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Ours brun (Ursus arctos Linnaeus, 1758) au parc animalier Hoenderdaell à Anna Paulowna, Pays-Bas. Crédit: René Cortin (CC BY-SA 4.0) / Brown bear (Ursus arctos Linnaeus, 1758) at the Hoenderdaell animal park in Anna Paulowna, The Netherlands. Credit: René Cortin (CC BY-SA 4.0). https://commons.wikimedia. org/wiki/File:Brown_bear_at_the_Hoenderdaell_animal_park_in_Anna_Paulowna_3.jpg

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Neither fish nor fowl. Isotopic evidence of a plant-based diet in (captive?) brown bears from Roman Augusta Raurica, Switzerland

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ABSTRACT

In Roman times, the brown bear (Ursus arctos Linnaeus, 1758) was one of the most important hunted wild animal species. Bears were killed for e.g. their furs, their teeth and their meat. One of the reasons for catching bears alive was for their use in the context of public entertainment, i.e., animal hunts in amphitheatres. Bear bones from the Roman settlement of Augusta Raurica, NW Switzerland, attest the tradition of hunting (or trading?) bears in this part of the Roman Empire. Archaeozoological investigations of several complete bear skeletons from this site indicated that at least one bear was kept in captivity for some period. The remains of four bears, deposited in two wells, were selected for stable carbon and nitrogen isotope analysis to explore whether life (stages) in captivity had an impact on the diets and in consequence to the stable isotope ratios in bear bone collagen. A comparison with (herbivorous) horses and (omni-)carnivorous dogs from the same Roman city and with bears from other prehistoric and modern contexts indicates that the diet of the adult brown bear specimen from Augusta Raurica was plant-based and does not provide evidence of human-influenced feeding in (prolonged) captivity. Nitrogen enrichment in the young bears is most likely explained by suckling. Human-influenced additional feeding in captivity cannot be completely ruled out but the enrichment results from stable isotope data from wild brown bear data from the literature and from dogs and equids from the same site argue suggest that this was not taking place.

KEY WORDS Stable carbon and nitrogen isotopes, Roman period, NW Switzerland, diet, captivity.

RÉSUMÉ

Ni poisson ni volaille. Indication isotopique d'un régime à base de plantes chez des ours bruns (captifs?) du site romain d'Augusta Raurica, Suisse.

À l'époque romaine, l'ours brun (Ursus arctos Linnaeus, 1758) était l'une des plus importantes espèces d'animaux sauvages chassées. Il était tué notamment pour sa fourrure, ses dents et sa viande. Une raison pour laquelle on capturait les ours vivants, était leur utilisation pour le divertissement public, par exemple les chasses aux animaux dans les amphithéâtres. Des os d'ours découverts dans la colonie romaine d'Augusta Raurica, dans le nord-ouest de la Suisse, attestent de la chasse (ou du commerce?) de l'ours dans cette partie de l'Empire romain. L'étude archéozoologique de plusieurs squelettes complets, indique qu'au moins un de ces ours a été tenu en captivité pour une certaine période. Les restes de quatre ours d'âges différents, déposés dans deux puits, ont été sélectionnés pour une analyse des isotopes stables du carbone et de l'azote, afin d'étudier si la vie en captivité a eu un impact sur le régime alimentaire et par conséquent sur les proportions des isotopes stables dans le collagène des os. La comparaison avec des chevaux (herbivores) et des chiens (omni-carnivores) de cette ville romaine, mais aussi avec des ours d'autres contextes préhistoriques et modernes, indique que le régime alimentaire de l'individu adulte d'Augusta Raurica était à base de plantes et ne fournit pas de preuve d'une alimentation influencée par l'homme. L'enrichissement en azote chez les jeunes ours s'explique probablement par l'allaitement. On ne peut pas exclure entièrement que l'enrichissement isotopique résulte d'une alimentation influencée par l'homme, mais la comparaison des isotopes stables des ours bruns sauvages et des chiens et chevaux du même site contrarie cette hypothèse.

KEY WORDS Isotopes stables du carbone et de l'azote, période romaine, nord-ouest de la Suisse, alimentation, captivité.

INTRODUCTION

The history of the relationship between humans and bears is complex and reaches back to the Palaeolithic period, when the bear seems to have played an important role, as indicated by bear tooth pendants, artificially modified bear bones, and the occurrence of bear engravings in cave and rock art (Kunst & Pacher 2019). Up until the 20th century, captivated bears were trained as dancing bears in fairgrounds and today bears are kept in zoological gardens and (increasingly rarely) perform in circus shows. In the Roman period, bears were kept by so-called *usarii* to serve in amphitheatre circus games (Wiedemann 2001). Bear baiting and bear dancing are traditions that were cultivated before the modern era and are still alive in some parts of Asia (D'Cruze et al. 2011). In the archaeological record, however, skeletal remains of brown bears (Ursus arctos Linnaeus, 1758) are rare (Kunst & Pacher 2019). There are a few finds of bear bone remains from Roman period contexts in Switzerland, e.g. from Avenches, Kempraten, Mollis-Hüttenböschen, Neftenbach, Oberwinterthur, and Augusta Raurica (Schmid 1963; Deschler-Erb 2001; Deschler-Erb & Akeret 2010; Deschler-Erb 2013; Marti-Grädel 2022). Although they are rare, these finds provide important information about hunting and keeping bears and about the relationship between humans and this animal species.

Various sources provide insights into human-bear-relationships in Roman times. A central context where bears play an important role are bear hunts or fights (*venationes*) in Roman amphitheatres, not only in Rome but also in the Roman provinces, as reported in ancient written literature, stone reliefs and through archaeozoological remains. Osteological remains of several bears were found in the drainage channels of the colosseum in Rome (dating to the 2nd to 5th centuries AD) and in other close architectural structures, i.e., the Meta Sudans (dating to the 5th and 6th centuries AD) (De Grossi Mazzorin et al. 2005). In Virunum, Austria, a votive stone relief shows a man, interpreted as a venator or bestiarius, with a whip taming a young bear (Gugl 2004). The epigraphic evidence is supported by the finds of the skeletal remains of two brown bears, interpreted as being killed in an amphitheatre bear hunt and subsequently deposited together (Gostenčnik 2009). For the purpose of venationes, bears had to be captured alive and held in captivity. There is evidence that for these purposes, bears were captured not only locally but also from regions further away and transported over long distances (De Grossi Mazzorin & Minniti 2023). Written and archaeological sources provide evidence for the management of wild and semi-domesticated animals in Roman farms in the Mediterranean (Mielsch 1987) and in other parts of the Roman Empire (Allen 2014). Other (written and archaeological) evidence is provided for bears being killed for their furs and teeth used as pendants as well as for their meat (Eichinger 2005).

