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Mobility and origin of camels in the Roman Empire through serial stable carbon and oxygen isotopes variations in tooth enamel

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Abstract

Although camels are not indigenous to Europe, they have been found at several sites from several Roman provinces dating from the beginning of the 1st century AD onwards. It must have been beneficial to bring them there. Based on finds of remains from juvenile individuals (e.g. from Tanais), it has been suggested that the Romans might have systematically bred camels within Europe. For this study we took serial samples of the enamel of four camels from European sites (Innsbruck-Wilten, Mamer-Bertrange, Tongeren, and Trier) dating to the 2nd - 4th century AD. We measured the relative abundances of carbon and oxygen isotopes of the carbonate fraction from the tooth enamel. The continuous record of oxygen and carbon isotopic composition of the intra tooth enamel serial samples reflects the climate and habitat in which an individual lived during the time of tooth mineralization. We used these data to make a rough evaluation of the areas of origin consistent with the relative abundances of the isotopes from the enamel of the camels and attempt to reconstruct their life history and mobility behavior based on the different ecological characteristics of the habitats represented in the isotopic data. Furthermore, the data can function as an additional proxy for species determination, due to the different habitats of Camelus bactrianus and Camelus dromedarius. This work also yields interesting insights on the similarities in the mobility pattern of the camels from Mamer-Bertrange and Trier. In combination with archaeological evidence, it was possible to tentatively connect them with specific military units, i.e. the detachments of the Legio VIII Augusta.

Keywords

animal mobility, enamel, intra-tooth serial sampling, stable isotopes, carbonates, Roman era

1. Introduction

Without camels, many places in the world would be uninhabitable for humans. Although camels are not indigenous to Europe, their skeletal remains have been found at several sites in different Roman provinces, dating from the beginning of 1st to the 4th century AD. Currently, 70 sites with finds of camel or dromedary bones are known (Dövener et al., 2017). In the last decades, several studies have investigated camels from the Roman Empire (Morales Muñiz et al., 1995; Bartosiewicz, 1996; Bartosiewicz and Dirjec, 2001; Grossi Mazzorin, 2006; Pigière and Henrotay, 2012; Vuković and Bogdanović, 2013; Bălăşescu, 2014; Daróczi-Szabó et al., 2014; Vuković-Bogdanović and Blažić, 2014; Oelschlägel and Dövener, 2016; Tomczyk, 2016; Dövener et al., 2017). Camels are especially useful in arid regions, but their translocation to Europe, with its very different climatic conditions, in Roman times, suggests that they had a special role there.

In general, camels are multifunctional animals that can be used in many different ways. In the Roman Empire they were used as beasts of burden, both in a military and civil trade context. The camel rider units of the Roman army, the so-called *dromedarii*, were mostly used for the logistics that accompanied warfare (Toynbee, 1973; Peters, 1998; Link, 2006). Probably the first function one might think of is them being part of caravans, transporting trade goods. This was of greatest importance in North Africa, the Near East associated with the incense trade in Arabia, and along the trade routes to Central Asia and China, for example along the so-called Silk Road. The Bactrian camels found in the Greek cities on the northern shore of the Black Sea served this purpose (Kron, 2014). In addition to their adaption to arid environments, they were also superior to other means of transport available at that time for other reasons. Unlike carts, camels do not rely on roads and require a smaller work force. In addition, they are also a faster option when compared to oxcarts in arid conditions (Bulliet, 1975).

As some of the finds were associated with amphitheaters (e.g. Cartago Nova (Morales Muñiz et al., 1995), Paris-Arènes de Lutèce (Dierkens et al., 2005), and Vindonissa (Schmid, 1952-1953)), they could also have played a role in the *ludi*, public festivals which included sports, artistic activities, animal fighting, and initially also religious rites (Freyburger, 2006). Historical sources definitely mention camels as being part of races in the *circus* (Geoponica XVI, 22; Scriptores Historiae Augustae, Elagabalus XXIII, 1; Suetonius, Nero XI, 1; Cassius Dio, LX, 7), but they could have also just been put on display given their exotic nature.

Additionally, there is pictorial evidence from North Africa of camels harnessed to ploughs and of their use in agricultural contexts, for example on a Roman tombstone from Libya (Benecke, 1994). Considering the climatic conditions in Europe, which are not favorable for the health of dromedaries in particular, but also for Bactrian camels, usage as draught animals in agriculture was probably not one of the reasons why the Romans brought them into these areas. Camel products like milk, meat and hair were used in the areas where these animals are indigenous. There is some evidence

that their milk was also at least occasionally used in the Roman Empire (Pliny the Elder, XI, 96; Pliny the Elder, XXVIII, 33). Elagabalus (Scriptores Historiae Augustus, Elagabalus XX, 5) allegedly ate the heels of the feet of camels as a delicacy. Another historical source, a papyrus letter from Egypt, also mentions the consumption of camel meat (Reinard, 2016). Butchery marks on camel bones have been detected previously, for example on a cervical vertebra from La Bourse, a Roman site in Marseille (Pigière and Henrotay, 2012) and in *Viminacium* (Serbia), where bone marrow was extracted (Vuković and Bogdanović, 2013). However, this is not the case for any of the four sites analyzed in this study.

1.1 Aims

The aim of this study is threefold. First, we want to use the isotopic data to estimate possible areas of origin and especially excluding others. Changes of habitat visible in the continuous record of relative abundances of C and O isotopes along the tooth crown will be used to reconstruct their mobility through their early life. In combination with archaeological and historical data we will attempt to infer the use of these four camels in the Roman Empire. Second, with our data we will contribute to the still debated question of whether the Romans bred camels in Europe or not. The breeding of camels outside of their indigenous habitat during the Roman Empire has already been suggested based on the find of a juvenile camel at Tanais, Russia (Tomczyk, 2016). However, this has not been able to be confirmed with any direct evidence until now. Our data could test if an individual camel spent its early years of life in a temperate habitat with a purely C_3 vegetation like Europe or not. Additionally, we also wanted to test if our data can be used as an additional proxy to distinguish between Bactrian camels (C. bactrianus) and dromedaries (C. dromedaries) based on the complementary geographical distribution of both camel species. Distinguishing between them solely on skeletal morphology is very difficult.

1.2 Biological Background

genus Camelus comprises two extant species, C. dromedarius and The *C. bactrianus*, whose habitats are complementary distributed with only a small area of overlap in the east and west of the Black Sea (Fig. 1). Both species are adapted to dry habitats with annual precipitation of 500 mm or less: C. dromedarius occurs in Africa; Arabia and the Near and Middle East, whereas C. bactrianus inhabits the areas north of the 21 °C isotherm from, Asia Minor to China (Sorge, 2006). Distinguishing the two camel species solely based on the osteological record is very difficult as most of the measurements overlap (Lesbre, 1903; Smuts and Bezuidenhout, 1987; Olsen, 1988; Köhler-Rollefson, 1989; Steiger, 1990; Martini et al., 2017). Therefore species identification is mostly done qualitatively based on osteomorphology (Steiger, 1990). Moreover, most of the studies focused solely on the postcranium. Species identification is further complicated as growth is heavily influenced by castration and its timing, and the Romans already practiced hybridization to get bigger and stronger individuals (Peters, 1998). The earliest zooarchaeological evidence for deliberately breeding camel hybrids comes from

Mleiha (United Arabian Emirates, 1st – 2nd century AD) (Jasim, 1999; Uerpmann, 1999), Troy (western Turkey, Roman era) (Uerpmann, 1999, p. 113), and Pella (Jordan, 747 AD) (Köhler-Rollefson, 1989).

