ET AL. 1997A, MACFADDEN ET AL. 1999). The occurence of a C_4 component in the diet of herbivorous mammals is interpreted as the use of C_4 grass and thus feeding in open grasslands. However, this approach is only applicable to settings in which C_4 grasses occur. A differentiation of browsers and grasers in a pure C_3 ecosystem based on enamel $\delta^{13}C$ values alone is not possible. The first grass fossils occur in rocks about 50 Ma (Palaeocene/Eocene; CREPET & FELDMAN 1991), but grasslands did not become globally widespread until the Miocene (JACOBS ET AL. 1999). The first fossils of C_4 grasses with the typical Kranz microanatomy were found in Middle Miocene deposits (~10 Ma) of North America (TIDWELL & NAMBUDIRI 1989). Based on analysis of fossil mammal teeth and ancient soil carbonates, C_4 plants do only occur as a major component in global ecosystems since the late Miocene (~7 Ma) when C_4 grasslands developed on most continents, excluding Europe (CERLING ET AL. 1993, 1997b). C_4 grasses are thus not expected to form a major food source for the middle Miocene mammals from Sandelzhausen in central Europe, but, C_3 grasses may have occurred.

Significant variability of carbon isotope compositions exists even within pure C_3-plant-dominated ecosystems, because of variations in light intensity, temperature, nutrient and water availability that all influence the $\delta^{13}C$ value in C_3 plants (EHLERINGER ET AL. 1986, 1987; FARQUHAR ET AL. 1989; EHLERINGER & MONSON 1993; HEATON 1999). Most C_3 plants have $\delta^{13}C$ values between –25 and –29 and average about –27 (DEINES 1980; FARQUHAR ET AL. 1989). However, in densely forested ecosystems subcanopy plants growing in closed canopy rain forests have very low $\delta^{13}C$ values between –32 and –36‰ because of low irradiance and ^{13}C-depleted CO_2 from biomass degradation near the forest floor (VAN DER MERWE & MEDINA 1989, 1991; CERLING ET AL. 2004). In contrast, water stressed C_3 plants in open and/or arid environments have more positive $\delta^{13}C$ values of up to –22‰ because they can close their stomata to decrease water loss and in doing so inhibit the CO_2 transport and fractionate less against ^{13}C (FARQUHAR ET AL. 1989; CERLING ET AL. 2004). Such differences in plant carbon isotope compositions are transferred to the fauna feeding on these plants. Therefore, such environmentally induced carbon isotope differences in C_3 plants can be used to discrimiate resource partitioning and habitat use of vertebrates in modern and ancient C_3 environments (QUADE ET AL. 1995; BLONDEL ET AL. 1997; DRUCKER ET AL. 2003; CERLING ET AL. 2003b, 2004; MACFADDEN & HIGGINS 2004; FERANEC & MACFADDEN 2006; FERANEC 2007; NELSON 2007; ZANAZZI & KOHN 2008).

Plant carbon ingested by herbivores is metabolized and incorporated into the mineralized skeletal tissues of the animals in the form of carbonate ion (CO_3^{2-}) that substitutes to 2-4 wt.% (DRIESSENS & VERBEEK 1990) for the PO_4^{3-} and OH group in the enamel hydroxy apatite ($Ca_5(PO_4)_3OH$). Skeletal carbonate hydroxyapatite forms in isotopic equilibrium with the blood and its dissolved inorganic carbon and the bioapatite carbonate is enriched in ^{13}C several permil relative to the diet (TIESZEN & FAGRE 1986; PASSEY ET AL. 2005). An extensive field stuy of wild E African large herbivorous ungulates (including grazers and browsers as well as foregut and hindgut fermenters) found an average $^{13}C_{enamel\text{-}diet}$ enrichment factor of 14.1±0.5‰ relative to the plant diet (CERLING & HARRIS 1999). However, in a recent controlled feeding study PASSEY ET AL. (2005) found a different $^{13}C_{enamel\text{-}diet}$ enrichment factors of 13.3±0.3‰ for non-ruminants pigs and +14.6±0.3‰ for ruminant cows raised on an isotopically identical diet. Therefore, different digestive physiology (e.g. the rate of ^{12}C-rich

methane production and its loss) can have an important influence on the $^{13}C_{enamel\text{-}diet}$ enrichment factor (PASSEY ET AL. 2005). Enamel $\delta^{13}C$ values mostly reflect the diet of the animal but may be additionally affected to some degree by its digestive physiology (PASSEY ET AL. 2005; ZANAZZI & KOHN 2008). Such a physiological influence will become increasingly important in an ecosystem with an isotopically similar diet, such as C_3-dominated ecosystems.

As modern atmospheric CO_2 ($\delta^{13}C_{CO2}$ = –8‰) is 1.5‰ depleted in ^{13}C compared to pre-industrial CO_2 with an $\delta^{13}C$ value of –6.5‰, due to the fossil fuel burning of ^{12}C-rich hydrocarbons (FRIEDLI ET AL. 1986). In this study we assume a $\delta^{13}C_{CO2}$ value of –6.5‰ for the Miocene atmosphere. Miocene C_3 and C_4 plants assimilating such CO_2 are then expected to have mean $\delta^{13}C$ values of –25.5‰ (range: –20.5 to –34.5‰) and –11.5‰ (range –8.5 to –13.5‰), respectively. Applying the average $^{13}C_{apatite\text{-}diet}$ enrichment factor of +14.1‰ for large ungulates (Cerling & Harris 1999), enamel $\delta^{13}C$ values for large Miocene mammalian herbivores feeding in a pure C_3 ecosystem should have a mean value of –11.4‰ and a range from –6.4 to –20.4‰.

Taxa that fed in more closed and mesic habitats are expected to have more negative carbon isotope values relative to those feeding in more open and/or arid environments (CERLING ET AL. 2004, KOHN ET AL. 2005). The most negative $\delta^{13}C$ values are expected to occur in close, dense forest environments due to the canopy effect, the recycling of isotopically light carbon in the form of CO_2 from the degrading biomass (VAN DER MERWE & MEDINA 1989, 1991; CERLING ET AL. 2004). Subcanopy ungulates can have about 6 permille lower $\delta^{13}C$ values than gap-clearing folivores, for example (CERLING ET AL. 2004). Therefore, in C_3 plant dominated ecosystems the effect of envrionments (open versus closed, humid versus arid, enlighted versus shaded) on the $\delta^{13}C$ values of food plants and thus herbivore body tissues is important.

Carbon isotope composition of enamel are considered to be diagenetically robust over geological time scales (e.g. LEE-THORP & VAN DER MERWE 1987; WANG & CERLING 1994). For example, expected differences in enamel $\delta^{13}C$ values between browsers and grazers eating isotopically distinct C_3, respectively, C_4 plants have been preserved for millions of years (LEE-THORP & VAN DER MERWE 1987; LEE-THORP & SPONHEIMER 2005). Therefore, given such a preservation for Tertiary mammel teeth, the carbon isotope compositions of fossil enamel allows for palaeodietary and palaeoenvironmental reconstructions e.g. if the animal was a grazer, mixed-feeder or browser or how closed or open its habitat was (see also reviews in KOCH 1998, 2007; KOHN & CERLING 2002).

Oxygen isotopes

The oxygen isotope composition ($\delta^{18}O_{H2O}$) of meteoric water varies within ecosystems due to changes in air temperature and/or amount of precipitiation or evaporation (DANSGAARD 1964; ROZANSKI ET AL. 1993). These oxygen isotope differences in meteoric water, which is used as drinking water by the mammals, are recorded in their skeletal tissues, that form in isotope equilibrium with the body water, and can be used to infer climatic conditions such as air temperature and aridity as well as animal drinking behaviour (LONGINELLI 1984; KOHN 1996; KOHN & CERLING 2002; LEVIN ET AL. 2006; TÜTKEN ET AL. 2006). Most of the oxygen in the enamel apatite is bound as both phosphate (PO_4^{3-}) and carbonate (CO_3^{2-}) ions. The major portion of this is in the phosphate group, as the carbonate rarely makes up more than 2-4 wt.% (Driessens & Verbeek 1990). The phosphate ($\delta^{18}O_{PO4}$) and carbonate ($\delta^{18}O_{CO3}$) oxygen isotope composition of bone and enamel apatite are positively correlated and have an

equilibrium offset of about 8.5 permille (BRYANT ET AL. 1996; IACUMIN ET AL. 1996). Therefore, both the $\delta^{18}O_{PO4}$ and $\delta^{18}O_{CO3}$ values reflect the isotopic composition of ingested water.

Herbivorous mammals derive their water from three sources: surface water, water from the food, and metabolic water from the food processing during oxidation of carbohydrates (BRYANT & FROELICH 1995; KOHN 1996). The body water $\delta^{18}O$ value of obligate drinkers, such as most large mammals, is linearly related to that of the drinking water (LONGINELLI 1984; KOHN 1996; KOHN ET AL. 1996). However, in addition to rainwater $\delta^{18}O$ values, several other physiological, environmental, and behavioural factors can affect enamel $\delta^{18}O$ values (e.g. KOHN, 1996, KOHN ET AL. 1996). An important factor is the water dependency of the animal (LEVIN ET AL. 2006). Mammals that drink frequently do have enamel $\delta^{18}O$ values that are dependent on rainwater $\delta^{18}O$ values whereas drought-tolerant evaporation sensitive animals usually have higher $\delta^{18}O$ values (AYLIFFE ET AL. 1990; LEVIN ET AL. 2006) because they obtain proportionally more water from evaporatively ^{18}O-enriched food sources such as leaves, fruits or seeds. Water in plant roots and stems is isotopically similar to meteoric water, but leaf water is relatively enriched in $H_2{}^{18}O$ due to preferential evapotranspiration of the lighter $H_2{}^{16}O$ molecule (DONGMANN ET AL. 1974; EPSTEIN ET AL. 1977; STERNBERG 1989; YAKIR 1992, 1997). The diet thus has a strong effect on the body water oxygen isotope composition, so that sympatric herbivores may have $\delta^{18}O$ values that can differ by as much as 8-9‰ (BOCHERENS ET AL. 1996; KOHN ET AL. 1996; SPONHEIMER & LEE-THORP 1999b). Browsing taxa often have higher relative ^{18}O content compared to grazing taxa of the same age and region, because they ingest a higher proportion of ^{18}O-enriched water with their food (KOHN ET AL. 1996; SPONHEIMER & LEE-THORP 1999b). Carnivores, however, have lower $\delta^{18}O$ values for their enamel relative to sympatric herbivores (SPONHEIMER & LEE-THORP 1999b).