The rare bear finds of the Roman period in Switzerland are mainly restricted to urban contexts, i.e., cities, and connected to animal hunts and exhibitions (if alive) or ornamentation (teeth, skin, fur) (Deschler-Erb 2001). Based on archaeozoological evidence, e.g. the increase of hare bones (as an indicator for landscape opening), and the intense agricultural use of the landscape, it can be assumed that in Roman times, bears were probably no longer native to the area of modern northwest Switzerland, although it cannot be excluded that some individuals lived in the Jura Mountains. The Black Forest is another close potential area of retreat (Deschler-Erb 2001). An *usarii* inscription from the Zurich area (CIL XIII 5243;

Dressel 1899; Walser 1979) suggests the presence of local bear populations in the Roman period. With the exception of some military camps, the frequency of wild animals in civilian towns and vici was low and hunting had no economic importance. A higher frequency (but still only c. 5%) of wild animals is known from Roman villae (Deschler-Erb et al. 2002). Hunting was therefore interpreted as a leisure activity undertaken by high-status people (Deschler-Erb 2017). Despite the rare evidence of bear osteological remains from Roman Switzerland, four complete brown bear skeletons have been recorded at the Roman city of Augusta Raurica. These are important and unique finds and a good opportunity to study human-bear-relationships using archaeozoological, palaeopathological, isotopic and genetic analysis. The bones of the four bears were therefore included in the Swiss National Science Foundation (SNSF) funded project "HumAnimAl -New insights in the human-animal relationship of earlier times as a basis for current social discussions". Here, we present the results of stable carbon and nitrogen isotope analysis, which was applied to investigate the diet of these bears in potential captivity as part of an exploration of the purpose of their presence in the city.

METHODOLOGICAL BACKGROUND AND ARCHAEOLOGICAL CONTEXT

Stable carbon and nitrogen isotope analysis allows us to gain information on feeding ecology and ecophysiology of fauna (Crawford et al. 2008; Ben-David & Flaherty 2012). In respect to the investigation of human and faunal skeletal tissues, stable carbon isotope analysis enables a distinction between C₃ and C_4 plants due to different CO_2 uptake during photosynthesis (O'Leary 1988; Farquhar et al. 1989) and between terrestrial and marine food components (Chisholm et al. 1982). Wild C₄ plants are uncommon in central Europe (Collins & Jones 1986; Pyankov et al. 2010), and domesticated C₄ plants first appear in Switzerland with the introduction of millet during the Bronze Age (Varalli et al. 2021). Besides dietary factors, environmental factors (e.g. precipitation, temperature, altitude, tree cover) can also add to δ^{13} C variability (Körner *et al.* 1991; Heaton 1999; Diefendorf et al. 2010). The mean offset between diet and bone collagen in herbivores is c. 5‰, with an additional increase in δ^{13} C of 1‰ with each step in the food chain (Van der Merwe 1989). Stable nitrogen isotope analysis is applied to distinguish between plant-based and animal protein-rich food, and $\delta^{15}N$ values increase 3-5‰ with each trophic level (Bocherens & Drucker 2003; Hedges & Reynard 2007). Environmental factors, e.g. precipitation, temperature and altitude, have a limited impact on $\delta^{15}N$ values in soils and plants (Amundson et al. 2003) and (via the food chain) the bone collagen of their consumers. Stable carbon and nitrogen isotope analyses are usually undertaken on bone collagen. Animal bones have varying turnover rates, depending on the skeletal element but also on the age of the individual (Hedges et al. 2007).

Brown bears are the largest carnivores in Europe (García-Vázquez *et al.* 2022). Stable isotope analysis on bear remains has previously mainly been applied to modern bear populations both inside (e.g. Careddu et al. 2021; García-Vázquez et al. 2022) and outside (e.g. Hilderbrand et al. 1999; Hobson et al. 2000) Europe to distinguish between ecological factors and dietary preferences. In archaeozoology, studies have focused on Pleistocene fauna including brown bear (Ursus arctos), steppe brown bear (Ursus priscus Goldfuss, 1818) and cave bear (Ursus spelaeus Rosenmüller, 1794) (e.g. Bocherens et al. 2004; Richards et al. 2008; Bocherens et al. 2015; García-Vázquez et al. 2018). For later prehistoric and historic periods, stable isotope studies focussing on brown bears are missing or not yet published (e.g. https:// boxofficebears.com/, last consultation on 27th April 2023) and stable isotope data have rarely been obtained in the course of human dietary reconstruction since bear is not considered a frequent food resource.

The Roman city of Augusta Raurica is located at the river Rhine in modern northwestern Switzerland (Fig. 1). In 15 BC the city was established on the Augst plateau and a military camp nearby on the plains towards the river Rhine, which served as the border of the Roman Empire at this time (Pfäffli 2010). When the border of the Empire was shifted further northwards after 50 AD, a redesign of the town involving stone constructions took place. In the decades after the fall of the Limes (c. 260 AD), Augusta Raurica was again located at the border, the Rhine, its population decreased and retreated into the (now) fortified Kastelen hill. At around 300 AD, the fort Castrum Rauracense was erected at the riverside taking the role of the Kastelen fortification. After its destruction in 351-352 AD by Germanic tribes, habitation continued until c. 401 AD. The site has been intensively archaeozoologically studied with almost 500000 (hand) collected animal bone remains making it the most archaeozoologically investigated site in Roman Switzerland (Deschler-Erb et al. 2021). Wild animals are rare (c. 2%) and played a marginal role (Schibler & Furger 1988; Deschler-Erb 2017). The evidence of four almost complete brown bear skeletons from the well house in Insula 8 and the well MR12 in the area Auf der Wacht, however, is unique for Swiss Roman contexts. They all date to the mid-3rd century AD, and brown bear remains from contexts before and after this period are rare (Deschler-Erb et al. 2021).