As the two camel species inhabit complementary distributed habitats (Fig. 1) with different environmental conditions (Fig. 2), isotopic analysis can be used as an additional proxy for species determination. Oxygen isotope values (δ^{18} O) are sensitive to temperature (Koch, 2007) thus the difference between hot and cold arid habitats of the dromedaries and Bactrian camels respectively should be clearly visible in the data. The carbon isotope values (δ^{13} C) on the other hand, differ between C₃ and C₄ plants, as they use different photosynthetic pathways for carbon fixation (Koch, 2007). These plant types are not distributed evenly across the globe (Ehleringer, 2005; Osborne et al., 2014). Bactrian camels predominantly live in areas where the C₄ plants are much less abundant than the areas where dromedaries live, which should again lead to significantly different carbon isotopic abundances.

1.2.1 Stable isotope analysis

The isotopes of an element differ in the number of neutrons. Due to the slightly different masses, they do not react in the exact same way in chemical or physical processes. Depending on the element that is used in stable isotope analysis, this fractionation gives information on various characteristics of past environments, such as temperature and aridity in the case of oxygen (O) or diet and vegetation in the case of carbon (C).

The carbon atoms incorporated in the carbonate fraction of the enamel originate from the diet of an organism. In herbivores, this is an indicator for the plants they have eaten during the time of incorporation by the analyzed tissue. Bioapatite is enriched by ~ 14 ‰ in large ruminant mammals such as in cattle or camels in comparison to their diet (Cerling and Harris, 1999; Passey et al., 2005). Carbon isotopes are very useful in distinguishing C_3 and C_4 plants (Deines, 1980; Martinelli et al., 1991). Different plant species use different pathways and therefore develop distinctive isotopic ratios. The two main photosynthetic pathways are called C_3 (or Calvin cycle, which is present in all plants) and C₄ (or Hatch and Slack cycle) pathway. The first stable photosynthetic product in the Hatch and Slack cycle is oxaloacetate, which contains four carbon atoms, in contrast to phosphoglycerate in the C₃ pathway, which only contains three carbon atoms. Due to this difference in carbon fixation, C₄ plants discriminate less against the heavier carbon isotope, resulting in higher δ^{13} C values ranging from -10 to -20 ‰ (Bender, 1971; Pfadenhauer and Klötzli, 2014). Measurements of carbon isotope ratios of modern plants result in average $\delta^{13}C$ values of -27 ‰ for C₃ and -13 ‰ for C₄ taxa (Bender, 1971). Considering the isotopic fractionation between enamel and diet in large ruminant mammals, their enamel exhibits δ^{13} C values of around -13 % when they are feeding on C₃ plants only and around 1 ‰ when their diet consists entirely of C₄ plants (Cerling and Harris, 1999). In predominantly C₃ environments like Europe, δ^{13} C values also differentiate open habitats from ones with closed canopy (Drucker et al., 2008; Hofman-Kaminska et al., 2018).

The δ^{18} O values of skeletal tissue result from the isotopic composition of body water (Ambrose and Norr, 1993; Tieszen and Fagre, 1993). More than half of the oxygen intake enters the body through the diet and drinking water. This influx is not subject to fractionation when incorporated into body water. There is nevertheless a constant offset between the δ^{18} O values of body water and carbonate (CO₃) within the bioapatite found in teeth and bone (ca. 26 ‰) (Koch, 2007).

Meteoric water or precipitation is the source for the majority of terrestrial water sources. Fractionation occurs during evaporation, condensation and precipitation. The relative abundances of the oxygen isotopes are influenced by altitude, distance from the coast, amount of precipitation and temperature. Although the underlying principles are the same around the globe, their magnitude is dependent on local factors, such as geography and topography (Dansgaard, 1964; Pederzani and Britton, 2019). When plants are incorporating soil water no fractionation takes place (Wershaw et al., 1966; Dawson and Ehleringer, 1991). Therefore, the δ^{18} O values of leaf water are highly dependent on the isotopic composition of precipitation and local modifiers such as catchment areas of rivers. Although no fractionation takes place when plants take up water, they display highly elevated δ^{18} O values in leaf water. This is caused by evapotranspiration through leaf stomata (Barbour, 2007). The reason why it is so important to discuss leaf water is that species that are adapted to arid environments obtain a large quantity of the water necessary for their metabolism from the ingested plant parts that are enriched with ¹⁸O. These draught tolerant animals normally display more positive δ^{18} O values due to this behavior. This of course is also true for camels, which are an exemplary type of species adapted to dry environments that acquires a significant proportion of its water through its plant food. In contrast δ^{18} O values of obligate drinking species mirror closely the δ^{18} O values of precipitation.

The indigenous habitats of dromedaries and Bactrian camels, as well as European habitats differ significantly in their climatic and environmental conditions. Habitat changes are therefore anticipated to be visible as shifts within the continuous isotopic record obtained from the intra-tooth serial samples. Refering to global models of δ^{13} C and δ^{18} O values of vegetation, we expect the highest δ^{13} C and δ^{18} O values in North Africa. They should then continuously decrease in the Near and Middle East, Central Asia and Europe, which is a purely C₃ habitat with temperate climate (Fig. 2) (Ehleringer, 2005; Suits et al., 2005; West et al., 2018). Exceptions are areas like Italy where there has been evidence for millet cultivation since the Bronze Age (Tafuri et al., 2009).

1.2.2 Tooth mineralization

Tooth mineralization or amelogenesis is a discontinuous progress starting at the crown and ending at the root. The timing varies between species and between

different teeth within a species. Amelogenesis can be divided into two different processes. Firstly, matrix secretion occurs where a primary hydrated matrix forms, which is rich in proteins and poor in minerals (10 - 20 %). Then the maturation stage begins, during which the majority of the mineralization takes place (Passey and Cerling, 2002; Balasse, 2003). This is often referred to as secondary mineralization process. It proceeds in successive waves across the enamel layer. There are differences in the timing of enamel maturation between different locations of the tooth enamel. The innermost layer right above the dentine is the first to be heavily mineralized, whereas the outermost layer is the last one. Nevertheless studies of changes in the isotopic abundances over time can still be undertaken as the chronological sequence is still represented within the record (Balasse, 2003).

When the tooth is fully mineralized the root starts to grow and the tooth begins to erupt (Min Gan et al., 2018). Tooth eruption ages are therefore a good *terminus ante quem* for the interpretation of isotopic data obtained from enamel samples. Few researchers have studied the tooth eruption ages of different teeth in camels (Rabagliati, 1924; Silver, 1963) and there are no studies on the duration of mineralization. We inferred the period of mineralization from the eruption times, as there were no studies done on the mineralization of camel teeth until now. We based our estimations (Table 1) on studies of the mineralization of cattle teeth that suggest a period of six to seven months prior to eruption during which mineralization takes place (Balasse, 2002).