The higher the water dependency of a terrestrial animal the closer is its body water $\delta^{18}O$ values to that of meteoric water (KOHN 1996; CLEMENTZ & KOCH 2001; LEVIN ET AL. 2006). Taxa inhabiting preferentially closed-canopy forests or swampy environments will have lower enamel $\delta^{18}O$ values because of the high humidity of these environments and thus decreased leaf water ^{18}O-enrichment due to evapotranspiration (e.g. CERLING ET AL. 2004). Furthermore, aquatic or semiaquatic animals such as marine mammals or hippopotamuses have lower $\delta^{18}O$ values than sympatric terrestrial mammals (BOCHERENS ET AL. 1996; CLEMENTZ & KOCH 2001). Therefore, $\delta^{18}O$ values also can allow for inferences on the habitat properties, feeding ecology, drinking behaviour and humidity (AYLIFFE ET AL. 1990; KOHN ET AL. 1998; SPONHEIMER & LEE-THORP 1999; LEVIN ET AL. 2006; ZANAZZI & KOHN 2008).

In addition as teeth mineralize over several months to years they record seasonal changes in the isotope composition of water and their food intake (e.g., KOCH ET AL. 1989; FRICKE & O`NEIL 1996; KOHN ET AL. 1996). However, the seasonal amplitudes of these changes are dampened due to enamel maturation after initial tooth mineralization (PASSEY & CERLING 2002). Nevertheless, seasonality is recorded and $\delta^{18}O$ amplitude changes allow for an evaluation of climatic changes (FRICKE ET AL. 1998; SHARP & CERLING 1998; NELSON 2005, 2007).

Material and Methods

Material

In this study the carbon and oxygen isotope compositions of bulk enamel carbonate samples of 53 large mammal teeth from Sandelzhausen were analyzed (Table 1 and 2). The teeth sampled belong to 9 different large mammal species: the cervid *Heteroprox eggeri,* the palaeomerycid *Germanomeryx fahlbuschi,* the chalicothere *Metaschizotherium bavaricum,* the proboscidean *Gomphotherium subtapiroideum,* the equid *Anchitherium aurelianense,* the three rhinoceroses *Prosantorhinus germanicus, Plesiaceratherium fahlbuschi* and *Lartetotherium sansaniens*, and the suid *Hyotherium soemmeringi.* In addition to samples of the bulk enamel, the enamel growth zones of one ever growing *Gomphotherium subtapiroideum* tusk were sampled. 16 enamel samples were taken every 2-4 mm, perpendicular to the growth axis of the tusk (Table 3). Furthermore, the oxygen isotope composition of enamel phosphate ($\delta^{18}O_{PO4}$) was measured for four teeth, one *Anchitherium*, two rhinoceros and one *Gomphotherium* molars (Table 4). For four teeth, one *Anchitherium* molar and three *Gomphotherium* molars, also the strontium isotope compositions ($^{87}Sr/^{86}Sr$) were also measured (Table 5).
Bulk enamel samples were taken along the complete crown height available, drilling parallel to the growth axis of the tooth using a hand-held Proxxon minidrill with diamond studded drill tips. This bulk sample (30-50 mg´s) thus represents the average isotope composition over the interval of tooth formation encompassing several months to 2 years (KOHN 2004), depending on species, tooth type, and wear pattern. Mostly third and second molar teeth - in some cases also premolars - were sampled to retrieve post-weaning dietary and drinkingwater isotope compositions. With the exception of one sample, first molars (M1) that mineralize wholly or partly before weaning were avoided because they could be potentially biased by isotope effects of mother milk during consumption (BRYANT ET AL. 1994). However, for several molars the exact type was not identifiable and unintended sampling of some M1 teeth can not be excluded.

Methods

C and O isotope measurements of the carbonate in the apatite

Isotopic analysis for all samples was done using 10 mg's of enamel powder, which was chemically pretreated according to methods given by KOCH ET AL. (1997) to remove organics and diagenetic carbonate 2% NaOCl solution was used for 24 hours, followed by a 1 M Ca-acetate acetic acid buffer solution for another 24 hours, prior to analysis of the carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O_{CO3}$) isotopic composition of the carbonate in the apatite. About 2 to 3 mg´s pretreated enamel powder was reacted with 100% H_3PO_4 for 90 minutes at 70°C using a ThermoFinnigan Gasbench II (SPOETL & VENNEMANN 2003). Carbon and oxygen isotope ratios of the generated CO_2 were measured in continuous flow mode on a Finnigan Delta Plus XL isotope ratio gas mass spectrometer at the University of Lausanne. For this reaction an acid fractionation factor of 1.008818, the same as between calcite and CO_2, was assumed to be applicable. The measured carbon and oxygen isotopic compositions were normalized to the in-house Carrara marble calcite standard that has been calibrated against the international NBS-19 calcite standard. The isotope composition of tooth enamel apatite is reported in the usual δ-notation in per mil (‰) relative to the known isotope reference standard VPDB (COPLEN 1994).

$$\delta^{13}C \text{ or } \delta^{18}O\ (‰) = [(R_{sample}/R_{standard})-1] \times 1000,$$

where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ and $^{18}O/^{16}O$ ratios in the sample and standard, respectively. Precision for the carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopic composition of carbonate in the apatite is better than ±0.1‰ and ±0.15‰, respectively. The NBS 120c

Florida phosphate rock standard, also pre-treated after KOCH ET AL. (1997), gave values of $\delta^{13}C_{VPDB}$ = –6.29±0.08‰ and $\delta^{18}O_{VPDB}$ = –2.32±0.14‰ (n = 13).

O isotope measurements of the phosphate

The oxygen isotope composition of phosphate ($\delta^{18}O_{PO4}$) was measured on silver phosphate (Ag_3PO_4) precipitated according to a method modified after DETTMANN ET AL. (2001) and described in TÜTKEN ET AL. (2006). 4 mg´s of pretreated enamel powder was dissolved in 2 M HF in a 2 ml safe lock centrifuge vessel. After centrifuging, the HF solution was transferred into a new centrifuge vessel leaving the CaF_2 residue behind. After neutralisation with 25% NH_4OH the dissolved phosphate was precipitated as Ag_3PO_4 by addition of 2 M $AgNO_3$ solution. Ag_3PO_4 of each sample was analyzed in triplicate for its oxygen isotopic composition according to methods described in VENNEMANN ET AL. (2002) using a TC-EA at 1450°C, linked to a ThermoFinnigan Delta Plus XL gas mass spectrometer at the University of Lausanne. $\delta^{18}O_{PO4}$ values are reported in the usual δ-notation vs. VSMOW. The Ag_3PO_4 precipitated from the NBS 120c standard gave a mean $\delta^{18}O_{PO4}$ value of 21.6±0.4‰, (n = 25).

Sr isotope measurements

The preparation for Sr isotope analysis was done in a clean laboratory. A 1 mg aliquot of the pre-treated enamel powder was dissolved in 1 ml suprapure HNO_3. The Sr fraction was separated with a standard separation procedure on quartz glass columns filled with 5 ml cation exchange resin bed of BioRad AG 50W-X12, 200-400 mesh. The purified Sr was loaded on tungsten filaments coated with TaF_5 activator. The Sr isotopic composition was measured with a Finnigan MAT 262 thermal ionization mass spectrometer (TIMS) at the University of Tübingen. For each sample >200 $^{87}Sr/^{86}Sr$ ratios were measured in the static mode with an internal precision ≤10 x 10^{-6}. $^{87}Sr/^{86}Sr$ ratios were corrected for mass fractionation in the instrument, using the natural $^{88}Sr/^{86}Sr$ ratio of 8.375209. Measured $^{87}Sr/^{86}Sr$ ratios were normalized to the certified value of NBS 987 ($^{87}Sr/^{86}Sr$ = 0.710248). The NBS 987 gave a mean $^{87}Sr/^{86}Sr$ = 0.710246±9, (n = 7) during the period of Sr isotope measurements.

Results

Enamel $\delta^{13}C$ values

The enamel $\delta^{13}C$ values of the 53 individual teeth analyzed have a range from –9.2 to –13.9‰ (Fig 2, Table 1) and a mean value of –11.4±1.0‰. Mean $\delta^{13}C$ values of the different taxa range from –10.2 to –12.7‰ (Table 2).The *Metaschizotherium bavaricum* (–12.7±0.8‰) has the lowest mean $\delta^{13}C$ value of all large mammal taxa from Sandelzhausen analyzed. Only the rhinoceros *Prosantorhinus germanicus* (–12.4±0.7‰) has a similar low mean $\delta^{13}C$ value. The palaeomerycid *Germanomeryx fahlbuschi* (–12.0±0.8‰) also has a low $\delta^{13}C$ value. The three sympatric rhinoceros species have different mean $\delta^{13}C$ values: *Prosantorhinus germanicus* (–12.4±0.7‰), the lowest value of the three sympatric rhinoceros species, *Plesiaceratherium fahlbuschi* (–11.6±0.5‰) with intermediate, and *Lartetotherium sansaniense* (–11.0±0.7‰) with the highest value. Most other large mammals, such as *Anchitherium aurelianense* (–11.1±0.7‰), *Gomphotherium subtapiroideum* (–11.1±0.6‰), and *Heteroprox eggeri* (–11.0±0.7‰) have identical mean $\delta^{13}C$ values of around –11‰, only slightly more positive than the mean average value for all of –11.4‰. The *Gomphotherium suptapiroideum* tusk has a significantly lower mean $\delta^{13}C$ value of –11.9±0.1‰ (n = 16) that is lower than that of the the molars (Fig. 2, Table 3). Furthermore, variation for the analyzed zones of this tusk have a

$\Delta\delta^{13}C$ range of only 0.5‰. The suid *Hyotherium soemmeringi* (–10.2±0.7‰) has the highest mean $\delta^{13}C$ value of all taxa analyzed from Sandelzhausen, which is about 1‰ higher than the mean value for all taxa (Fig. 2). Most mammals have a similar intra-taxon $\delta^{13}C$ variability, $\Delta\delta^{13}C$, of around 2‰ (Fig. 3). However, the large rhinoceros *Lartetotherium sansaniense* has the smallest $\Delta\delta^{13}C$ value of 1.4‰ and that *Anchitherium aurelianense* has the highest $\Delta\delta^{13}C$ values of 2.3‰ of all taxa (Fig. 3).