MATERIALS AND METHODS

Single finds of brown bear are spread across the excavated area of Augusta Raurica, e.g. in the amphitheatre, in insulae 24, 29, 30, in region 5C, in the Kastelen layers (Mráz 2018: 159) and in Kaiseraugst-Schmidmatt 1 horizon 2 phase 2 (Marti-Grädel 2022). In addition, the remains of four almost complete brown bear skeletons were recovered from a well (MR 12, area Auf der Wacht, region 17C) and a subterranean well house in Insula 8 at the bottom of the Kastelen hill (Fig. 1).

The well house in Insula 8 was excavated in 1999, and an almost complete skeleton of a young bear was found together with skull fragments of an older bear specimen and the bones of wild and domestic animals, e.g. red deer (*Cervus elaphus*)



Fig. 1. — Map of Switzerland with the location of Roman Augusta Raurica (bottom right) and location of features with (almost) complete skeletons of brown bears (*Ursus arctos* Linnaeus, 1758) discussed in the text: MR 12 and well house Insula 8. Credit: image, Claudia Zipfel, Römerstadt Augusta Raurica. Abbreviations: **A**, Austria; **D**, Germany; **F**, France; **I**, Italy.

Linnaeus, 1758), horse (Equus caballus Linnaeus, 1758), and dog (Canis familiaris Linnaeus, 1758). With a minimum number of individuals (MNI) of 60, dogs were especially numerous. It is assumed that dead animals were disposed in the well after it was no longer in use. (Fig. 2; Schmid et al. 2011). According to the archaeozoological analysis, the individual HUM 69.1 is a young bear of 1.5 years of age. In 2012, three further bears were discovered in well MR12 (Fig. 2; Mráz 2018). The remains of three bears were found together with domestic and wild animals, e.g. cattle, horse, sheep, pig, and chicken (Mráz 2018: supplementary table 3). Again, dogs were very abundant with a MNI of 41. This suggests that there was a large dog population in the city. There are indications that the fur of the animals was used, and it can be assumed that their remains were later disposed of in the well shaft. The three bears were found in the lower backfill of the well, in features G01664 and G01663: the individuals with laboratory identification number HUM 16.1 (corresponding to bear 2) in Mráz 2018), HUM 17.1 (i.e., bear 3 in Mráz 2018), and HUM 18.1 (i.e., bear 1 in Mráz 2018). Archaeozoological analysis (Mráz 2018) has showed that HUM 16.1 was 1.5-2 years of age when it died. HUM 18.1 was also very young, <2 years of age. The gracile bones showed signs of a bone disease, maybe osteomyelitis. HUM 17.1 was an older individual, 6-8 years or >9 years at the time of death (Mráz 2018; S. Deschler-Erb, pers. comm.). The proximity of the three bear finds indicates that the animals were deposited (almost) contemporaneously (Mráz 2018) pointing to an intentional killing event rather than natural deaths. The butchery marks as well as missing fore and hindlimb elements suggest that the bears were killed for their furs (Mráz 2018: 159, fig. 19, 160). This interpretation is further supported by the location of the well close to a supposed workshop for leather and horn processing.

Use wear analysis demonstrated that the teeth of HUM 16.1 were manipulated by humans leading to changes in the bone structure of the nose (Mráz 2018: 160, 161, figs. 20, 21, 23). All three remaining canines were shortened using a saw leaving the pulp of the teeth open and damaging the neighbouring premolars. It is assumed that a bacterial inflammation altered the bone structure of the jaw and the snout. Based on the results of the use wear analysis, Mráz (2018: 160) concluded that this happened when the bear was alive and saw this as an indication of captivity over several weeks to months.

All four individuals (HUM 16.1, 17.1, 18.1, 69.1) were selected for stable carbon and nitrogen isotope analysis. Samples were taken from two tibiae (HUM 16.1, 18.1) and



Fig. 2. — Subterranean well house in Insula 8 and well MR12. Brown bears (*Ursus arctos* Linnaeus, 1758) are coloured in grey. The animal silhouettes represent the minimum number of individuals (MNI), mainly agreeing with complete or almost complete carcasses. Credit: image, Claudia Zipfel, Römerstadt Augusta Raurica. Scale bar: 1 m.

two ulnae (HUM 17.1, 69.1). Stable carbon and nitrogen isotopes found in the bone collagen of tibiae and ulnae provide dietary information over several years or – depending on the animal species and the age of the analysed animal – the complete life of the individual (Hedges *et al.* 2007).

The four bear bones were analysed at the University of Basel, Switzerland. Sample preparation followed Longin (1971) with modifications as described by Knipper *et al.* (2017). Compact bone portions were cut and the surfaces removed. Between 400 and 700 mg of sample were demineralized in 10 ml of 0.5 NHCl at initially 4°C and later at room temperature for 14 days, rinsed to neutrality and reacted with 10 ml of 0.1 M NaOH for 24 h at 4°C, rinsed again to neutrality and gelatinized in 4 ml of acidified H2O for 48 h at 75°C. Insoluble particles were separated using EZEE filter separators, and the collagen frozen and lyophilized. Analysis was conducted in duplicates. About 0.8 mg of collagen was placed into tin capsules and loaded onto an INTEGRA2 EA-IRMS instrument (Sercon Ltd., Crewe, United Kingdom) at Biogeochemistry, Department of Environmental Sciences, University of Basel. Raw nitrogen and carbon isotope data were blank-, linearity, and drift-corrected and then normalized to the air (AIR) and Vienna Pee Dee Belemnite (VPDB) scales, respectively, by means of two-point calibrations based on EDTA (in-house

TABLE 1 List of analysed material and isotopic results	of the four brown bears (Ursus arctos Linnaeu	s, 1758) from Roman Augusta Raurica. Abbreviations: AD, Age
at death (years); AIR, air; Atom., atomic; C, carbon; CY	collagen yield; FC, find complex; N, nitrogen	; SE, skeletal element; VPDB, Vienna Pee Dee Belemite scale.