This means that during the mineralization of the M1 the camel still depends on milk from its mother. Even after weaning, during the mineralization of the M2, they still have a strong bond to their mother and are not fully independent from her. Camels cannot bear heavy loads until the age of 3.5 to 4 years, because of lacking developmental maturity. So, they cannot be used as beasts of burden before the mineralization of the M3 (Potts, 2005).

2. Material

The four adult camels that we analyzed for this study (Tab. 2) all originate from civilian settlement contexts located on or near a major Roman road. With the exception of Mamer-Bertrange, all the remains were highly fragmented. All four camels were adult and found in association with faunal waste assemblages interpreted as the remains of food processing and bone working.

2.1 Innsbruck-Wilten

The site of Innsbruck-Wilten belonged in Roman times to the city of *Veldidena*. It occupies its northwestern edge. The Roman city lay on an important pass over the Alps, the Brenner, which was part of the north-south trade and transit route connecting *Augusta Vindelicorum* (Augsburg) with Verona. This road is documented in the *Tabula Peutingeriana* and the *Intinerarium Antonini* (Gietl, 2004). The camel remains were found during excavations at the corner of Anton-Melzer-Straße and the

Fritz-Konzert-Straße in a part of the Roman city interpreted as a *canabae legionis*, a civilian settlement forming adjacent to a long-term military base. They date from the 2^{nd} to 3^{rd} century AD and due to the highly fragmented skeletal remains a determination of species, age at death or sex was not possible (Picker, 2006; Pucher, 2006).

2.2 Mamer-Bertrange

The site of Mamer-Bertrange is a Roman small-town, probably a *vicus*, providing baths and a temple precinct, in the west of nowadays Luxembourg (Dövener, 2015). The Roman settlement was located on a main Roman road from Trier (*Augusta Treverorum*) via Arlon (*Orolaunum*) to Reims (*Durocortorum* or *Civitas Remorum* after the Gallic War) (Folmer, 1973). The camel remains were discovered in the filling of well 2 that was used as a dump site for carcasses and workshop waste from the second half of the 3rd century AD onwards, in an area of the site called "Bierg". The complete carcass of the animal was deposited in the well shaft. It was therefore possible to determine that the male dromedary died at the age of 6 – 7 years. (Dövener et al., 2017).

2.3 Tongeren

The Roman city of Tongeren (*Atuatuca Tungrorum*) is situated in what is today eastern Belgium near the border to the Netherlands. It was well connected by the Roman road network, situated on the crossing of two important trade routes: one from Boulogne s. M. (*Gesoriacum*) to Cologne (*Agrippina*) and the other one connecting it with Leiden and Nijmwegen (*Noviomagum*) (Miller, 1916; Vanderhoeven and Ervynck, 2007). Long distant trade is evident from the finds of white and coloured marble. These indicate connections to present-day Greece, Turkey, Egypt, Tunisia, and Italy (Dreesen et al., 2013). The camel remains were found during the excavation in the Vermeulenstraat in the late Roman ditch. Based on the tooth measurements the individual is most likely a male dromedary, although an identification as a hybrid could not be excluded completely (De Winter and De Cupere, 2017; De Winter et al., 2018). Therefore, DNA analysis is currently being undertaken on this individual.

2.4 Trier

Trier (*Augusta Treverorum*), in nowadays Germany, owed a major part of its prosperity during the Roman Empire to its central position in a network of trunk roads, like the one leading from Lyon (*Lugdunum*) to Cologne (*Colonia Claudia Ara Agrippinensium*) or the road from Reims (*Durocortorum*) to Mayence (*Mogontiacum*). Furthermore, Trier was situated on the banks of the Moselle, which was another important transport axis towards the Rhine and, indirectly via the Saône, to the Rhône (Miller, 1916; Wightman, 1970; Heinen, 1985). These routes crossed with many other roads, thus it was easy to reach Tongeren or the *vicus* of Mamer-

Bertrange starting from Trier. During the excavations of the site at Zurmaiener Straße 101-106 in Trier, an area south-west of a spacious villa complex was explored. South of a late Roman necropolis, in a trench system that either separated fields or demarcated the premises belonging to the villa, a maxilla fragment of a camel was discovered dating from the second half of the 3rd century AD (Hupe, 2017).

2.5 The reference material

For our study we used already published reference data of other herbivores and analyzed some camel bones as well as some bovid teeth from Mamer-Bertrange and Tongeren (Table 3). We used published δ^{13} C and δ^{18} O values from the carbonate fraction of middle and large sized herbivores dental enamel or bone. On the majority of published reference material, strontium (Sr) isotopic analysis has been conducted as well. Only in the case of the Israeli site Tell es-Safi/Gath significant large scale mobility was detected. Hence, the data set was split in this case into two groups. One representing Israel, and one Egypt (Arnold et al., 2016). A detailed discussion for each site can be found in the Supplementary Materials section. On the basis of the interpretations made in the publications, large scale mobility that would make a dataset problematic for our purposes is not to be expected.

As there is no known difference in C or O fractionation between bioapatite of teeth and bone, the difference in tissue does not represent a problem. It should be mentioned however, that bone is more susceptible to diagenetic changes. Bone constantly remodels during life and therefore reports a different period in the life of an individual compared to enamel. As the reference material is from modern or subfossil bone (bone that is not fossilised yet), it is unlikely that they have been diagenetically altered. The different time span in an individual's life that enamel and bone represent is also irrelevant for the purposes of this study.

The difference in time period from which the samples originate definitely has to be considered. We decided that the variability in climate is small enough between the different time periods from which the studied and the reference material originated to legitimate a comparison between the two. Nevertheless, it has to be mentioned that the results become more robust the closer the reference material is to the studied material in time.

Another potentially problematic aspect is the difference between species: *C. bactrianus* and *C. dromedarius* are both drought adapted species and therefore non-obligate drinkers. That means that they obtain a bigger fraction of their water intake from food than obligate drinkers like bovids, equids and ovicaprids. Non-obligate drinkers are therefore more likely to display elevated δ^{18} O values, due to the evapotranspiration in leaves and grasses as explained earlier.

3. Method

For the analysis, we took several intra-tooth samples (Fig. 3) perpendicular to the growth axis of the tooth. Their exact number per tooth depended on the respective crown height and varied between 3 and 8 (Table 2). Before sampling, the uppermost 0.5 mm of enamel were removed to reduce the risk of contamination. Then, 10-12 mg of sample was collected in 1.5 ml Eppendorf vials by drilling horizontal bands. This sampling technique is used for the majority of studies using intra-tooth isotope analysis. There is a certain risk of introducing biases due to the duration of the tooth mineralization, the difference in timing between the inner- and outermost parts of the enamel, and its individual steps. Nevertheless, a chronological sequence can be obtained and used when studying changes in habitat, climate, or nutrition (Balasse, 2003). Intra-individual serial sampling allows us to obtain isotopic ratios from different moments in the early life of an individual. Each sample has preserved the isotopic ratio of ${}^{18}O/{}^{16}O$ and ${}^{13}C/{}^{12}C$ at a certain phase of tooth mineralization. Plotting the δ values together in a graph, they form a continuous record for this time period (Fig. 3). Changes in climate, diet or habitat become visible this way as well as their relative chronology during the life history of the studied individual.