Enamel $\delta^{18}O_{CO3}$ values

The $\delta^{18}O$ values of the mammal teeth display a range from –4.5 to –9.8‰ (Table 1) and a mean value of –7.4±1.1‰ (n = 53). The suid *Hyotherium soemmeringi* (–8.4±0.9‰) has the lowest mean $\delta^{18}O$ value of all large mammal taxa from Sandelzhausen analyzed. *Gomphotherium subtapiroideum* (–8.1±1.0‰) and *Heteroprox eggeri* (–8.1±1.6‰) have similar low mean $\delta^{18}O$ values. Most other mammals do have higher mean $\delta^{18}O$ values of around –7 to –7.5‰ (Fig. 2; Table 2). The three sympatric rhinoceros species have identical mean $\delta^{18}O$ values: *Prosantorhinus germanicus* (–7.2±0.7‰), *Plesiaceratherium fahlbuschi* (–7.2±0.7‰) and *Lartetotherium sansaniense* (–7.3±0.6‰). Only slightly lower is the mean $\delta^{18}O$ value of *Metaschizotherium bavaricum* (–7.5±0.8‰). *Anchitherium aurelianense* (–6.6±0.9‰) has a slightly higher $\delta^{18}O$ value. The palaeomerycid *Germanomeryx fahlbuschi* (–5.7±1.7‰) has the highest mean and single $\delta^{18}O$ value of all analyzed taxa (Fig. 3). Furthermore, *Germanomeryx fahlbuschi* and *Heteroprox eggeri* also have the highest variability of $\delta^{18}O$ values expressed with a $\Delta\delta^{18}O$ value of 3‰ (Fig. 3). The *Gomphotherium suptapiroideum* tusk has a mean $\delta^{18}O$ value of –9.7±0.5‰ (n = 16), lower than any other mammal teeth (Fig. 2, Table 3). The intra-tusk $\Delta\delta^{18}O$ range is 1.8‰ (Fig. 4).

Enamel $\delta^{18}O_{PO4}$ values

The $\delta^{18}O_{PO4}$ VSWOW values of one *Anchitherium* molar, one *Gomphotherium* molar and two rhinoceros molars are 19.0‰, 17.9‰ and 15.9 to 18.2‰, respectively (Table 4). These $\delta^{18}O$ values indicate the use of water sources with $\delta^{18}O_{H2O}$ values of –5.3 to –7.0‰ VSMOW (Table 4).

Sr isotope composition

The enamel $^{87}Sr/^{86}Sr$ ratios of the *Anchitherium* tooth (0.71033) and the *Gomphotherium* teeth (0.71013 to 0.7106) are similar and range from 0.71013 to 0.71063 (Table 5). The $^{87}Sr/^{86}Sr$ ratios are higher than those of teeth from sympatric Miocene mammals of the Molasse basin (Fig. 5).

Discussion

Despite the small overall range of isotope compositions some of the 9 analyzed large mammal taxa do have inter-taxon differences for their enamel carbon and oxygen isotope composition (Fig. 2). Although most skeletal remains in Sandelzhausen were found disarticulated, most of them lack transport marks, so that a transport over long distances and thus potential mixing of bones and teeth of animals from ecologically distinct habitats is unlikely. Furthermore, the inter-taxon isotope differences are not due to significant time averaging because of the short deposition time of the sediment succession at Sandelshausen. This is further supported by the fact that enamel samples of teeth from the same taxon in the lower and upper part of the sediment profile, which are seperated by a thin coaly layer, do not have taxon-wise

differences in their carbon and oxygen isotope compositions. Thus, no significant changes in diet and/or habitat for the anlyzed taxa are associated with the evolution from a more fluvial to a limnic depositional environment. Therefore, enamel samples from both stratigraphic units are pooled for each taxon for the following discussion of the data. The observed inter-taxon differences in isotope compositions can either be attributed to dietary, environmental or physiological differences such as different feeding ecology, habitat use or digestive strategy.

Carbon isotopes – general consideration

Carbon isotope values are interpreted based upon certain cutoff values for diets of C_3 versus C_4 vegetation as well as for closed versus open habitats. The $\delta^{13}C$ values for enamel apatite of modern pure C_3 feeding mammals have a general range from approximately –8‰ to –22‰, with the extremes representing distinctive habitats, low values closed canopy rainforest and high values open xeric habitats (CERLING ET AL. 1997b, 2004; CERLING & HARRIS 1999). In terms of habitat for modern mammals, low enamel $\delta^{13}C$ values (–14 to –22‰) are indicative for feeding in mesic closed-canopy forests (CERLING ET AL. 2004), intermediate values (–13 to –8‰) for feeding in woodlands and open woodlands and high values (around –8‰) for feeding in xeric C_3 grasslands (CERLING & HARRIS 1999). In contrast, pure C_4 feeders have higher $\delta^{13}C$ enamel values of –1 to +4‰. Intermediate values (–8 to –1‰) would characterize mixed C_3 and C_4 plant feeders (CERLING & HARRIS 1999). For fossil mammals the above mentioned values are shifted 1.5‰ towards more positive values due to the fossil fuel burning effect (FRIEDLI ET AL. 1986).

The teeth from all large herbivores sampled from Sandelzhausen have a mean enamel $\delta^{13}C$ value of –11.4±0.7‰ and a range from –9.2 to –13.9‰ clearly indicating that all herbivores fed on C_3 plants only. The range of enamel $\delta^{13}C$ values is comparable to that of large herbivorous mammals from other Miocene C_3 plant dominated settings, e.g. Ternan, E Africa (14.0 Ma): –8.6 to –13‰ (CERLING ET AL. 1997a); Panama (15 Ma): –10.1 to –15.9‰ (MACFADDEN & HIGGINS 2004) and the Siwaliks, Pakistan (9.2 Ma): –8.1 to –14.6‰ (NELSON 2007). In such a pure C_3 plant ecosystem the inter-taxon differences in enamel $\delta^{13}C$ values (Fig. 2) are related to feeding on C_3 plants with distinct $\delta^{13}C$ values which are either related to differences in habitat (e.g. vegetation openness, humidity, biomass recycling; EHLERINGER ET AL. 1986, 1987; VAN DER MERWE & MEDINA 1989) and/or plant tissues (e.g., leaves, stems, fruits; HEATON 1999; CERLING ET AL. 2004). The enamel $\delta^{13}C$ values of all Sandelzhausen mammals are well in accordance with foraging in woodlands and open woodlands.
However, different digestive physiology, especially the rate of methan formation, can also cause inter-taxon differences in enamel $\delta^{13}C$ values (PASSEY ET AL. 2005). PASSEY ET AL. (2005) found a total range of 5‰ for enamel $\delta^{13}C$ values of different small and large mammals raised on a controlled diet with the same carbon isotopic composition. However, for large ruminant and non-ruminant herbivorous mammals they only found a difference of around 1.3‰. Inter-taxon $\delta^{13}C$ differences larger than that must be caused by other factors. For extinct mammals such as metaschizotheres or palaeomerycids, which have the most distinct isotope compositions of all Sandelzhausen mammals (Fig. 2), the digestive strategy is unknown, hence, its effect on enamel $\delta^{13}C$ values can not be determined. But for Sandelzhausen mammals, a systematic difference in enamel $\delta^{13}C$ values exists even between species using the same digestive physiology, especially between the three sympatric rhinoceros species (Fig. 2), which are all hindgut fermenters. This supports dietary and/or habitat differences being a major factor controlling enamel $\delta^{13}C$ values of the mammal foraging in the C_3 plant ecosystem of Sandelzhausen.

None of the enamel $\delta^{13}C$ values from Sandelzhausen are consistent with a diet derived from closed canopy conditions. In such environments with dense forestcover low light intensities and CO_2 recycling (VAN DER MERWE & MEDINA 1989) herbivores have enamel values lower than –14 to 15‰ (CERLING ET AL. 2004; KOHN ET AL. 2005). However, enamel $\delta^{13}C$ values of ≤ –12‰ and lower for *Metaschizotherium*, *Prosantorhinus* and *Germanomeryx* (Fig. 2) suggest feeding in a closed forest or woodland habitat, relative to the other sympatric mammals. Most taxa, such as *Gomphotherium*, *Lartetotherium*, *Anchitherium* and *Heteroprox* have very similar mean enamel $\delta^{13}C$ values of around –11‰ (Fig. 2), as expected for mammals feeding on average Miocene C_3 plants with a $\delta^{13}C$ value of around –25‰. These taxa were probably non-selective feeders and did not feed on certain food plants and/or in closed or open environments only. The forest hog *Hyotherium* has the highest mean $\delta^{13}C$ value (−10.2‰) and thus ingested the most ^{13}C-rich diet of all taxa from Sandelzhausen and possibly was omnivorous.

Oxygen isotopes – general consideration

Differences in enamel $\delta^{18}O$ values between mammals suggest different sources of ingested waterand may be correlated with feeding ecology and/or the degrees of water dependency (BOCHERENS ET AL. 1996; SPONHEIMER & LEE-THORP 1999; LEVIN ET AL. 2006). Obligate drinkers are expected to have lower $\delta^{18}O$ values compared to mammals that derive most (or all) their water from plant sources (AYLIFFE ET AL. 1990; KOHN 1996) such as leaves or fruits, which are evaporated compared to the source water (DONGMANN ET AL. 1986; YAKIR 1992, 1997).
The palaeomerycid *Germanomeryx fahlbuschi* has the highest mean $\delta^{18}O$ value (–5.7‰) and together with the cervid *Heteroprox eggeri* also the largest range of $\delta^{18}O$ values ($\Delta\delta^{18}O$ = 3.2‰) of all taxa (Fig. 3). Probably *Germanomeryx* foraged preferentially on leaves from the canopy that are ^{18}O-enriched. Most other taxa have mean enamel $\delta^{18}O$ values around –7.5±0.3‰ identical to the locality mean of –7.4‰. Only the *Anchitherium* has a slightly higher mean $\delta^{18}O$ value of –6.6‰, possibly related to feeding on a somewhat more ^{18}O-enriched diet and/or feeding in a more open environment. In contrast, *Heteroporx eggeri* (–8‰) and especially the forest hog *Hyotherium* (–8.4‰) have the lowest mean $\delta^{18}O$ values of all taxa. They probably fed in a more humid environment and/or were more water dependent. Water dependent species track the $\delta^{18}O$ value of meteoric water (LONGINELLI 1984; KOHN 1996; LEVIN ET AL. 2006). Most species in Sandelzhausen have $\delta^{18}O$ values expected for obligate drinkers and the mean $\delta^{18}O$ value is similar to those of large mammals from other localities in southern Germany (Tütken et al. 2006).