Lab-ID	Excavation	FC	SE	AD	CY (mg)	CY (%)	% C	% N	Atom. C/N	δ13C (‰ vs VPDB)	δ15N (‰ <i>vs</i> AIR)
HUM 16.1	2012.001	G01663	Tibia	1.5-2	65.4	10.9	40.6	14.6	3.2	-20.1	7.0
HUM 17.1	2012.001	G01663	Ulna	6-8 or >9	40.5	5.8	38.2	13.8	3.2	-20.4	4.7
HUM 18.1	2012.001	G01664	Tibia	<2	89.0	13.3	39.1	14.2	3.2	-19.6	6.7
HUM 69.1	1999.06	E04245	Ulna	c. 1.5	33.7	8.8	41.2	14.9	3.2	-19.8	7.4

standard) and IAEA N2 or EDTA and IAEA CH6, respectively. Nitrogen and carbon isotopic compositions are reported in δ -notation in per mil relative to VPDB for carbon and AIR for nitrogen. Reproducibility of internal and external standards was better than $\pm 0.25\%$ for δ^{15} N and better than $\pm 0.1\%$ for δ^{13} C. Data evaluation and statistical analysis have been performed in Microsoft Excel and the add-in XLStat (version 2021.3.1).

RESULTS

Results of the stable carbon and nitrogen isotope analysis are reported in Table 1. All four bear samples fulfilled the quality criteria for ancient collagen as suggested by Ambrose (1990) and Van Klinken (1999) and yielded between 5.8 and 13.3% of collagen, 38.2 and 41.2% of C, 13.8 and 14.9% of N, and had atomic C/N ratios of 3.2.

The δ^{13} C values range from -20.4 to -19.6%, averaging $-20.0 \pm 0.3\%$, and the δ^{15} N values range from 4.7 to 7.4‰, averaging 6.4 ± 1.2‰. While the δ^{13} C values show a low variability (0.8‰), the δ^{15} N values are more variable (2.7‰) due to the outlier value (4.7‰) of HUM 17.1. Young bears (<2 years of age, n = 3) show isotopic differences to the juvenile-adult bear (n = 1) and have a δ^{15} N mean value of 7.0 ± 0.3‰ vs 4.7‰ and a δ^{13} C mean value of $-19.8 \pm 0.2\%$ vs -20.4%. Due to the small sample number of specimens, it was not possible to test the differences between the ontogenic stages with statistical methods.

Figure 3 shows a comparison of the stable isotope data of the four bears to the results from dogs (Canis familiaris) as typical examples of carni-omnivores and equids (Equus caballus) as examples of herbivores from Roman Augusta Raurica and Iron Age Basel-Gasfabrik (Appendix 1). The bears differ in both, carbon and nitrogen stable isotope values, in comparison to both animal species. The animal species from both archaeological sites are very similar in their stable isotope values: Equids average $-22.1 \pm 0.4\%$ and $5.1 \pm 1.1\%$ (Augusta Raurica) $vs - 22.2 \pm 0.3\%$ and $5.5 \pm 0.7\%$ (Basel-Gasfabrik). Dogs average $-19.6 \pm 1.0\%$ and $8.8 \pm 0.6\%$ (Augusta Raurica) $vs-19.3 \pm 1.0\%$ and $8.9 \pm 0.7\%$ (Basel-Gasfabrik). In respect to δ^{15} N, the bears are in the range of the herbivorous equids thus showing a strong impact of herbivorous food sources. In respect to δ^{13} C, however, the bears match the range of the dogs. The lower δ^{13} C values in horses can be explained by metabolic differences (Hedges 2003) and have also been observed elsewhere (e.g. Le Huray et al. 2006; Stevens et al. 2010; Knipper et al. 2017).

DISCUSSION

Despite the small sample size (n = 4), a couple of observations based on the stable isotope data can be discussed.

Reasons for depositing brown bear skeletons in Augusta Raurica

An interesting question concerns the reasons for the depositions of (complete) brown bear skeletons within the city of Augusta Raurica. In Roman times, wild animals played an insignificant role for the human diet, with general proportions of <6% (and always <12%) across animal bone assemblages (Deschler-Erb 2001: 59). Among wild animals, the brown bear is of very low importance. Additionally, the remains of wild animals connected with hunting activities were predominantly found in rural *villae rusticae* and military contexts, e.g. the officer's kitchen at Vindonissa (Flück 2022), rather than cities and are connected to luxurious (and Romanised?) lifestyles (Jacomet et al. 2002: 37-39; Deschler-Erb 2017). Based on pollen and archaeobotanical analysis the environment surrounding Augusta Raurica was shaped by human impact, and consisted mainly of open landscapes and a few wooded areas during the first centuries AD (Wick 2015; Deschler-Erb et al. 2021), but the Jura Mountains and the Black Forest, both not far away, were potential habitats for brown bears at that time.

A potential reason for hunting (and killing) bears is the consumption of their meat, as e.g. known from Roman written sources. While the bear bone from Kaiseraugst-Schmidmatt 1 showed cut marks suggesting the consumption of bear meat (Marti-Grädel 2022: 157, fig. 156), archaeozoological analysis of the three bear specimens from well MR12 do not support this kind of interpretation. In addition, meat consumption has been ruled out for the skeleton of a young (and complete) brown bear found in a Roman well in Pforzheim, south Germany (Kuss 1957). The results of the archaeozoological analysis suggest that the bears in the Augusta Raurica wells were killed for their furs (Mráz 2018).

The three bear skeletons showed butchery marks in the area of the skull and lower jaw, as well as on the wrists and ankles (Mráz 2018: 159, fig. 19, 160). Further, finger, metatarsal and metacarpal bones are missing. Taken together with the location of the finds close to a suspected workshop for horn and leather processing this suggests that the bears were killed for their furs. The use of the skins has also been suggested as the main reason for death in the case of some of the equids and dogs of MR 12 (Mráz 2018: 155, 157).



Fig. 3. – Scatter plot of δ¹³C and δ¹⁵N values from bone collagen of the four brown bears (*Ursus arctos* Linnaeus, 1758) from Augusta Raurica compared to equids (*Equus caballus* Linnaeus, 1758) and dogs (*Canis familiaris* Linnaeus, 1758) from Augusta Raurica (this study; Granado *et al.*, unpublished data) and Basel-Gasfabrik (Knipper *et al.* 2017).