For the bone reference material, a chunk of around 500 mg was sampled and immersed in chloroform (CHCl₃), and methanol (CH₃OH) in the proportion 1:2. The chloroform-methanol mixture removes all the lipids from the bone samples. The samples were then placed on a shaker at 450 rpm for one hour. Afterwards, the solution was removed using Pasteur pipettes. Then, MilliQ-water was added and the samples were placed on the shaker again. The rinsing with water was repeated twice. After that the samples were put in the drying oven at 40 °C until completely dry. Following this, the bones were ground to a grain size of < 0.7 mm, and 30 mg of sample was placed in an Eppendorf vial for pretreatment.

During the pretreatment of the samples, 1.35 ml of sodium hypochlorite (NaOCI) at a concentration of 2.5 % was added to each Eppendorf vial. This removes the organic fraction of the enamel powder. The solution was mixed using a vortex for approximately 30 seconds and the enamel and bone samples were placed on a shaker for 24 or 72 hours respectively. The increased reaction time for the bone samples ensured that the markedly bigger organic fraction (~30 % in bone and only ~1% in enamel) was removed completely. In addition, the NaOCI was replaced every 24 hours. Subsequently, the samples were rinsed three times with Milli-Q H₂O to remove all of the NaOCI. In between the rinses, the samples were centrifuged to separate the solution from enamel. During the next step, 1.35 ml of 1 M acetic acid buffered solution (CH₃COOH) was added to remove all secondary carbonates (Bocherens et al., 1994; Koch et al., 1997; Wright and Schwarcz, 1999). The samples were then mixed using a vortex and were left to react for 24 hours during which they were constantly shaken. Afterwards, the samples were rinsed three times with Milli-Q H₂O and centrifuged in between each rinse. The samples were then placed in an oven to dry at 40 °C for 72 hours. Only 2.5 – 3 mg of the structural carbonate proceeded into the IRMS-analysis (Koch et al., 1997). Two internal enamel standards (Elephant CRM, Hippo CRM; CRM stands for carbonate reference

material) were processed according to the same protocol, with every set of samples following the principle of identical treatment (IT principle) (Werner and Brand, 2001). As secondary isotopic reference materials (SIRMs) 0.1 mg of IAEA-603 (International Atomic Energy Agency), NBS-18 (National Bureau of Standards, now National Institute of Standards and Technology or NIST), and the internal LM standard (Laaser Mamor CRM) were used. A set of these three more or less pure carbonate standards together with enamel Elephant CRM and Hippo CRM were included at the beginning and the end of the MS-run as well as after every 15 samples. The absolute isotopic abundances of ¹³C and ¹⁸O of the internal and internal standards are reported in Table 4.

The samples were analyzed with continuous-flow isotope ratio mass spectrometry (IRMS) at the laboratory of the AG Biogeology at the University of Tübingen. The sample reacts with highly concentrated (~99 %) phosphoric acid (H₃PO₄). The resulting gaseous CO₂ is then analyzed five times over a period of 15 minutes with an Elementar IsoPrime 100 IRMS. These five measurements are then used to calculate a mean value and the corresponding standard deviation (SD). Therefore, the measurement precision can be reported very accurately (Szpak et al., 2017). The two in-house standards were used for the calibration with the Elementar IonOs software relative to VPDB (Vienna Pee Dee Belemnite) for C and VSMOW (Vienna Standard Mean Ocean Water) for O. The raw data undergoes a 2-point calibration using Elephant CRM and Hippo CRM. A trend line is calculated (y = mx + c) where the known/expected values of the standards are mapped against the measurements of the unknown isotope ratios of the archaeological and reference samples.

Measurement uncertainty was monitored using the in-house standards. In general, the analytical precision of the measurements is higher than 0.1 ‰ for carbon and better than 0.2 ‰ for oxygen isotopic values. The calibrated results are summarized in Table 5 and reported in Table 6 in the supplementary information, including the exact standard deviations for each sample. The δ -notation (in per mill) is used to facilitate easier reading and interpretation. Delta-values are calculated using the following formula, ^jX being the heavier and ⁱX the lighter isotope.

$$\delta^{j/i} X = \frac{({}^{j}X/{}^{i}X)_{sample}}{({}^{j}X/{}^{i}X)_{standard}} - 1$$

(Coplen, 2011, pp. 2554–2555; Bond and Hobson, 2012, p. 328)

Some of the δ^{18} O values from published reference data were only given relative to VPDB. Hence, these values had to be conversed to values relative to VSMOW. This was done using the following formula: $\delta^{18}O_{a/VSMOW} = 1.03086 \times \delta^{18}O_{a/VPDB} + 30.86$ (Friedman and O'Neil, 1977).

4. Results

4.1 Innsbruck-Wilten

The δ^{13} C values of the M³ and P⁴ from Innsbruck-Wilten were very stable (Fig. 4, top right). There was minimal intra-tooth variation of the values. To express this stability with a statistic metric the variance (s²) for each tooth was calculated. It was 0.05 for the M³ and 0.02 for the P⁴. Both teeth combined had a variance of 0.04 in their δ^{13} C values signifying a very small inter-tooth variation. According to our approximation on the mineralization times, the M3 and the P4 of both the mandible and the maxilla represent the same age. While the δ^{13} C values are uniform across the two teeth, there is more variation in the δ^{18} O values. Slight differences in the timing of mineralization of these two teeth cannot be excluded as a cause for these variations since no in-depth studies were conducted in this direction. As the δ^{18} O values plot in the same range, the variation is not considered problematic for this study.

Considering the results of this study, it is apparent that the δ^{18} O values show more variability in comparison to the δ^{13} C values. This was also the case with the samples from Innsbruck-Wilten. The M³ showed a continuous trend towards slightly lower δ^{18} O values with the exception of one outlier (s² = 0.18). Measurements near the root of the P⁴ showed the most fluctuation (s² = 0.15).

4.2 Mamer-Bertrange

The δ^{13} C values of the M₁ and M₃ from Mamer-Bertrange were again very uniform (Fig. 4, top left) with a variance of 0.19 and 0.1, respectively. Nevertheless, when the values of the two teeth were compared to one another they did differ significantly. The M₁ ranged from -4.5 to -5.8 ‰ whereas the M₃ returned values from -10.2 to -10.4 ‰. In contrast to these two teeth, the M₂ expressed a continuous decrease in δ^{13} C values plotting even lower than the level of the M₃. These very low values were the ones most similar to the ones obtained from the two bovid molars (M₂ and M₃) from Mamer-Bertrange. An arrow in the figure indicates their level. These reference values too were very stable ranging from -12.3 to -12.7 ‰ with a variance of 0.01.