The 4 teeth analyzed for their phosphate oxygen isotope composition ($\delta^{18}O_{PO4}$) allow a mean meteoric water $\delta^{18}O_{H2O}$ value of –5.7±0.7‰ VSMOW to be calculated, given their species-specific $\delta^{18}O_{PO4}$– $\delta^{18}O_{H2O}$ relations for modern horses (HUERTAS ET AL. 1995), elephants (AYLIFFE ET AL. 1992), and rhinoceroses (TÜTKEN ET AL. 2006). This value provides an estimate of a mean $\delta^{18}O$ value for the Middle Miocene meteoric water and is similar to those reconstructed for other Miocene localities of Germany (TÜTKEN ET AL. 2006, Tütken unpublished data). Using a MAT–$\delta^{18}O_{H2O}$ regression based on modern precipitation and air temperature data for Germany and Switzerland (see TÜTKEN ET AL. 2006 for details), a mean MAT of 18.7±1.7°C can be calculated for Sandelzhausen, which is about 10°C warmer than today. Due to the small sample size this derived MAT has to be considered with caution, but it is reasonable because the Middle Miocene was the warmest period of the Neogene (ZACHOS ET AL. 2001). Furthermore, it is in good agreement with a MAT estimate >17.4°C based on

the occurence of thermophilic lower vertebrates in Sandelzhausen and southern Germany (BÖHME 2003).

In the following the isotopic results for each of the 9 investigated mammal taxa from Sandelzhausen will be discussed in more detail and in the context of known information about their diet.

Diet of *Metaschizotherium bavaricum*

Metaschizotherium bavaricum, the extinct, large, claw-bearing Perissodactyl, is a rare faunal element in the Sandelzhausen fauna. The occurrence of *Metaschizotherium* indicates the presence of trees, although not necessarily with a dense tree cover. Metaschitzotheres were probably bipedal brachydont browsers mostly interpreted to be leaf-eating herbivores (e.g., HEISSIG 1999). However, their diet is still a matter of debate. Recent mesowear results suggest that *Metaschizotherium bavaricum* was a browser that fed on both non-abrasive plants but also abrasive fibrous and tough plant material such as bark, twigs, and branches likely in a closed, non-dusty forest environment (SCHULZ ET AL. 2007; COOMBS this issue; SCHULZ & FALKE this issue). Feeding in a more closed, forested environment is well in accordances with the lowest mean (–12.7‰) as well as the lowest single enamel $\delta^{13}C$ value (–13.9‰) for *Metaschizotherium* of all Sandelzhausen mammals. However, this value was obtained from a first molar (M1). Assuming a similar dental development strategy as for other large mammals, this value might be influenced at least to some extend by the mother milk composition as the M1 mineralizes after birth and mostly before weaning. But even excluding the M1, the mean value (–12.4‰) is still low. Only the small rhinoceros *Prosantorhinus germanicus* has a similarly low mean $\delta^{13}C$ value (Fig. 2). Such a low mean $\delta^{13}C$ value of below –12‰ also supports feeding in a forested woodland (e.g., PASSEY ET AL. 2002), but the values are not as low as would be expected from forest-dwelling subcanopy browsers in a closed canopy environment (CERLING ET AL. 2004). Within a modern rainforest canopy plants growing in gaps of the canopy or leaves, fruits and seeds from the canopy have about 4 to 5‰ higher $\delta^{13}C$ values compared to subcanopy plants (VAN DER MERWE & MEDINA 1989; CERLING ET AL. 2004). Therefore, subcanopy frugivores and folivores as well as omnivores living in open areas within the forest have higher $\delta^{13}C$ values compared to subcanopy browsers (CERLING ET AL. 2004). The magnitude of such canopy effects on plant $\delta^{13}C$ values is much less developed in sparsely forested realms. But still *Metaschizotherium* was probably not using fruits and seeds from the canopy as a major food source because higher enamel $\delta^{13}C$ and especially $\delta^{18}O$ values would be expected as fruits and seeds tend to be enriched in ^{18}O relative to the source water similar as leaves (YAKIR 1992, 1997). However, *Metaschizotherium* has enamel $\delta^{18}O$ values similar to most other large mammals and not such high values as the sympatric palaeomerycid *Germanomeryx fahlbuschi*, that probably was a canopy folivore.

Diet of the rhinoceroses

Rhinoceros are the most abundant large mammals in the Sandelzhausen fauna and there were three sympatric species: *Prosantorhinus germanicus*, *Plesiaceratherium fahlbuschi*, and *Lartetotherium sansaniense* (HEISSIG 1972, 2005 pers. comm.). These rhinoceroses are all relatively well adapted to moist, swampy habitat and indicate a water-rich environment (HEISSIG 2005 pers. comm.). *Prosantorhinus germanicus* is the smallest and most frequent of the three species. It has short legs and mesodont cheek teeth adapted to a somewhat abrasive diet, possibly reeds or other abrasive plants in a swampy environment (HEISSIG 2005 pers. comm.). *Plesiaceratherium fahlbuschi* is a medium-sized species. *Lartetotherium sansaniense* is the least frequent and largest rhinoceros species present in Sandelzhausen. It has low-

crowend cheek teeth and likely fed on a soft diet (HEISSIG 2005 pers. comm.). *Lartetotherium* was probably a less specialized feeder occurring in different habitats and was a long-lived species (HEISSIG 1972).
All three rhinoceros taxa have different mean enamel $\delta^{13}C$ values (Fig. 2), especially the two most abundant species *Prosantorhinus* and *Plesiaceratherium*, which have 1‰ difference in their mean enamel $\delta^{13}C$ values. This indicates the use of isotopically different foodplants due to niche partitioning and/or habitat differences of the sympatric rhinoceros. *Prosantorhinus* has the lowest $\delta^{13}C$ value and could well have been a browser in a partly more closed, forested habitat. *Plesiaceratherium* has an intermediate and *Lartetotherium* the highest mean enamel $\delta^{13}C$ value, hence *Lartetotherium* was probably feeding in a more open environement than the other two species.
All three rhinoceros species seem to have been water dependent species and probably obligate drinkers as they have identical enamel $\delta^{18}O$ values of –7.3‰ similar to the locality mean (Fig. 2). The three rhinoceros species plot distinct from each other in the $\Delta\delta^{18}O$–$\Delta\delta^{13}C$ diagram (Fig. 3). Together with the slightly different mean enamel $\delta^{13}C$ values this supports niche-partitioning of the sympatric rhinoceros. Higher $\Delta\delta^{13}C$ and $\Delta\delta^{18}O$ values indicate the use of different food sources with variable isotope compositions. If this is true, then *Prosantorhinus* would have been the more flexible or generalistic feeder and *Lartetotherium* a more specialized feeder. However, this seems to be in contradiction with palaeontological interpretations (HEISSIG 1972, 2005 pers. comm.). Alternatively, there might also be an influence of body mass on the turnover rate of the blood carbonate pool buffering its isotopic composition from which skeletal apatite forms, as large taxa seem to have lower $\Delta\delta^{13}C$ and $\Delta\delta^{18}O$ values (Fig. 3). A further investigation of dental meso- and microwear might allow better constraints on the dietary niches and feeding behaviour of the sympatric rhinoceros.

Diet of the suid: *Hyotherium soemmeringi*

Hyotherium, a relatively small suid is the most abundant of two suids in Sandelzhausen and the most common Early and early Middle Miocene suoid of Europe (VAN DER MADE this issue). It is interpreted to have lived in humid and closed environments as it is well known from Miocene brown coal deposits and associated with swampy woodland settings (VAN DER MADE this issue).
Hyotherium has the highest mean enamel $\delta^{13}C$ value (–10.2‰) of all taxa from Sandelzhausen (Fig. 2). This value is about 1.2‰ higher than the locality mean $\delta^{13}C$ value of –11.4‰. Due to differences in digestive physiology the carbon isotope fractionation in suids is slightly smaller than for other large mammals (HARRIS & CERLING 2002; PASSEY ET AL. 2005). PASSEY ET AL. (2005) recently determined a $^{13}C_{diet\text{-}enamel}$ enrichment factor of 13.3±0.3‰ for pigs raised on isotopically controlled diet which is smaller than the 14.1‰ for large ungulate mammals (CERLING & HARRIS 1999). Using this smaller enrichment factor *Hyotherium* fed on plants with a $\delta^{13}C$ value of around –23.5‰, while most other large herbivores fed on plants with $\delta^{13}C$ values of about –25‰ or lower. This might either indicate feeding in a more open habitat or feeding on canopy derived fruits or leaves that have higher $\delta^{13}C$ values than subcanopy plants (CERLING ET AL. 2004). As *Hyotherium* is associated with closed, humid environments (VAN DER MADE this issue), feeding in a more open habitat seems unlikely. However, the use of fruits and also scavenging of meat is known from modern African forest hogs (KINGDON 1997; CERLING & HARRIS 2002). Frugivory of *Hyotherium* could explain the elevated $\delta^{13}C$ values, however, frugivory should imply also elevated $\delta^{18}O$ values as fruits tend to be ^{18}O-enriched relative to the source water (YAKIR 1997). But the mean enamel $\delta^{18}O$ value of *Hyotherium* is the lowest for all mammal taxa (Fig. 2, Table 2). An omnivorous diet of *Hyotherium* could explain ^{18}O-depleted values relative to the other

herbivores because carnivores have lower $\delta^{18}O$ values than sympatric herbivores (Sponheimer & Lee-Thorp 1999b; KOHN ET AL. 2005). But due to a smaller carbon isotope fractionation lower enamel $\delta^{13}C$ values are to be expected for carnivores and hence omnivores compared to sympatric herbivores (BOCHERENS 2000). A significant consumption of meat by *Hyotherium* seems thus unlikely. Therefore a fugivorous diet for *Hyotherium* is more likely, especially as modern frugivorous primates in a rain forest setting have lower enamel $\delta^{18}O$ values than sympatric folivorous primates (CERLING ET AL. 2004). Furthermore, the low $\delta^{18}O$ values indicate a high water depencence of *Hyotherium* because obligate drinking mammals tend to have the lowest $\delta^{18}O$ values in terrestrial faunas (KOHN 1996; LEVIN ET AL. 2006). This is in good agreement with observations for modern forest hogs being highly water dependent animals (HARRIS & CERLING 2002) as well as the palaeontological data indicating a humid, closed environment for *Hyotherium* (VAN DER MADE this issue).