The manipulation on the teeth of bear 2, however, implies that the animal(s) were kept in captivity for some time, making it unlikely that the bear was hunted and immediately killed only for its fur. It is likely that the bear was (probably primarily) caught for another purpose, i.e., for use in amphitheatre animal hunts. Two amphitheatres are known at Augusta Raurica: Augst-Neun Türme (built c. 110 AD and in use until c. 170 AD), superseded by Augst-Sichelgraben (in use until c. 270/280 AD) (Hufschmid 2009). Bears were frequent animals in the Roman *venationes*. Dozens of these animals (besides elephants and African predatory animals) were killed in the first reported *venatio*, organised in the framework of the ludi, in Rome in 186 BC (Bernstein 1998; Shelton 2014). Venationes were also popular in the Roman provinces and animals were traded over long distances for this purpose. Information on animal trade to supply amphitheatre shows is provided by ancient authors. Brown bears, found in large numbers in the Colosseum in Rome, for example, are suggested to have originated from Caledonia, Lucania (Martial, Ep. 7, 8), Dalmatia (Symmachus, Ep. 7, 121; 9, 132, 142), Tagus and the Pyrenees (Claudian, De Cons. Stil. 3, 302 ss.) (De Grossi Mazzorin & Minniti 2023).

Since the three bears from MR12 were found in the same find context, it cannot be ruled out – although not archaeozoologically proven – that the other two individuals were also kept in captivity for some time before being killed for their furs and deposited in the well. The deposition is likely to have happened after the use of the well because water was probably not drinkable with faunal remains deposited there, as has been noted for the Roman well in Pforzheim (Kuss 1957).

FEEDING ECOLOGY

In contrast to the cave bear that followed a predominantly herbivorous diet (e.g. Nelson *et al.* 1998; Bocherens *et al.* 2011; Naito *et al.* 2016), the modern brown bear feeds on an omnivorous diet (Pasitschniak-Arts 1993) consisting of vegetation (e.g. grasses, leaves, roots, mosses, berries, nuts, fungi) and animal-derived food (e.g. small mammals, insects, birds, larvae). In addition, bears also eat carrion as well as fish.

Our data can be compared to that of Late Pleistocene and Holocene brown bears from Cantabria, Spain (García-Vázquez et al. 2018) and with very strong restrictions to that of modern brown bears (obtained from hair not bone) from mountainous areas of southern Europe (García-Vázquez et al. 2022). In respect to the latter, we consider a correction factor of +2‰ for the modern bear specimen due to the $\delta^{13}C$ decrease in atmospheric CO₂ as a result of the use of fossil fuels since the Industrial Revolution around 1880 AD (Long et al. 2005; Dombrosky 2020). The δ13C values of the Augusta Raurica bears fall in the centre of both the ancient bear data distribution ($\delta^{13}C = -20.1\% \pm 0.3$, n [MNI] = 39 and the modern bear data distribution $(\delta^{13}C = -20.33\% \pm 0.89, n = 32)$. Small variations in $\delta^{13}C$ can be explained by ecological differences, e.g. precipitation, temperature and forest density. While the bears <2 years old from Augusta Raurica plot are above the upper end of the δ^{15} N range of the ancient Cantabrian brown bears (and at the top of the south European modern brown bears), the adult individual from Augusta Raurica falls in the upper half of the ancient Cantabrian brown bear data range

 $(\delta^{15}N = 3.3\% \pm 1.0, n [MNI] = 39)$ (and in the lower half of the modern data range [$\delta^{15}N = 5.56\% \pm 1.64$, n = 32]). García-Vázquez et al. (2018) suggested a predominantly herbivorous diet for the ancient Cantabrian brown bears. The stable isotope data obtained from modern Cantabrian and Apennine brown bear hair samples (García-Vázquez et al. 2022) suggested a similar proportion of herbivorous and carnivorous food sources, while bears from the Pyrenees followed a more carnivorous diet, according to the authors. These results agree with (non-stable isotope based) observations on modern brown bears from Cantabria (e.g. Rodríguez et al. 2007). Scavenging (of large carcasses like mammoth) was suggested as a dietary component of the brown bear from the Gravettian site Předmostí I in the central Moravian Plain (Bocherens et al. 2015). Since the bear isotope data from Augusta Raurica does not show any signs of significant ¹⁵N enrichment, scavenging is unlikely to have played a major role.

For the modern Hokkaido brown bear in Japan it has been recorded that salmon was consumed on a very regular basis and sometimes in high proportions (>30%), but varying by location, age and sex (Matsubayashi *et al.* 2014). Very high salmon intake (>60%) was observed for North American grizzly bears along the Pacific coast, but again with large variability within the populations and depending on locations (Mowat & Heard 2006). For Europe, however, evidence for salmon consumption is missing (Swenson *et al.* 2007). At the Iron Age site Basel-Gasfabrik, salmonids were strongly enriched in ¹⁵N and averaged 13.5 \pm 0.4‰ (Knipper *et al.* 2017). Since the bear isotope data from Augusta Raurica does not show any sign of significant ¹⁵N enrichment, salmon consumption can likely be ruled out as food source.

There are distinct isotopic differences between C₃ and C₄ plants due to varying photosynthetic pathways. While modern C3 plants have $\delta^{13}C$ values between -30 and -25%, C₄ plants δ^{13} C values usually range from -13 to -11% leading to significantly different $\delta^{13}C$ values in the bone collagen of their consumers (Kohn & Cerling 2002). Since C₄ plants are very rare in Central Europe, and account for c. 1% of the plants in modern Switzerland (Collins & Jones 1986), a significant C₄ plant intake in the investigated brown bears would point to the import of captivated bears from regions with natural C₄ vegetation, i.e., warmer areas (probably outside Europe, cf. Collins & Jones 1986), or feeding on food including C₄ plants such as millet during captivity. The δ^{13} C values of the four bears from Augusta Raurica average at $-20.0 \pm 0.3\%$, and do not point to an appreciable influence of C_4 plants. This indicates a European origin of the bears and C3 plant based diets, obtained either from the natural environment or deliberate feeding. The marginally lower δ^{13} C mean value of $-20.0 \pm 0.3\%$ in the bone collagen of the bears from Augusta compared to the bear bone collagen values from cave sites in the Mont Ventoux region, southern France $(n = 41, c. 5000 \text{ BC}, \delta^{13}\text{C} - 19.6 \pm 0.5\%; \text{ Bocherens et al.}$ 2004) can most likely be explained by ecology. An unpaired

two-sample two-sided t-test was found to be statistically non-significant at a significance level of 0.05 (t[43] = 1.52, p = 0.137). Palynological investigations in southern France suggest a relatively open environment with a mosaic pattern of wooded areas (Bocherens *et al.* 2004) as also indicated for the hinterland of Augusta Raurica in the first centuries AD (Wick 2015; Deschler-Erb *et al.* 2021), although precipitation and temperature differences could explain these variations. Due to large chronological differences, however, these observations regarding the environment and vegetation must be considered with caution, and could also relate to temperature differences.