The isotopic results for oxygen mirrored the ones for carbon as the M_1 again displayed much higher abundances of the heavier isotope, and therefore higher δ^{18} O values ranging from +27.8 to +27.2 ‰ (s² = 0.08). The M_2 and M_3 combined were ranging from +25.7 to +24.3 ‰. Like for carbon, the M_2 returned δ^{18} O values with a high variance of 0.23 compared to the variance of the M_3 (s² = 0.09). The bovid reference samples ranged from +27 to +25.3 ‰ with a variance of 0.38. Again, the M_2 was closest to the values expected for European habitats in general and the bovine reference samples from the *vicus* of Mamer-Bertrange in particular.

4.3 Tongeren

The δ^{13} C values from Tongeren (Fig. 4, bottom left) were homogenous within the single teeth with variances of 0.02 for the M¹, 0.03 for the M², and 0.01 for the M³. Values of the M¹ and the M² were very close together. The M³ showed slightly

elevated δ^{13} C values. The mean δ^{13} C values of the M¹ and the M³, and the M² and the M³ differed by 1.3 ‰ and 1.1 ‰ respectively. In comparison with the bovid reference samples from Mamer-Bertrange, the three third molars from Tongeren were more variable with a variance of 0.52. The values from the bovid teeth of Tongeren ranged from –11.6 to –13.9 ‰, with M¹ and M² plotting within this range.

In comparison with the δ^{13} C values, the δ^{18} O values were much more variable on an intra- as well as an inter-tooth scale. The M² expressed the most variability (s² = 0.82 compared to s² = 0.2 in the M¹, and s² = 0.08 in the M³) as its δ^{18} O values rose with a steep slope to +27 ‰. The M³ was the only tooth plotting within the range of the bovid reference samples from Tongeren which spread from +23.9 to +20.3 ‰ (s² = 1).

4.4 Trier

The δ^{13} C values of the M³ and the P⁴ from Trier (Fig. 4, bottom right) were again very homogenous on an intra-tooth scale. Their variances are 0.01 and 0.03 respectively. On an inter-tooth scale, the P⁴ was slightly more depleted in ¹³C than the M³. The M¹ and M² showed a higher variability with variances of 0.16 for the M¹ and 0.82 for the M². Compared with the other two teeth from Trier, the M¹ and M² had generally higher δ^{13} C values ranging from –8.8 to –8.1 ‰ and –7.1 to –9.9 ‰ respectively.

The variations of the δ^{18} O values along the crown of the teeth were similar to the trends in δ^{13} C values. For example, the M² first shows a downwards trend before the δ^{18} O values rise again. A similar pattern was also visible in the δ^{13} C values of the same tooth. The M³ and the P⁴ displayed the biggest differences between the trends of the δ^{13} C and the δ^{18} O values. Moreover, the variances of the M³ (s² = 0.21) and the P⁴ (s² = 0.45) were considerably higher than the ones of the M¹ (s² = 0.03) and the M² (s² = 0.13).

5. Discussion

5.1. Origin and species identification

All of the three individuals from which the M1 could be sampled (Mamer-Bertrange, Tongeren, Trier) display different δ^{13} C and δ^{18} O values, which is consistent with them originating from different places. Furthermore, all of them could not be associated with any of our European reference sites. Our data is therefore not consistent with camel breeding in Europe, at least in places in Europe that were considered in this study. The M₁ from the dromedary from Mamer-Bertrange falls within the range of the reference data from Chad (Fig. 2) and in the general area of values expected for North African habitats. The stable isotopic data is in line with the species identification as *C. dromedarius* based on the skeletal morphology. The individual from Trier is most closely associated with the reference data from the Iranian sites (Fig. 2), this would be consistent with a Near or Middle Eastern origin. This indicates that it is more likely to be a dromedary than a Bactrian camel. The dromedary from

Tongeren was born in a habitat that among the three individuals sampled resembles the European reference sites the most. Considering its slightly higher δ^{18} O values, it could reflect a warmer and more arid habitat. Nevertheless, it cannot be associated with any of the reference sites. The sampling strategy for a follow up project should definitely include Eastern Europe, Iberia, and the northern Mediterranean coast as well as increasing the database for Egypt and Chad.

5.2. Mobility pattern and life history

The two individuals from Mamer-Bertrange and Trier clearly show a similar mobility pattern. The M₁ from Mamer-Bertrange is most closely associated with the reference data from North Africa, so, as discussed in the previous section, the journey of this dromedary probably started even further away from Europe, than the one of the dromedary from Trier. The M₂ of the Mamer-Bertrange dromedary is consistent with migration to cooler but still arid regions, for example the Near or Middle East. The samples taken closest to the CEJ (cemento enamel junction), which correspond to the part of the tooth that formed later in the life of the animal, do show the closest resemblance to values expected from temperate C₃ habitats like Europe. Isotopic, archaeological and historical data is consistent with movement of the Mamer-Bertrange dromedary from Northern Africa via the Near or Middle East (possibly Turkish-Iranian borderland) towards Europe during the first five years of its life. At the time of the migration the dromedary was 2-3 years old, an age at which it was still not completely independent from its mother and therefore probably accompanied by her. The isotopic signal of the M₃ is again consistent with warm and dry habitat with a partly C₄ vegetation, e.g. Turkey or the Near and Middle East. Between the age of 5.5 years and 6-7 years, it moved to the *vicus* at Mamer-Bertrange where it then died.

The M^1 as well as the M^2 of the camel from Trier fall within the range of the Iranian sites. It is therefore possible that it spent its first three years of life in the Near or Middle East. This would also be consistent with archaeological and historical evidence. Since the M^2 shows higher δ^{18} O values than the M^1 , the camel lived in a warmer and more arid region when it was 2 - 3 years old. There was then a shift in diet and habitat from the M^2 to the M^3 . The proportion of C₄ plant intake decreased significantly, which is indicated by the lower δ^{13} C values. They are even lower in the P⁴, although this difference is not as big. In addition, the δ^{18} O values decreased, indicating an approximation to more temperate, European-like habitats.

Two samples from the P^4 (a in particular and to a lesser extent also d) do show a marked tendency towards the values from the European reference sites. The isotopic data indicates that it could not have stayed in a temperate, C_3 dominated habitat for a long time, before moving back to some slightly warmer habitats.

When we combine isotopic, archaeological, and historical evidence, they are consistent with a connection of both these individuals with specific military units, the

detachments of the *Legio VIII Augusta* that were active on the eastern boundary of the Roman Empire in the 3rd century AD. The isotopic data does not contradict an association of both the Mamer-Bertrange and the Trier camel with habitats similar to those found in this region in the Near East. A connection of the two dromedaries with such military units is further supported by inscriptions from the European sites were the camels were found dating to the same period. One inscription is on the altar of Fortuna in Dalheim (the Roman *vicus Ricciacum*, ca. 19 km beeline south-east of Mamer-Bertrange) which documents that parts of the *Legio VIII Augusta* were present in the region around Mamer-Bertrange in 257 AD (Dövener et al., 2017). A votive inscription found at Arlon (ca. 16 km north-west from Mamer-Bertrange) is another historical source that connects this legion to this region (Krier, 2016), i.e. the territory of the *Civitas Treverorum*, and to camels, because camel remains were also found in Arlon (*Orolaunum*). Unfortunately, no teeth were preserved on this *vicus* site (Pigière and Henrotay, 2012; Dövener et al., 2017).