Diet of the equid*: Anchitherium aurelianense*

Anchitherium aurelianense is a brachydont equid with teeth lacking extensive cement. It is found in subtropical to warm-temperate habitats and is considered to be a forest-dwelling browser such as the North American *Anchitherium clarencei* (MACFADDEN 2001). However, recent mesowear analyses suggest that *Anchitherium* at Sandelzhausen was a mixed feeder close to the transition to the browsers thus being an opportunistic or at least flexible feeder (KAISER this issue). Such an opportunistic feeding strategy is supported by the fact that *Anchitherium* has the highest $\Delta\delta^{13}C$ value of all taxa from Sandelzhausen (Fig. 3), indicating the use of variable plant resources, however if one tooth enamel sample (FZ EQ SA 2) is excluded the range of $\delta^{13}C$ values is significantly reduced, cautioning the above interpretation. The mean $\delta^{13}C$ value, however, is indistinguishable from those of the largest, probably generalistic, herbivores *Lartetotherium* and *Gomphotherium* but also from the cervid *Heteroprox* (Fig. 2). The mean $\delta^{18}O$ value and also the $\Delta\delta^{18}O$ value of *Anchitherium* are higher than for most other herbivores except for *Germanomeryx fahlbuschi*. This supports incorporation of water from more ^{18}O-enriched and more varied water sources, which is in accordance with a significant consumption of leaves. Given the tooth morphology, the mesowear signal (KAISER this issue) and the enamel carbon and oxygen isotope composition, *Anchitherium aurelianense* from Sandelzhausen probably was a forest or woodland browser, though an intake of some C_3 grass cannot be excluded. In conclusion *Anchitherium* was likely a more flexible feeder than assumed so far.

Diet of the cervid: *Heteroprox eggeri*

In the humid Molasse basin environment usually wet-prefering tragulids are more abundant than cervids, however, Sandelzhausen is an exception with only 10% of the ruminants being Tragulidae and 90% Cervidae (RÖSSNER 2004, this volume). Extensive supply of leaves due to a abundant forest can be assumed because of the high number of five sympatric ruminants at Sandelzhausen (RÖSSNER 2004, this volume). Based on mesowear data *Heteroprox eggeri*, as well as the sympatric ruminant ungulates *Lagomeryx*, *Dorcatherium* and *Germanomeryx* were classified as pure browsers (KAISER & RÖSSNER 2007). The *Heteroprox* mean enamel $\delta^{13}C$ value of -11‰ is indistinguishable from those of *Lartetotherium*, *Gomphotherium*, and *Anchitherium*. Thus *Heteropox* ingested C_3 plants with an average $\delta^{13}C$ value and did not feed in a closed forest environment. *Heteroprox* has a slightly lower $\delta^{18}O$ value than most of the other mammals, except for *Hyotherium*. Therefore, *Heteroprox* was probably not a canopy browser such as *Germanomeryx* because if so, higher $\delta^{18}O$ values would be expected. More likely, *Heteroprox* was a water dependent understory browser in a partially closed forest

environment not ingesting large proportions of water from ^{18}O-enriched plant tissues such as leaves. However, a high $\Delta\delta^{18}$O value indicates that *Heteroprox* has ingested water with variable δ^{18}O values (Fig. 3).

Diet of the palaeomerycid: *Germanomeryx falbuschi*

The extinct paleomerycids were ruminants that are comparable to the extant Okapi living in dense African rainforests. Palaeomerycidae occur in relative high abundance in Sandelzhausen compared to other Miocene sites in S Germany (RÖSSNER 2004, this volume). However, it is not clear whether this is due to sampling bias because of the detailed excavation at Sandelzhausen or is ecology-related due to relatively dense forest in the more proximal basin position (RÖSSNER 2004). Mesowear data of the extraordinary large palaeomerycid *Germanomeryx fahlbuschi* are comparable to the Sumatran rhinoceros and identify the brachydont *Germanomeryx fahlbuschi* as a browser feeding on soft plants while its metapodial bones are interpreted as an adaptation towards swampy ground (KAISER & RÖSSNER 2007; RÖSSNER this volume).
The palaeomerycid *Germanomeryx fahlbuschi* has a mean enamel δ^{13}C value (–12‰) lower than the locality mean and than most other mammals. Only the rhinoceros *Prosantorhinus* and the *Metaschizotherium* have slightly lower δ^{13}C values (Fig. 2). Therefore *Germanomeryx* was probably feeding in a closed woodland which is in good aggreement with ecomorphological data (RÖSSNER this issue). *Germanomeryx* has the highest mean enamel δ^{18}O value (–5.7‰) and together with ther cervid *Heteroprox* also has the largest range of δ^{18}O values (3.2‰) of all herbivores (Fig. 3). Thus *Germanomeryx* ingested water from an ^{18}O-enriched water source, most likely ^{18}O-enriched leaves. Modern girafs as well as giraffids in Miocene settings generally had higher values relative to other faunal elements (CERLING ET AL. 1997a) because of their feeding in the upper canopy where leaf-water δ^{18}O values are high. Therefore, a similar canopy feeding on ^{18}O-enriched leaves seems likely for the palaeomerycid *Germanomeryx fahlbuschi.*

Diet of the proboscid: *Gomphotherium subtapiroideum*

The proboscideans of Sandelzhausen are dominated by *Gomphotherium subtapiroideum* that makes up >95% of the proboscidean remains. Deinotheres are lacking, probably due to ecological reasons as they occur contemporarily in other sites in the Molasse basin (SCHMIDT-KITTLER 1972; GÖHLICH this issue). From the *Gomphotherium* mostly juvenile specimens and many decidous teeth are present (SCHMIDT-KITTLER 1972). One decidous D4 tooth (FZ MA SA 2) that formed pre-weaning is likely influenced by the consumption of milk and has slightly lower δ^{13}C and δ^{18}O values than the molars. Milk lipids are five-times depleted in ^{13}C compared to carbohydrates and proteins (DENIRO & EPSTEIN 1978), thus enamel apatite synthesized before weaning may have lower δ^{13}C values than bioapatite synthesized after weaning. The magnitude of this effect depends on the lipid content of the consumed milk. Therefore, this decidous tooth is excluded in Fig. 2 and for the further discussion.
Interestingly, the mean δ^{13}C value of the tusk enamel samples is about 1‰ lower than the mean δ^{13}C value of the five molar teeth (Fig. 2). Similar systematic differences between *Gomphotherium* molar and tusk enamel have been observed for North American *Gomphotherium* (FOX & FISHER 2004). The reasons for this offset are not clear. Continously growing tusks and finite growing molars represent different periods of the ontogeny and may therefore record different dietary compositions. This, however, does not explain why tusk enamel always has lower δ^{13}C values compared to molar enamel. An effect from the mother milk consumption on the isotope composition is unlikely as the tip of the tusk is the oldest

portion and the basal region which was analyzed (Fig. 4) also formed after weaning. However, the preservation of such small but significant differences in enamel $\delta^{13}C$ values between tusk and molar enamel indicates that such differences in isotope composition have not been biased by diagenetic alteration. Based on the enamel $\delta^{13}C$ values *Gomphotherium subtapiroideum* was probably a browser or mixed feeder with preference for C_3 browse with no seasonal variation in diet, similar as North American *Gomphotherium* (FOX & FISHER 2004). This is in agreement with its subtapiroid-bunodont and brachydont morphology of the cheek teeth and the interpretation relating *G. subtapiroideum* to a humid woodland biotope (SCHMIDT-KITTLER 1972; GÖHLICH this issue).

From one *Gomphotherium* tusk part of the enamel band was serially sampled (Fig. 4). The sampled interval of 65 mm of the *Gomphotherium subtapiroideum* tusk enamel band probably represents about 1.5 years of tusk growth, assuming a similar tusk growth rate of 45 mm/year as for Miocene North American *Gomphotherium* (FOX 2000). The small intra-tusk variability of the enamel $\delta^{13}C$ values (–11.9±0.1‰, n = 16) of the *Gomphotherium* tusk suggests a fairly constant carbon isotope composition of the C_3 plants ingested by this individual over the period of enamel mineralization. No seasonal change in dietary resource use and/or habitat is recorded in the $\delta^{13}C$ values. Similarly low intra-tusk $\delta^{13}C$ variability has been found for North American *Gomphotheriums* (FOX & FISHER 2001, 2004). This might relate to a generalistic, unselective feeding strategy of such a large herbivore or mobility over larger landscape scales integrating a variety of food resources as proboscideans are known to migrate over several 100 km even on a seasonal basis (HOPPE ET AL. 1999).

Intra-tusk $\delta^{18}O_{CO3}$ values have only a small range of 1.8‰ and display no clear seasonal pattern (Fig. 4). Even if some dampening of the environmental $\delta^{18}O$ input signal is likely due to enamel maturation (PASSEY & CERLING 2002), no pronounced seasonality is recorded. The proximity of groundwater-fed sources and the large body size may explain a certain isotopic buffering of *Gomphotherium* body water. Nevertheless, surface drinking water resources used by this *Gomphotherium* did not have a pronounced seasonal $\delta^{18}O$ cyclicity. This is in agreement with the warm, subtropical to temperate Middle Miocene climate in S Germany (BÖHME 2003, this study) and the relatively humid conditions in the floodplain environment of Sandelzhausen with year-round high groundwater level (SCHMID 2002).