Without the possibility of analysing potential food sources, an approach is to compare the stable isotope data of the investigated brown bears with those of herbivorous, omnivorous and carnivorous animal species from the same archaeological contexts (Fig. 3). The adult bear falls within the same $\delta^{15}N$ range as the herbivorous equids from Augusta Raurica, which is probably the result of a largely herbivorous diet with limited (or no?) meaty/fishy components. As discussed further below, the higher $\delta^{15}N$ values of the young bears is probably the result of suckling. The δ^{13} C values in bear bone collagen match the range of the dogs from Augusta Raurica and are typical for a terrestrial food. As described above, the lower δ^{13} C values in horses result from metabolic differences between horses and other animal species such as ruminants (Hedges 2003) and have also been observed elsewhere (e.g. Le Huray et al. 2006; Stevens et al. 2010; Knipper et al. 2017). A comparison with the only so far isotopically analysed human skeleton deriving from Roman Augusta Raurica ($\delta^{13}C = -19.5\%$), δ^{15} N = 10.7‰; Gerling & Doppler 2021) confirms that the diet of the investigated bears was omnivorous with a very large herbivorous influence.

$\delta^{15}N$ enrichment due to suckling

We observed an enrichment in $\delta^{15}N$ in the bone collagen of young bears (<2 years of age, n = 3) compared to the adult bear (n = 1) with 7.0 ± 0.3‰ vs 4.7‰. The reverse is seen in respect to $\delta^{13}C$ with -19.8 ± 0.2‰ vs -20.4‰. ¹⁵N enrichment, likely due to suckling, is also observed in a young horse, a foal, from Augusta Raurica (Fig. 3). A strong discrepancy in the stable isotope values of young and adult bears were also observed for the Mont Ventoux population (Bocherens *et al.* 2004). The 3-month-old cubs showed average $\delta^{15}N$ values of 5.8 ± 0.8‰ and average $\delta^{13}C$ values of -19.7 ± 0.6‰ (n = 25), while and the adult bears showed average $\delta^{15}N$ values of 3.5 ± 0.3‰ (n = 9) and average $\delta^{13}C$ values of -19.3 ± 0.3‰ (n = 9), respectively.

Our data can be compared to those obtained from modern polar bears *Ursus maritimus* Phipps, 1774 in Canada, for which temporal variation in the δ^{13} C and δ^{15} N values of the plasma for cubs and their mothers during the two-year maternal care period has been established. After a lactation period of several months, the cubs continue to be nursed while additionally consuming other food (Polischuk *et al.* 2001). It must be noted that polar bears are not directly

comparable to brown bears due to large dietary differences. Polar bears feed primarily on ringed seals and occupy a high trophic position in the food chain (Hobson & Welch 1992). They also undergo a seasonal cycle of feasting and fasting based on their location and the availability of their prey (Ramsay & Stirling 1988). General trends in isotopic variation caused by suckling, however, can be compared. Polischuk et al. (2001) found the plasma of first year cubs to be enriched in spring in ¹⁵N by 1.0‰ depleted in ¹³C by 0.8% relative to the plasma of their mothers probably because of the consumption of mother's milk. A similar isotopic spacing has been detected by Jenkins et al. (2001) in modern grizzly bears (Ursus arctos horribilis Ord, 1815) from the USA. The plasma of the grizzly bear cubs differed by $1.2 \pm 0.5\%$ for ¹⁵N to that of their mothers. A ¹⁵N-enrichment of up to 5‰ and ¹³C-depletion of 2.4‰ in the bone collagen of neonates/cubs compared to adults has also been detected in fossil bones of the European cave bear (Ursus spelaeus Rosenmüller & Heinroth, 1794) from Slovenia (Nelson et al. 1998) and was interpreted as the effect of suckling (in combination with metabolic processes, i.e., hibernation and growth; Lidén & Angerbjörn 1999). In this study, the adult-offspring-differences disappeared to a great extent during the second year. Hissa (1997) noted that the lactation period in the European brown bear lasts for at least 4-5 months.

The young bears in our study are <2 years of age. At this age it is expected that they were largely relying on their mother's milk with an addition of solid food (Glenn *et al.* 1976; Pasitschniak-Arts 1993; Lidén & Angerbjörn 1999) – if not completely fed by food replacement when living in captivity. The ¹⁵N enrichment in the bone collagen of the young bears suggests that they were suckled (and as a consequence living together with their mother). It cannot be distinguished, however, if this happened in freedom or in captivity.

$\delta^{15}N$ enrichment due to hibernation

Bears are considered to be hibernators (Nores et al. 2010). Hibernation during winter dormancy can affect both stable carbon and nitrogen isotope values in bears (Nelson et al. 1998; Lidén & Angerbjörn 1999). This is due to metabolic processes, i.e., an 815N enrichment because of urea recycling (Barboza et al. 1997). The correlation between stable isotope values and metabolism has been investigated in modern bears, but also in ancient bears, e.g. Lidén & Angerbjörn 1999. Bocherens et al. (1994) suspected that the δ¹⁵N enrichment in the young bears from Mont Ventoux can be partly explained by the metabolic processes during hibernation in female lactating bears, but assumed that the $\delta^{15}N$ enrichment happening during hibernation is recorded in bone collagen only to a small extent. They also pointed out that "a more detailed knowledge of the factors that influence the isotopic enrichments during winter dormancy in modern bears" are needed to better understand this aspect (Bocherens et al. 2004). Not all bears hibernate, however (e.g. Hellgren & Vaughan 1987 on American black bears). Winter dormancy in captivity is not well understood. Observations on 60 modern semicaptive brown bears from northern Spain indicated that while most bears hibernated in winter, some individuals remained active without eating. The bears that did not hibernate, however, mostly slowed down (Nores *et al.* 2010). In hibernating bears δ^{13} C bone collagen values are expected to show shifts from ¹³C depleted fatty acid influences during hibernation to protein-influenced metabolism in the rest of the year (Bocherens *et al.* 2004 citing e.g. Tieszen & Boutton 1989; Hissa 1997). HUM 17.1 is 0.6‰ more depleted in ¹³C than the young bears. This could be considered an indicator of hibernation for only this individual, or the stronger impact of the ¹³C shifts during hibernation in this individual due to age differences.