The other two analyzed camels differ drastically from this pattern. The δ^{13} C values from the dromedary from Tongeren only show a slight increase in the M³, otherwise they are relatively stable indicating a stable diet consisting of mostly C₃ plants. The δ^{18} O values differ substantially and along with one data point from the M² increasingly lower throughout the early years of the dromedary's life (Fig. 4). This indicates that it moved to habitats characterized by decreasing temperature and increased openness or abundance of C₄ plants during its first five years in life.

The individual from Innsbruck-Wilten does not exhibit any significant variation in either its δ^{13} C or the δ^{18} O values (Fig. 4). Hence, no direct evidence for mobility or changing living conditions is detected for the part of the animal life-time recorded in the analyzed teeth. This does of course not imply that the animal spent all its lifetime in one place. The reduced amplitude of δ^{18} O values could be an indicator for a mobility pattern that evened out any effect of seasonal variability in the oxygen isotope composition at one place. However, as the tooth crowns of the individuals were quite worn in our sample it is more likely that this was the cause of the reduction of amplitude of δ^{18} O values. Another reason for this low variability of isotopic ratios along the tooth crown could be that C and O are incorporated into the tooth enamel at a slower rate in camels. Considering the current lack of studies on camel physiology and formation and mineralization of their enamel this cannot be excluded as a cause for such a pattern. The diet of the camel from Innsbruck-Wilten consisted predominantly of C₃ plants, but with a marked contribution of C₄ plants.

6. Conclusion

For the three camel individuals where the M1 was sampled, we could roughly estimate a broad area from which they could have originated from and exclude some areas where they could not have originated from. This information can also give indications for species identification of these camels. For Mamer-Bertrange, the

isotopic data was in concordance with the morphometric identification as a *C. dromedarius*. The possible connections of the camel from Trier with the Near or Middle East and the detachments of the *Legio VIII Augusta, as discussed above,* do point towards it also being a dromedary. Until now, no species identification was attempted on its skeletal material to which the interpretation based on the isotopic evidence could be compared. For the camel from Tongeren, the isotopic evidence is too inconclusive for species identification as its M^1 could not be associated with any of our reference sites.

The serial sampling along the tooth crown allowed the tracking of habitat changes in chronological order and in the case of Mamer-Bertrange and Trier, we can presume a connection of their movement with specific military units of the *Legio VIII Augusta*. Our case study clearly shows the power of stable carbon and oxygen isotopes for studies of migration in general and long-distance animal migration in particular. With our data, we did obtain a good overall idea about the life history of the four camels.

The results also allowed us to make first, very tentative inferences about camel husbandry in the Roman Empire. The combination of the isotopic data and the archaeological record enabled us to support the interpretation of the presence of the dromedaries from Mamer-Bertrange and Trier in a military context, although both were found in civilian settlement contexts. They could have been used as either beasts of burden or as mascots. In our small sample, we found no evidence for centralized camel breeding. Each individual was born in a different region and could not be associated with one of our reference sites from Europe. Our results therefore are not consistent with the hypothesis that camel breeding did take place in Europe during the Roman Empire. Egyptian papyri mention the practice of camel breeding in various locations by local farmers (Davies, 1969). The isotopic data from the four camels that were analyzed for this study so far does not contradict this historical source. Nevertheless, it has to be emphasized that our sample size is much too small to be regarded as a solid indicator of the way camel husbandry and breeding was organized in the Roman Empire. In addition to the high variation in origin, there are no patterns as to the age at which the camels were first introduced to Europe. Camel husbandry therefore cannot be regarded as a systematic and centrally controlled practice in Europe during the Roman era based on our data.

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Figure Captions

Fig. 1 Map showing the four archaeological sites from which the camels were samples as well as all the reference sites. The shading indicates the distribution of the two camel species (Sorge 2006).

Fig. 2 Maps a) and b) represent the distribution of C₄ grasses over the globe. In a) the relative abundance of C₄ grasses is indicated by different shading, b) illustrates the species richness of C₄ grasses in these areas. In c) a model of the global mean annual δ^{18} O values of leaf water (modified after (Osborne et al., 2014) (a and b) and (West et al., 2018) (c)). Below the δ^{18} O values of some of our reference areas converted to leaf water values according to the constant offset between diet and carbonate of 26 ‰ (Koch, 2007) are indicated as box and whisker plots. The continuous decrease in δ^{18} O values from very hot an arid North Africa to cooler and more temperate areas such as for example Germany is clearly visible.

Fig. 3 M³ of the camel from Innsbruck-Wilten after sampling.

Fig. 4 δ^{13} C (solid lines) and δ^{18} O (dashed lines) results of the serial samples taken from the four camels. The data points in colour represent the bovid reference samples taken from Mamer-Bertrange and Tongeren. On the x-axis the samples are spread according to evaluated distance from CEJ (cemento enamel junction). The datapoint farthest left on each tooth is the one that mineralised earliest, hence is located further away from the CEJ on the tooth crown (e. g. for the P⁴ from the Trier camel: TR-1-PM-a). The space separating the different teeth and indicates that a continuity between them cannot be assumed, due to different mineralization times and levels of abrasion.

Table Captions

Table 1 Summary table of the tooth eruption times and the inferred periods of tooth mineralization of the camel teeth used for this study. As the estimated ages at tooth mineralization do not differ between maxillary and mandibulary teeth it is not differentiated between them between the two.

Table 2 Summary of the Roman camel remains that were analyzed for this study.

Table 3 Summary of all the reference material including mean and standard deviation for each. For sites from which we used already published data the references are reported.

Table 4 Absolute isotopic abundances of the international and internal standards used.

Table 5 Summary table that reports the mean δ^{13} C and δ^{18} O values as well as the variance for each tooth and for the individual camel or in case of the bovid reference samples for the site.

Table 6 Table reporting the δ^{13} C and δ^{18} O values of the four Roman camels and all the reference material that was analyzed for this study.

Supplementary Material

Local or non-local provenience of the fauna from the reference sites

Because we used a lot of published reference data, it is necessary to discuss the local or non-local provenience of the fauna for each site in more detail. At Tell es-Safi/Gath (Arnold et al., 2016), Hundisburg-Oldetal (Winter-Schuh et al., 2018), Knossos (Isaakidou et al., 2019), and Sagalassos (D. Frémondeau, personal communication) strontium (Sr) isotopic analysis were conducted in addition to carbon and oxygen. With some exceptions all data was consistent with the Sr ratios of the local bedrock.