Mobility of the large mammals

The strontium isotope compositions ($^{87}Sr/^{86}Sr$ = 0.710382±0.0002, n = 4) of the *Anchitherium* tooth and three *Gomphotherium* teeth is relatively similar and significantly more radiogenic than enamel of other Miocene large mammal teeth from the Molasse basin realm (Fig. 5, TÜTKEN ET AL. 2006). The bioavailable Sr ingested by these mammals during the period of enamel mineralisation thus originates from soils and rocks with high $^{87}Sr/^{86}Sr$ ratios ≥ 0.710. The clastic sediments of the floodplain in the eastern part of the Molasse basin, mostly alpine detritus, seem to have higher bioavailable $^{87}Sr/^{86}Sr$ ratios than those in other localities in southern Germany and Switzerland (Fig. 5). At least the four investigated mammals did not take up large amounts of food in areas with bioavailable $^{87}Sr/^{86}Sr$ ratios lower than 0.710, such as the marine Jurassic limestone rocks of the Swabian and Franconian Alb ($^{87}Sr/^{86}Sr$ ~ 0.707 to 0.708) north of the Molasse Basin, the western Molasse basin ($^{87}Sr/^{86}Sr$ ~ 0.708 to 0.709), or volcanic areas such as the Hegau Province ($^{87}Sr/^{86}Sr$ < 0.704 to 0.707) NW of Lake Constanz (Fig. 5). Therefore, the mammals have probably lived most of the time on the floodplain environment in the eastern part of the Molasse basin. As the cystalline bedrocks of the Bohemian Massive outcrop in about 50 km distance NE of Sandelzhausen (Fig. 5) a migration and uptake of Sr with high $^{87}Sr/^{86}Sr$ ratios in areas of such old crustal rocks seems

possible. However, it is not possible to infer individual home ranges or exact migrational history from the limited data. Inter- and intra-tooth analyzes, e.g. the serial sampling of proboscid tusks (HOPPE ET AL. 1999), could provide evidence for such potential migrational movements.

Conclusions

All large herbivorous mammals of the Middle Miocene fossil site Sandelzhausen were browsers that fed on C_3 plants with an average $\delta^{13}C$ value of –25.5±1‰. However, niche partitioning and different habitat use within the humid, low relief floodplain C_3 plant ecosystem is indicated by small but significant inter-taxon enamel carbon and oxygen isotope differences. The forest hog *Hyotherium soemmeringi* has the highest $\delta^{13}C$ and lowest $\delta^{18}O$ value of all taxa, possibly related to a frugivorous diet. *Anchitherium* may have had a larger dietary variability than assumed from palaeontological evidence so far. *Metaschizotherium bavaricum*, the small rhinoceros *Prosantorhinus germanicus* and the palaeomerycid *Germanomeryx fahlbuschi* fed in partially closed forests or woodlands. *Germanomeryx* was probably a canopy brower feeding preferentially on ^{18}O-enriched leaves. However, most of the mammals were water dependent browsers in a humid environment as they have similar mean enamel $\delta^{18}O$ values. A $\delta^{18}O_{H2O}$ value of –5.7±1.1‰ VSMOW for the Middle Miocene (~16 Ma) precipitation can be reconstructed from enamel $\delta^{18}O_{PO4}$ values. The herbivores lived in a warm climate with a MAT of about 19°C and low seasonality. Enamel Sr isotope compositions indicate that they ingested their food in the eastern Molasse basin and not in the western Molasse basin or the Franconian Alb plateau.

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Table 1

$\delta^{13}C$ and $\delta^{18}O$ values of enamel apatite

sample	specimen-Nr.	species	tooth position	$\delta^{13}C$ VPDB (‰)	SD	$\delta^{18}O$ VPDB (‰)
FZ CE SA 1	1959 II 6619	*Heteroprox eggeri*	M3	-12.0	0.04	-7.7
FZ CE SA 3	1959 II 6621	*Heteroprox eggeri*	M3	-10.6	0.04	-9.4
FZ CE SA 4	1959 II 4146	*Heteroprox eggeri*	M3	-10.4	0.05	-6.0
FZ CE SA 7	1959 II 4164	*Heteroprox eggeri*	M2	-11.1	0.07	-9.2
FZ CE SA 8	1959 II 5196	*Germanomeryx fahlbuschi*	M	-11.1	0.05	-7.7
FZ CE SA 9	1959 II 5202	*Germanomeryx fahlbuschi*	M dext.	-12.4	0.03	-5.0
FZ CE SA 10	1959 II 5186	*Germanomeryx fahlbuschi*	M	-12.6	0.09	-4.5
FZ CH SA 1	1952 II	*Metaschitzotherium bavaricum*	M	-12.3	0.07	-7.9
FZ CH SA 2	no Nr.	*Metaschitzotherium bavaricum*	P2 or P3	-12.8	0.04	-7.8
FZ CH SA 3	no Nr.	*Metaschitzotherium bavaricum*	M1	-13.9	0.03	-7.1
FZ CH SA 4	no Nr.	*Metaschitzotherium bavaricum*	P4	-12.6	0.05	-8.3
FZ CH SA 5	no Nr.	*Metaschitzotherium bavaricum*	M	-11.9	0.05	-6.3
FZ MA SA 1	BSPG 1959 II 11416	*Gomphotherium subtapiroideum*	I2 dext.	-11.9	0.13	-9.6
FZ MA SA 2	BSPG 1959 II 11326	*Gomphotherium subtapiroideum*	D4 dext	-11.5	0.08	-8.8
FZ MA SA 3	1959 II 44	*Gomphotherium subtapiroideum*	M	-11.5	0.06	-7.2
FZ MA SA 4	no Nr.	*Gomphotherium subtapiroideum*	M	-11.2	0.05	-8.2
FZ MA SA 5	no Nr.	*Gomphotherium subtapiroideum*	M	-10.6	0.04	-8.3
FZ MA SA 6	no Nr.	*Gomphotherium subtapiroideum*	M	-10.2	0.06	-6.8
FZ MA SA 7	no Nr.	*Gomphotherium subtapiroideum*	M	-10.8	0.05	-7.5
FZ EQ SA 1	1959 II 577	*Anchitherium aurelianense*	P2	-11.4	0.10	-6.6
FZ EQ SA 2	no Nr.	*Anchitherium aurelianense*	M or P	-9.5	0.04	-6.5
FZ EQ SA 3	no Nr.	*Anchitherium aurelianense*	M	-11.2	0.05	-7.7
FZ EQ SA 4	no Nr.	*Anchitherium aurelianense*	M	-11.3	0.05	-6.0
FZ EQ SA 5	no Nr.	*Anchitherium aurelianense*	M or P	-11.7	0.05	-7.9
FZ EQ SA 6	no Nr.	*Anchitherium aurelianense*	M	-11.8	0.08	-5.5
FZ EQ SA 7	no Nr.	*Anchitherium aurelianense*	M	-10.6	0.07	-5.7
FZ EQ SA 8	1959 II 5215	*Anchitherium aurelianense*	M	-11.1	0.04	-7.0
FZ RH SA 1a	1959 II 6793	*Plesiaceratherium fahlbuschi*	M3	-11.3	0.04	-6.3
FZ RH SA 1c	1959 II 6793	*Plesiaceratherium fahlbuschi*	M1	-11.6	0.06	-7.5
FZ RH SA 2a	1959 II 6793	*Plesiaceratherium fahlbuschi*	P4	-11.0	0.05	-7.7
FZ RH SA 2b	1959 II 4416	*Plesiaceratherium fahlbuschi*	P3	-11.1	0.07	-7.8
FZ RH SA 3	1959 II 5149	*Plesiaceratherium fahlbuschi*	M3	-11.4	0.04	-6.0
FZ RH SA 4	1959 II 3530a	*Plesiaceratherium fahlbuschi*	M3	-11.9	0.04	-7.7
FZ RH SA 5	1959 II 7002	*Plesiaceratherium fahlbuschi*	M2	-12.0	0.04	-7.4
FZ RH SA 6	1959 II 6748	*Plesiaceratherium fahlbuschi*	M3	-12.5	0.03	-7.3
FZ RH SA 7a	no Nr.	*Lartetotherium sansaniense*	M3	-11.5	0.04	-7.8
FZ RH SA 7b	no Nr.	*Lartetotherium sansaniense*	M2	-11.6	0.06	-7.7
FZ RH SA 8	no Nr.	*Lartetotherium sansaniense*	M3	-10.7	0.05	-7.1
FZ RH SA 9	1959 II 3817	*Lartetotherium sansaniense*	P2	-10.2	0.02	-6.5
FZ RH SA 10	1959 II 6742	*Prosantorhinus germanicus*	P4	-12.9	0.05	-6.0
FZ RH SA 11	no Nr.	*Prosantorhinus germanicus*	M3	-11.8	0.04	-8.1
FZ RH SA 12	1959 II 2595	*Prosantorhinus germanicus*	M3	-13.6	0.03	-7.1
FZ RH SA 13	1959 II 2676	*Prosantorhinus germanicus*	M2	-11.7	0.05	-7.1
FZ RH SA 14	no Nr.	*Prosantorhinus germanicus*	P3	-12.5	0.04	-7.6
FZ RH SA 15	no Nr.	*Prosantorhinus germanicus*	M3	-12.1	0.05	-7.4
FZ SU SA 1	1959 II 311	*Hyotherium soemmeringi*	M2	-10.8	0.05	-9.8
FZ SU SA 2	1959 II 238	*Hyotherium soemmeringi*	M3	-9.6	0.04	-8.2
FZ SU SA 3	1959 II 265	*Hyotherium soemmeringi*	P	-11.1	0.05	-7.8
FZ SU SA 4	1959 II 265	*Hyotherium soemmeringi*	P4	-11.2	0.06	-8.1
FZ SU SA 5	1959 II 266	*Hyotherium soemmeringi*	M	-10.1	0.06	-8.6
FZ SU SA 6	1959 II 266	*Hyotherium soemmeringi*	M	-9.9	0.06	-9.0
FZ SU SA 7	no Nr.	*Hyotherium soemmeringi*	P	-9.2	0.06	-6.7
FZ SU SA 8	no Nr.	*Hyotherium soemmeringi*	I	-9.6	0.07	-8.7