CONCLUSIONS

Based on the results obtained from stable carbon and nitrogen isotope analyses, the diet of the four investigated brown bears (Ursus arctos) from Roman Augusta Raurica is likely to have been plant-based with limited impact from other food sources such as meat or fish. The observed patterns are largely consistent with those of prehistoric and modern wild bears considered to have eaten omnivorous diets with a significant impact from plant food sources. The nitrogen isotope values are also similar to herbivorous horses and significantly below those of (omni-)carnivorous dogs from the same archaeological site. The differences between young bears and the juvenile-adult individual can most likely be explained by physiological and metabolic processes, i.e., ¹⁵N enrichment due to suckling. Another possible explanation for the differences is metabolic variability due to hibernation. This is known to influence nitrogen isotope ratios in bone collagen, although in captive bears hibernation does not necessarily occur. It cannot be ruled out that the nitrogen enrichment is the result of human-influenced additional feeding in captivity but stable isotope data from ancient and modern brown bears from southern Europe and those from horses and dogs from the same site argue against this interpretation. In conclusion, the isotopic data do not indicate human-influenced dietary behaviour as a consequence of (prolonged) captivity. Shorter periods of captivity, archaeozoologically proven for at least one of the four bears can, however, not be ruled out due to delayed incorporation of isotope values into body tissues and hence a missing isotopic visibility.

There is lots of potential for future research. A methodological expansion including compound specific isotope analysis of amino acids can help to further investigate the feeding and keeping of brown bears during Roman times. An intense interdisciplinary study of Roman and historically documented captive and free living brown bears would most likely provide important results and could probably serve as a powerful case study for human-animal relationship studies in the past.