One case in which large scale mobility could be detected was the Israeli site of Tell es-Safi/Gath. The ass found in a sacrificial context as well as one of the goats could be associated with Egypt based on comparison with reference data from some Egyptian sites. Trade connections between nowadays Israel and Egypt have been known since the Bronze Age. The other ovicaprids fall within the range of the local baseline established by vegetation samples from the vicinity of the site in Israel (Arnold et al., 2016). Unfortunately, the reference data used to associate the two animals with Egypt could not be used for our study as it did not include carbon and oxygen measurements on the carbonate fraction of bioapatite. However, we used the ass and the goat as reference data for Egypt. The second case in which larger scale mobility could be detected was the Early Byzantine site of Sagalassos in Turkey. Three individuals were identified as non-local, but their Sr ratios were nevertheless consistent with Western Anatolia (D. Frémondau, personal communication).

The specimen of the Mongolian dataset of sympatric wild and domesticated ovicaprids were collected from local herds using the pastures in the surrounding area. The wild specimen were collected from carcasses found in the same area. Large scale migration outside of the desert steppe environment north of the Gobi desert is not expected (Makarewicz and Pederzani, 2017).

As for the other studies on archaeological sites, the focus was mostly herd management and animal husbandry. The faunal assemblage from Volders in Tyrol was interpreted as livestock living in the archaeological settlement and was part of the herds that were driven seasonally up to the alms. Only three animals probably originated from outside of the Inn valley, but still their origin was limited to the circumalpine areas north and south of the site in Germany and Italy respectively (McGlynn, 2007). The reference data from Mycenae was interpreted in the original study as identifying different faunal management schemes that were associated with different consumption contexts. All ovicaprids were herded on small scale pastures leading to a restricted diet in regards of plant diversity. Only a part of the bovids, the ones found at the cult centre, showed a little more variance in the relative isotopic abundances of carbon and oxygen. This was interpreted as them having broader foraging ranges and showing connections of the elites with the surrounding nonpalatial settlements. Larger scale migration has not been implied (Price et al., 2017). At the two Iranian sites domestic caprids and wild ass were compared regarding their foraging and seasonal mobility pattern. There was only evidence for vertical transhumance in the domestic specimen, but no outliers hinting towards large scale mobility (Bocherens et al. 2001). At Kösk Höyük, a Chalcolithic site in Turkey the isotopic data pointed towards seasonal migration to winter pastures, which have been interpreted to be located nearby the settlement (Makarewicz et al., 2017).

The only slightly problematic data set is the one from Sudan, as the high variance between the Neolithic humans could indicate a semi-nomadic population. The switch from C₄ plants to a more C₃ based diet similar to the one in the Neolithic humans, is consistent with domestication of these animals. Semi-nomadic behaviour therefore is also possible for the bovids. The small sample size did not allow for more detailed interpretation. However, the overall relative isotopic abundances of C and O are consistent with our expectations for this area with very high δ^{18} O values and δ^{13} C values indicating the ingestion of C₄ plants. We considered these limitations of the data set in our interpretation.

Site	Country	Period	Species	N°	N°	Tissue	Element	δ^{13}	C _{VPDB}	δ ¹⁸ C	SMOW	Reference
Sile	Country	Fellou	•	individuals	samples	115506	Liement	mean	SD	mean	SD	Reference
Volders	Austria	Early Medieval	Bos, Capra, Cervus, Equus, Ovis	14	14	bone	not reported	-13.39	0.75	21.19	1.31	(McGlynn, 2007)
Tongeren	Belgium	Roman	Bos	3	32	enamel	M ³	-12.82	0.72	22.11	1.00	This study
Kolle	Chad	modern	C. dromedarius	2	2	bone	phalanx, carpus/tarsus	-2.28	3.65	28.36	2.31	This study
Kossom Bougoudi	Chad	modern	C. dromedarius	2	2	bone	phalanx	-3.31	1.39	27.24	0.11	This study
Tell es- Safi/Gath	Egypt (Israel)	Early Bronze Age	Capra, Equus	2	30	enamel	M1 – M3	-3.36	2.93	32.65	2.32	(Arnold et al., 2016)
Hundisburg- Oldetal	Germany	Late Neolithic	Bos	5	91	enamel	МЗ	-11.62	0.44	23.25	1.18	(Winter-Schuh et al., 2018)
Knossos	Greece	Late Bronze Age	Capra, Ovis	7	88	enamel	M2, M3	-11.17	0.65	28.91	1.67	(Isaakidou et al., 2019)
Mycenae	Greece	Late Bronze Age	Bos, Capra, Ovis	62	62	bone	not reported	-12.56	1.00	29.13	1.35	(Price et al., 2017)
Sagzabad	Iran	Iron Age	Capra, Equus	2	19	enamel	P4, M1, M2	-9.03	1.83	27.63	2.12	(Bocherens et al., 2001)
Zageh	Iran	Neolithic	Capra, Equus	2	23	enamel	M1 – M3	-8.31	1.21	27.45	2.10	(Bocherens et al., 2001)
Tell es- Safi/Gath	Israel	Early Bronze Age	Capra, Ovis	4	16	enamel	M1 – M3	-10.75	1.66	33.89	1.52	(Arnold et al., 2016)
Mamer- Bertrange	Luxembourg	Roman	Bos	2	10	enamel	M ³	-12.57	0.10	25.98	0.61	This study
Baga Gazaryn Chuluu	Mongolia	modern	Ovis/Capra	12	12	enamel	M2, M3	-9.51	1.53	23.54	2.27	(Makarewicz and Pederzani, 2017)
Ras Al- Junayz	Oman	modern	C. dromedarius	1	1	bone	vertebra	-9.73	0.00	27.42	0.00	This study
Al Khiday	Sudan	Neolithic	Bos	2	2	bone	not reported	-9.35	0.78	31.90	0.57	(lacumin et al., 2016)
Khartoum	Sudan	modern	Bos, Capra, Ovis	4	4	bone	not reported	-1.20	8.46	38.50	0.51	(lacumin et al., 2016)
Manisa	Turkey	Sub-modern	Camelus sp.	1	1	bone	rib	-14.15	-	22.67	-	This study
Köşk Höyük	Turkey	Chalcolithic	Capra, Ovis	15	15	enamel	M2, M3	-9.35	1.23	24.72	1.38	(Makarewicz et al., 2017)
Sagalassos	Turkey	Early Byzantine	Bos	15	290	enamel	M ₂	-9.01	1.59	27.11	1.81	D. Frémondeau, personal communication
Dehistan Plain	Turkmenistan	modern	C. dromedarius	1	1	bone	mandible	-6.75	-	24.52	-	This study

Al-Madam	United Arabian Emirates	modern	C. dromedarius	1	16	enamel	$M_{1} - M_{3}$	-6.57	0.88	29.37	0.90	This study
Mleiha	United Arabian Emirates	3rd c. BC- 3rd c. AD	C. dromedarius	3	3	pone	phalanx, long bone	-5.65	1.11	31.45	1.11	This study

Journal Pre-proof

Tooth	Age at tooth erup	otion (in years) ¹	Age at tooth mineralization (in years)
	(Rabagliati, 1924)	(Silver, 1963)	
M1	1 – 1.25	1	0.5 – 1.25
M2	2.5 – 3	3	2-3
M3	5 – 5.5	5	4.5 – 5.5
P4	5 – 5.5	4 – 5	4.5 – 5.5