Table 2
Mean enamel $\delta^{13}C$ and $\delta^{18}O$ values

species	n	$\delta^{13}C_{VPDB}$ (‰)	SD	range	$\delta^{18}O_{VPDB}$ (‰)	SD	range (‰)
Germanomeryx fahlbuschi	3	-12.0	0.8	-12.6 to -11.1	-5.7	1.7	-7.7 to -4.5
Metaschitzotherium bavaricum	5	-12.7	0.8	-13.9 to -11.9	-7.5	0.8	-8.3 to -6.3
Prosantorhinus germanicus	6	-12.4	0.7	-13.6 to -11.7	-7.2	0.7	-8.1 to -6.0
Plesiaceratherium fahlbuschi	8	-11.6	0.5	-12.5 to -11.0	-7.2	0.7	-7.8 to -6.0
Lartetotherium sansaniense	4	-11.0	0.7	-11.6 to -10.2	-7.3	0.6	-7.8 to -6.5
Gomphotherium subtapiroideum	7	-11.1	0.6	-11.9 to -10.2	-8.1	1.0	-9.6 to -6.8
Heteroprox eggeri	4	-11.0	0.7	-12.0 to -10.4	-8.1	1.6	-9.4 to -6.0
Anchitherium aurelianense	8	-11.1	0.7	-11.8 to -9.5	-6.6	0.9	-7.9 to -5.5
Hyotherium soemmeringi	8	-10.2	0.7	-11.2 to -9.2	-8.4	0.9	-9.8 to -6.7

Table 3
$\delta^{13}C$ and $\delta^{18}O$ values of serial sampled gomphotherium tusk enamel

Sample	Distance [mm]	$\delta^{18}O$ VPDB [‰]	SD	$\delta^{13}C$ VPDB [‰]	SD	$CaCO_3$ wt%
FZ MA SA 3-1	1	-9.0	0.3	-12.0	0.2	3.8
FZ MA SA 3-2	3	-9.0	0.2	-12.1	0.2	4.5
FZ MA SA 3-3	5	-9.4	0.2	-12.0	0.1	4.2
FZ MA SA 3-4	9	-10.3	0.3	-11.9	0.2	3.7
FZ MA SA 3-5	12	-9.7	0.2	-12.0	0.1	3.8
FZ MA SA 3-6	15	-10.1	0.2	-12.2	0.1	3.6
FZ MA SA 3-7	19	-9.6	0.3	-11.8	0.1	3.9
FZ MA SA 3-8	25	-9.3	0.2	-12.2	0.1	4.2
FZ MA SA 3-9	28	-9.6	0.2	-11.8	0.2	4.1
FZ MA SA 3-10	32	-9.9	0.2	-12.0	0.1	4.3
FZ MA SA 3-11	36	-10.2	0.2	-11.9	0.2	3.8
FZ MA SA 3-12	40	-9.4	0.2	-12.1	0.1	4.0
FZ MA SA 3-13	45	-10.8	0.2	-11.9	0.1	3.9
FZ MA SA 3-14	50	-9.2	0.1	-11.7	0.1	4.8
FZ MA SA 3-15	54	-9.7	0.2	-11.7	0.1	4.4
FZ MA SA 3-16	58	-9.3	0.1	-11.9	0.1	4.7

Table 4
Enamel $\delta^{18}O_{PO4}$ values and calculated drinking water $\delta^{18}O_{H2O}$ and MAT values

sample	$\delta^{18}O_{CO3}$ VSMOW (‰)	SD	$\delta^{18}O_{PO4}$ (‰)	SD	n	$\delta^{18}O_{H2O}$ VSMOW (‰)	MAT (°C)
FZ EQ SA 1	24.1	0.19	19.0	0.4	3	-5.6	19.3
FZ MA SA 4	22.4	0.09	17.9	0.3	3	-5.8	19.1
FZ RH SA 1	24.4	0.06	18.2	0.5	3	-5.3	20.1
FZ RH SA 7a	22.9	0.13	15.9	0.0	3	-7.0	16.2

Table 5
Strontium isotope composition of tooth enamel

sample	Species	$^{87}Sr/^{86}Sr$	2σ
FZ EQ SA 1	*Anchitherium aurelianense*	0.710319	0.000009
FZ MA SA 3	*Gomphotherium subtapiroideum*	0.710628	0.000009
FZ MA SA 4	*Gomphotherium subtapiroideum*	0.710427	0.000010
FZ MA SA 5	*Gomphotherium subtapiroideum*	0.710154	0.000010

Figure 1

Fig. 1. Fossil locality of Sandelzhausen in the North Alpine Foreland basin. Map from Göhlich (2002).

Figure 2

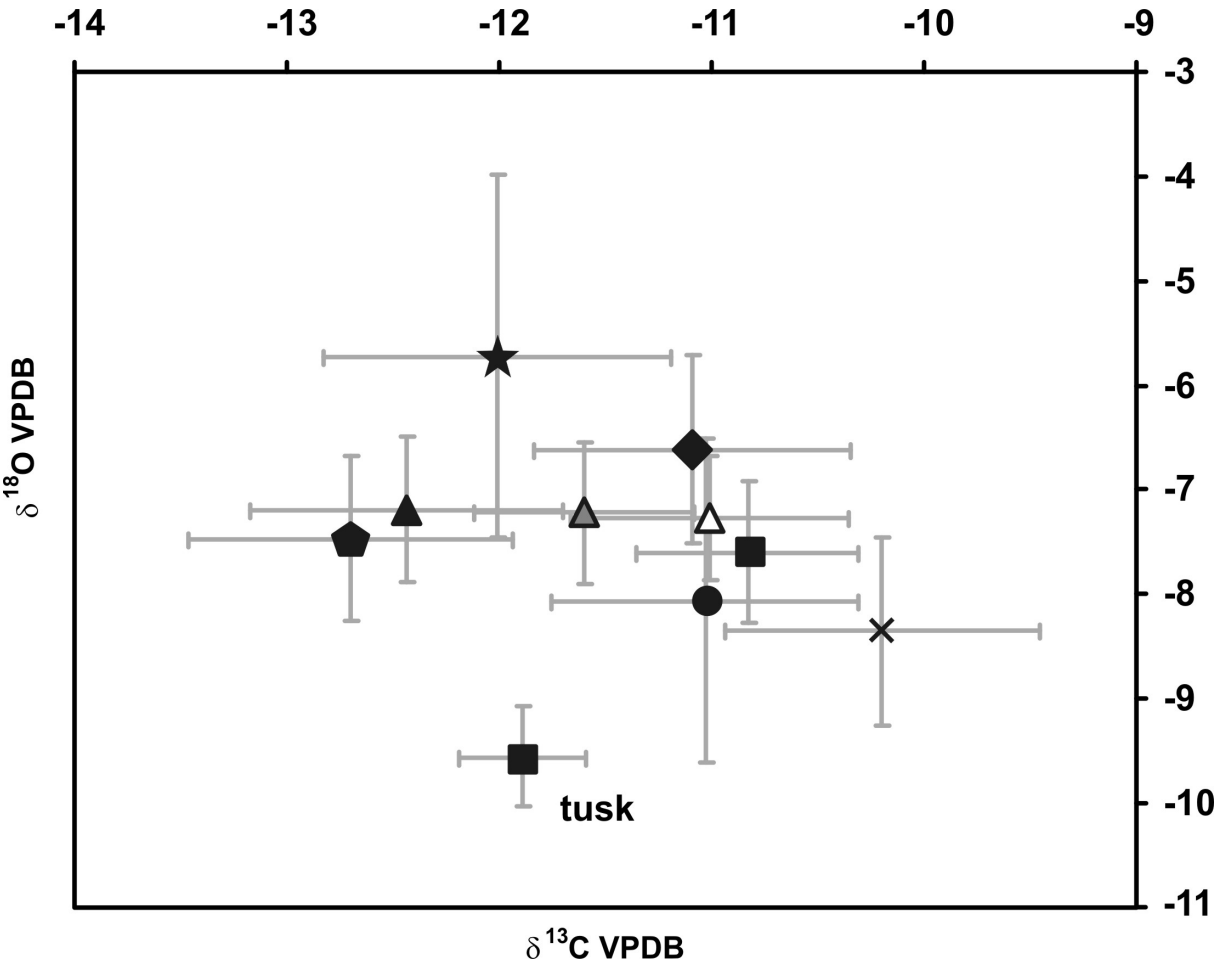

Fig. 2: Enamel carbonate mean $\delta^{13}C$ and $\delta^{18}O$ values and one standard deviations of the 9 analyzed mammal taxa from Sandelzhausen: *Metaschizotherium bavaricum* ⬟, the three rhinoceroses *Prosantorhinus germanicus* ▲, *Plesiaceratherium fahlbuschi* ◬, and *Lartetotherium sansaniense* △, the equid *Anchitherium aurelianense* ◆, the cervid *Heteroprox eggeri* ●, the palaeomerycid *Germanomeryx fahlbuschi* ★, the suid *Hyotherium soemmeringi* ✕, the proboscid *Gomphotherium subtapiroideum* ■. For the mean value of *Gomphotherium* the D4 tooth and tusk were excluded for reasons explained in the text. The mean value of the data from the tusk sample (Table 3) is shown separately. Analytical error is about the symbol size.