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Archaeological sit	e Sample ID	Excavation	FC	Species	SE	CY (%)	% C %	N Atom. C/N	613C (% vs VPDB)	δ ¹⁵ N (‰ vs A	IR) Publication
Augusta Raurica	HUM 15.1	2014.008	G05085	Equidae	Metacarpus	6.6	42.5 15.	3 3.2	-22.3	5.9	this study
Augusta Raurica	HUM 31.1	2000.060	E04388/ E04389	Equidae	Ulna	14.7	44.2 16.	0 3.2	-21.7	4.2	this study
Augusta Raurica	HUM 32.1	SBB-Umschlagplatz	B05579	Equidae	Metatarsus	8.8	33.4 12.	1 3.2	-21.6	4.9	this study
Augusta Raurica	HUM 33.1	1999.060	E04198	Equidae	Phalanx	7.6	41.6 15.	0 3.2	-22.6	2.2	this study
Augusta Raurica	HUM 34.1	1999.060	E04245	Equidae	Metatarsus	7.5	36.5 13.	1 3.3	-21.6	4.6	this study
Augusta Raurica	HUM 35.1	SBB-Umschlagplatz	B05579	Equidae	Metacarpus	5.4	40.8 14.	4 3.3	-21.6	7.2	this study
Augusta Raurica	HUM 46.1	1983 "Horizont 8"	B9279	Equus caballus	Metatarsus	3.3	39.8 14.	3 3.2	-22.4	5.1	this study
Augusta Raurica	HUM 47.1	1983 "Horizont 8"	B9279	Equus caballus	Metatarsus	2.7	39.2 13.	6 3.4	-21.9	5.1	this study
Augusta Raurica	HUM 48.1	1983 "Horizont 8"	B9279	Equus caballus	Metatarsus	2.6	39.8 14.	2 3.3	-22.1	6.2	this study
Augusta Raurica	HUM 49.1	1983 "Horizont 8"	B9261	Equus caballus	Metatarsus	6.9	41.3 14.	7 3.3	-22.3	4.9	this study
Augusta Raurica	HUM 50.1	1983 "Horizont 8"	B9195	Equus caballus	Metatarsus	2.4	38.1 13.	5 3.3	-23.1	4.3	this study
Augusta Raurica	HUM 51.1	1983 "Horizont 8"	B8466	Equus caballus	Metatarsus	6.7	15.1 5.	6 3.1	-22.4	5.5	this study
Augusta Raurica	HUM 52.1	1983 "Horizont 8"	B9279	Equus caballus	Metatarsus	3.7	39.9 14.	3 3.3	-21.8	4.6	this study
Augusta Raurica	HUM 53.1	1983 "Horizont 8"	B9279	Equus caballus	Metatarsus	3.3	38.4 13.	8 3.2	-22.4	4.9	this study
Augusta Raurica	HUM 54.1	1984 "Horizont 8"	B8478	Equus caballus	Metatarsus	6.7	40.8 14.	6 3.3	-21.6	5.9	this study
Augusta Raurica	HUM 55.1	SBB-Umschlagplatz	B05579	Equidae	Metatarsus	7.7	40.6 14.	6 3.3	-21.8	6.2	this study
Augusta Raurica	HUM 56.1	2000.060	E04391	Canis familiaris	Radius	17.0	44.2 16.	0 3.2	-20.0	8.6	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 58.1	2000.060	E04389.18	Canis familiaris	Femur	5.8	39.3 14.	1 3.3	-19.4	9.3	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 59.1	2000.060	E04389.15	Canis familiaris	Femur	5.4	39.0 13.	9 3.3	-19.6	9.1	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 70.1	2012.001	G01664	Canis familiaris	Humerus	9.0	38.6 14.	1 3.2	-19.0	8.4	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 71.1	2012.001	G01663	Canis familiaris	Humerus	7.0	33.0 12.	0 3.2	-16.3	8.1	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 72.1	2000.060	E04398.23	Canis familiaris	Femur	5.7	38.4 13.	6 3.3	-19.7	8.9	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 57.1	2000.060	E04235	Canis familiaris	Humerus	2.9	37.1 13.	8 3.1	-20.3	9.7	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 61.1	1991.65	D00180	Canis familiaris	Calcaneus	5.5	41.9 14.	9 3.3	-20.5	8.8	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 62.1	2004.65	E09387	Canis familiaris	Ulna	10.1	33.5 11.	5 3.4	-20.7	9.5	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 65.1	1999.060	E04198	Canis familiaris	Humerus	6.4	40.6 15.	2 3.1	-19.6	0.0	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 76.1	1999.060	E04185.1	Canis familiaris	Metacarpus	6.4	40.7 14.	7 3.2	-19.9	9.6	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 77.1	2012.001	G01621	Canis familiaris	Humerus	10.4	38.2 13.	9 3.2	-19.6	9.2	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 78.1	2003.006	E05689	Canis familiaris	Metacarpus	7.0	28.6 10.	5 3.2	-19.5	8.4	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 60.1	2000.060	E04231	Canis familiaris	Metatarsus	6.8	40.9 14.	7 3.2	-20.0	8.2	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 63.1	2000.060	E04206	Canis familiaris	Metatarsus	7.4	40.9 14.	7 3.3	-19.5	8.1	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 64.1	2000.060	E04245	Canis familiaris	Femur	3.9	41.4 14.	9 3.2	-19.9	8.5	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 73.1	2000.060	E04388	Canis familiaris	Metacarpus	7.0	41.2 15.	2 3.2	-18.2	7.4	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 74.1	2012.001	G01621	Canis familiaris	Humerus	6.0	36.3 13.	2 3.2	-19.8	9.8	Granado <i>et al.</i> (u.d.)
Augusta Raurica	HUM 75.1	2012.001	G01663	Canis familiaris	Humerus	5.7	39.8 14.	7 3.2	-20.1	8.8	Granado <i>et al.</i> (u.d.)
Basel-Gasfabrik	BGT 1	25169	Pit 293	Equus caballus	Humerus	13.4	42.9 15.	8 3.2	-22.1	6.3	Knipper <i>et al.</i> 2017
Basel-Gasfabrik	BGT 2	25232	Pit 293	Equus caballus	Femur	12.2	41.3 15.	3 3.2	-22.0	6.0	Knipper <i>et al.</i> 2017
Basel-Gasfabrik	BGT 3	25189	Pit 293	Equus caballus	Humerus	2.1	36.1 12.	8 3.3	-22.3	5.3	Knipper <i>et al.</i> 2017
Basel-Gasfabrik	BGT 4	20063	Pit 286	Equus caballus	Metacarpus	5.4	36.4 13.	4 3.2	-21.7	5.3	Knipper <i>et al.</i> 2017
Basel-Gasfabrik	BGT 5	20095	Pit 286	Equus caballus	Metatarsus	3.4	38.6 14.	0 3.2	-22.6	4.4	Knipper <i>et al.</i> 2017
Basel-Gasfabrik	BGT 23	25220	Pit 293	Canis familiaris	Mandibula	1.9	37.4 14.	0 3.1	-19.7	9.4	Knipper <i>et al.</i> 2017
Basel-Gasfabrik	BGT 24	25228	Pit 293	Canis familiaris	Humerus	11.8	43.0 16.	1 3.1	-20.1	10.1	Knipper <i>et al.</i> 2017
Basel-Gasfabrik	BGT 25	25265	Pit 293	Canis familiaris	Cranium	4.6	39.0 14.	5 3.1	-18.9	8.5	Knipper <i>et al.</i> 2017
Basel-Gasfabrik	BGT 26	25271	Pit 293	Canis familiaris	Maxilla dx	12.7	41.6 15.	5 3.1	-19.4	ເ ເ ເ	Knipper et al. 2017
Basel-Gastabrik	BG1 27	25048	Pit 129	Canis tamiliaris	Vertebra	4.7	40.6 15.	0 3.2	-18.8	9.7	Knipper <i>et al.</i> 2017

Appendix.

			C L		L		2					
Archaeological si.		EXCAVATION	2 2	species	Ä	(%) 10	ט %	N %	Atom. C/N	OLO (% VS VPUB)	O'N (% VS AIH)	Publication
Basel-Gasfabrik	BGT 28	25081	Pit 129	Canis familiaris	Mandibula	9.6	43.0	16.0	3.1	-20.2	8.6	Knipper et al. 2017
Basel-Gasfabrik	BGT 29	25147	Pit 129	Canis familiaris	Costa	6.6	39.1	14.3	3.2	-18.7	9.4	Knipper et al. 2017
Basel-Gasfabrik	BGT 30	22530	Pit 287	Canis familiaris	Radius	3.9	38.7	14.5	3.1	-19.6	8.5	Knipper et al. 2017
Basel-Gasfabrik	BGT 31	22986	Pit 287	Canis familiaris	Radius	10.4	38.9	14.4	3.1	-19.8	8.2	Knipper et al. 2017
Basel-Gasfabrik	BGT 32	23009	Pit 287	Canis familiaris	Radius	8.4	38.9	14.5	3.1	-20.4	8.1	Knipper et al. 2017
Basel-Gasfabrik	BGT 33	23102	Pit 287	Canis familiaris	Mandibula	3.9	37.9	14.1	3.1	-18.5	8.7	Knipper et al. 2017
Basel-Gasfabrik	BGT 34	20005	Pit 286	Canis familiaris	Mandibula	15.4	43.3	16.1	3.1	-16.4	10.1	Knipper et al. 2017
Basel-Gasfabrik	BGT 35	20057	Pit 286	Canis familiaris	Costa	8.7	39.9	14.8	3.1	-19.7	9.1	Knipper et al. 2017
Basel-Gasfabrik	BGT 36	20057	Pit 286	Canis familiaris	Maxilla	7.1	38.2	14.1	3.2	-19.7	8.9	Knipper et al. 2017
Basel-Gasfabrik	BGT 37	20062	Pit 286	Canis familiaris	Vertebra	3.3	39.7	14.4	3.2	-19.5	8.4	Knipper et al. 2017