Journal Pre-proof

Site			Jour	nai Pre-pro	pof		Current	
Sile	Age	Species	Teeth	N° samples	Element	Specimen number	specimen location	Reference
Innsbruck-	$2^{nd} - 3^{rd} c.$	Camelus	P ⁴	6	maxilla	FNr. 219	NHM Wien	(Picker, 2006;
Wilten	AD	sp.	M ³	8	Паліїа	1 11. 219		2000, Pucher
Mamer-		C.	M ₁	6			CNRA-	(Dövener et
Bertrange	3 rd c. AD	dromedariu	M ₂	5	mandible	2009-63/542		(Dovener et al., 2017)
Lornango		S	M ₃	5			Bertrange	
	1 st half of	C.	M ¹	5			Royal Belgian	(De Winter and De
Tongeren	the 4 th c. AD	dromedariu	M ²	8	maxilla	V613	Institute of	Cupere,
	the 4 C. AD	S	M ³	6			Natural	2017)
			P^4	6			Rheinisches	
Trier	2 nd half of	Camelus	M ¹	3	maxilla	FNr. 734	Landesmus	(Hupe,
	the 3 rd c. AD	sp.	M ²	8	maxina	1111.704	eum Trier	2017)
			M ³	7				

SIRM	Material	$\delta^{13}C_{VPDB}$	SD $\delta^{13}C$	δ ¹⁸ O _{VPBD}	SD δ ¹⁸ Ο	Reference
Elephant CRM	Enamel	-10.55	0.11	+1.80	0.42	Documentation AG Biogeologie
Hippo CRM	Enamel	-3.80	0.09	-2.10	0.32	Documentation AG Biogeologie
IAEA-603	Carbonate	+2.46	0.02	-2.37	0.04	(International Atomic Energy Agency, 2016)
LM CRM	Carbonate	+1.50	0.16	-5.20	0.31	Documentation AG Biogeologie
NBS-18	Carbonate	-5.01	0.035	-23.20	0.1	(International Atomic Energy Agency, 1995)

0:4-	Lab ID	Teet	Mean	Journal Pr	^{o-p} Mean	
Site	Lab-ID	Tooth	$\delta^{13}C_{VPDB}$	Variance C	$\delta^{18}O_{SMOW}$	Variance O
lan alamada	I-1-M3	M ³	-10.38	0.05	+24.70	0.18
Innsbruck- Wilten	I-1-P4	P^4	-10.45	0.02	+25.12	0.15
WIIICH	tota	I	-10.41	0.04	+24.88	0.20
	BBP-8	M_1	-5.15	0.19	+27.57	0.08
Mamer- Bertrange	BBP-9	M_2	-10.84	1.77	+25.13	0.23
	BBP-10	M_3	-10.25	0.01	+24.61	0.09
	tota	I	-8.52	7.89	+25.12 0.15 $+24.88$ 0.20 $+27.57$ 0.08 $+25.13$ 0.23 $+24.61$ 0.09 $+25.88$ 1.98 $+25.95$ 0.20 $+25.28$ 0.82 $+23.03$ 0.08 $+24.74$ 1.89 $+25.40$ 0.03 $+25.40$ 0.03 $+25.78$ 0.52 $+25.78$ 0.52 $+25.49$ 0.03 $+26.48$ 0.20 $+25.98$ 0.38 $+22.18$ 0.94	1.98
	TO-1-M1	M ¹	-11.69	0.02	+25.95	0.20
Tongeren	TO-1-M2	M^2	-11.44	0.03	+25.28	0.82
Tongeren TO-1-M3 M ³ -10.38 0.01 +23 total -11.17 0.34 +24 TR-1-M1 M ¹ -8.40 0.16 +25 TR-1-M2 M ² -8.98 0.82 +26	+23.03	0.08				
	tota	I	-11.17	6.15 0.19 $+27.57$ 0.08 0.84 1.77 $+25.13$ 0.23 0.25 0.01 $+24.61$ 0.09 8.52 7.89 $+25.88$ 1.98 1.69 0.02 $+25.95$ 0.20 1.44 0.03 $+25.28$ 0.82 0.38 0.01 $+23.03$ 0.08 1.17 0.34 $+24.74$ 1.89 8.40 0.16 $+25.40$ 0.03 0.89 0.82 $+26.54$ 0.13 0.89 0.01 $+25.24$ 0.21 1.49 0.03 $+25.77$ 0.45 0.09 1.79 $+25.78$ 0.52 2.62 0.00 $+25.49$ 0.03 2.51 0.01 $+26.48$ 0.20 2.57 0.01 $+25.98$ 0.38 2.72 0.08 $+22.18$ 0.94 3.58 0.08 $+22.49$ 0.97 2.13 0.18 $+21.69$ 0.89	1.89	
	TR-1-M1	M ¹	-8.40	0.16	+25.40	0.03
	TR-1-M2		-8.98	0.82	+26.54	0.13
Trier	TR-1-M3	M ³	-10.89	0.01	+25.24	0.21
Ther	TR-1-P4	P^4	-11.49	0.03	+25.57	0.45
	tota	I	-10.09	1.79	+25.78	B 0.20 0.08 0.23 0.09 1.98 0.20 0.82 0.08 0.82 0.08 0.82 0.08 0.82 0.03 0.03 0.03 0.13 0.021 0.45 0.03 0.52 0.03 0.20 0.03 0.94 0.097 0.89
Bovids	PA-44	M^2	-12.62	0.00	+25.49	0.03
Mamer-	PA-45	M ³	-12.51	0.01	+26.48	0.20
Bertrange	tota	I	-12.57	0.01	+25.98	0.38
	TO-2	M ³	-12.72	O.08	+22.18	0.94
Bovids	TO-3	M ³	-13.58	0.08	+22.49	0.97
Tongeren	TO-4	tal-10.410.04+24.880.20 M_1 -5.150.19+27.570.08 M_2 -10.841.77+25.130.23 D M_3 -10.250.01+24.610.09 M_3 -10.250.01+25.881.98 M_1 -8.527.89+25.881.98 M_1 -11.690.02+25.950.20 M_2 -11.440.03+25.280.82 M_2 -11.440.03+25.280.82 M_2 -11.170.34+24.741.89 M_3 -10.380.01+23.030.08 M_1 -8.400.16+25.400.03 M_2 -8.980.82+26.540.13 M_1 -8.400.16+25.770.45 M_2 -12.620.00+25.780.52 M_2 -12.620.00+25.490.03 M_3 -12.510.01+26.480.20 M_3 -12.570.08+22.180.94 M_3 -12.130.18+21.690.89	0.89			
	tota	I	-12.82	0.52	+25.13 0.23 $+24.61$ 0.09 $+25.88$ 1.98 $+25.95$ 0.20 $+25.28$ 0.82 $+23.03$ 0.08 $+24.74$ 1.89 $+24.74$ 1.89 $+25.40$ 0.03 $+26.54$ 0.13 $+25.77$ 0.45 $+25.78$ 0.52 $+25.49$ 0.03 $+26.48$ 0.20 $+25.98$ 0.38 $+22.18$ 0.94 $+22.49$ 0.97 $+21.69$ 0.89	



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Declaration of interests

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The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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