Figure 3

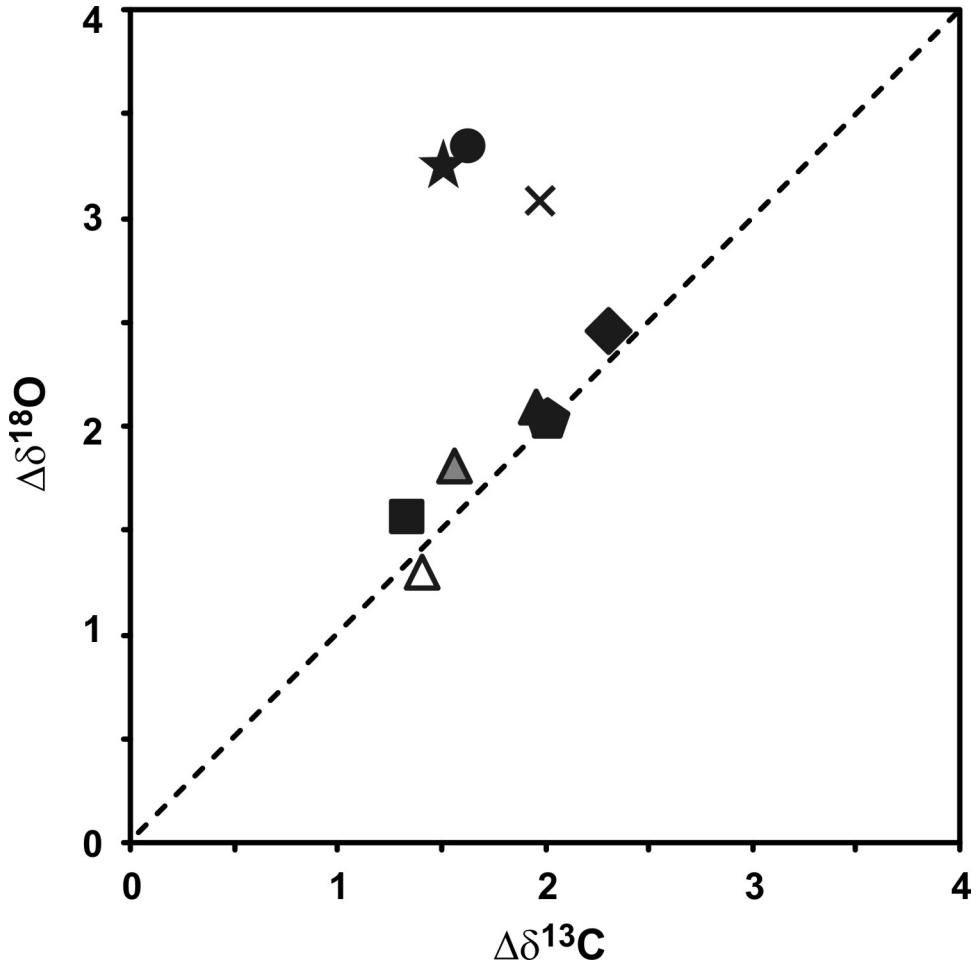

Fig. 3: Intra-taxon ranges of enamel carbon ($\Delta\delta^{13}C$) and oxygen ($\Delta\delta^{18}O$) compositions of the 9 analyzed mammal taxa from Sandelzhausen. Same symbols as in Figure 2. For *Gomphotherium* the D4 tooth and the tusk were excluded for reasons explained in the text.

Figure 4

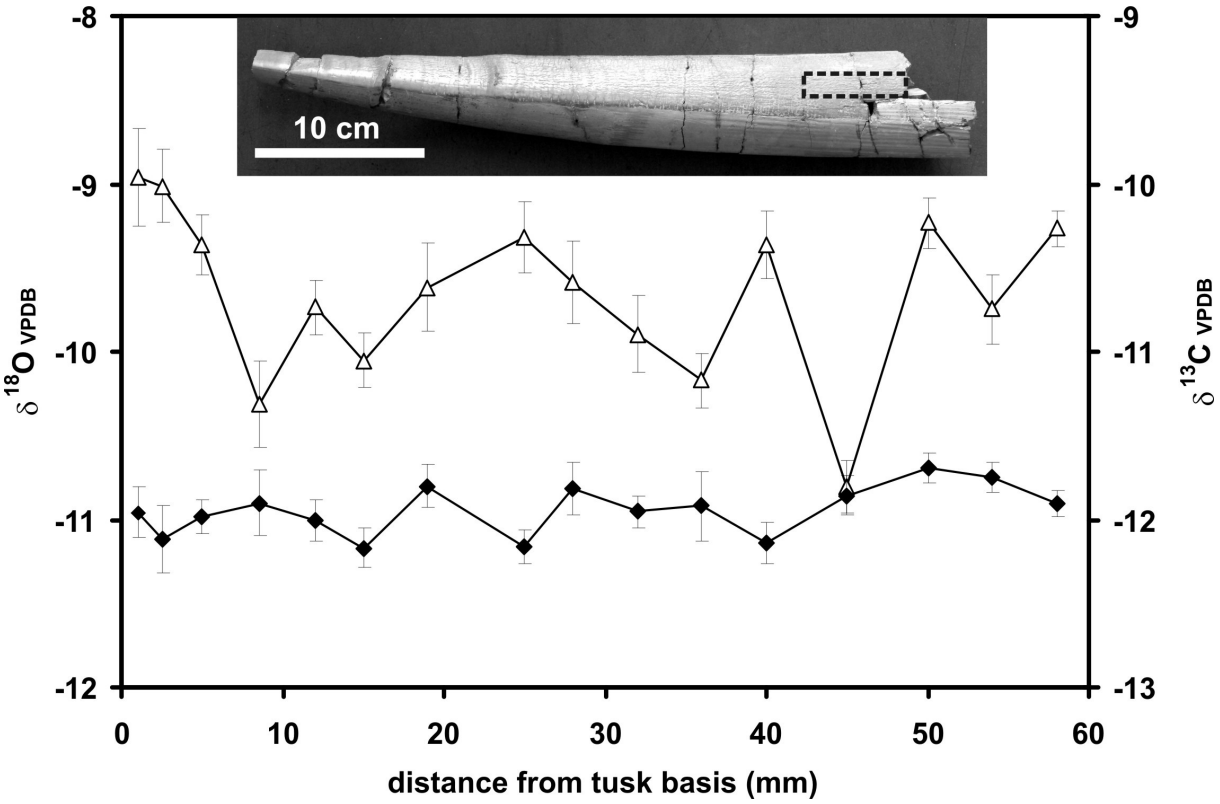

Fig. 4. Carbon (♦) and oxygen (Δ) isotope data from the serially sampled *Gomphotherium subtapiroideum* tusk (FZ MA SA 3, Table 3). The stippled rectangle in the inset photograph shows the part of the tusk from which the 16 samples were taken.

Figure 5

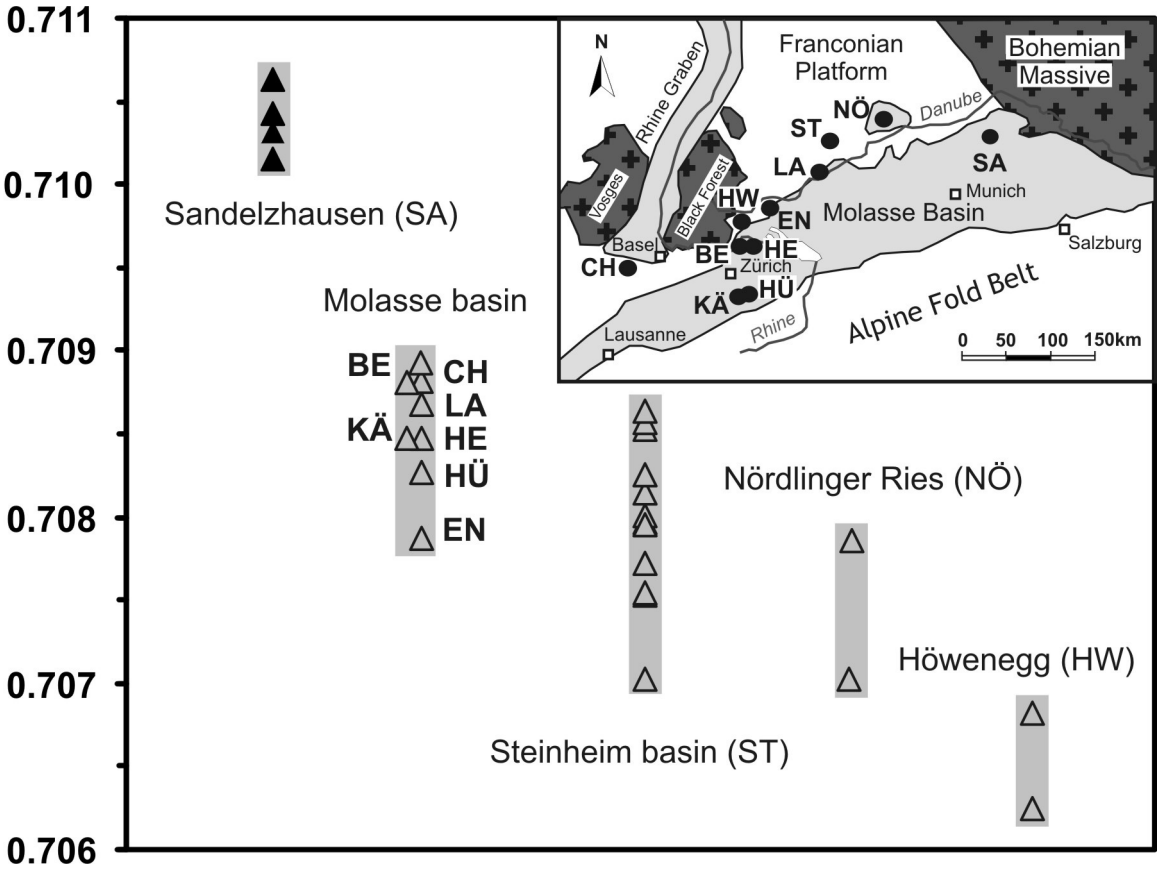

Fig. 5. Sr isotope compositions of enamel from fossil mammal teeth from Miocene localities in southern Germany and Switzerland. ▲ Sandelzhausen, this study ; ▲ $^{87}Sr/^{86}Sr$ data from Tütken et al. (2006) and Tütken unpublished data: **CH**: Charmoille, Switzerland; **BE**: Benken, Switzerland; **LA**: Ulm Langenau, SW Germany; **HE**: Helsighausen, Switzerland; **KÄ**: Käpfnach, Switzerland; **HÜ**: Hülistein, Switzerland; **EN**: Engelswiese, SW Germany; **ST**: Steinheim, Swabian Alb, SW Germany; **NÖ**: Nördlinger Ries, Swabian Alb, S Germany; **HW**: Höwenegg, Hegau, SW Germany.