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Investigating cave bear remains – an overview on methods with focus on radiocarbon dating and stable isotopes

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Abstract: Radiocarbon dating is generally the first choice to date younger Upper Pleistocene organic material. In caves, skeletal remains of animals or humans are often the only preserved datable finds. Routinely, collagen is extracted from bones for radiocarbon dating as it does not readily exchange carbon with its surrounding. However, collagen can also deteriorate and is sometimes not at all or only insufficiently preserved. Apart from the age determination, dietary habits are of special interest and are reconstructed using the stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). We describe the major challenges of radiocarbon dating and stable isotope analysis of cave bear remains from the Austrian Alps, Franconia (Germany) and fossil finds at a site near Bobenheim-Roxheim (Germany), but also the informative potential of successful application of the methods. We intent to sharpen the knowledge what to look out for to be able to obtain reliable ages of cave bear and other bone material. Moreover, we present two additional scientific methods, luminescence dating and dendroecology as further possibilities to disclose information about sites, their chronology and climatic conditions.

Kurzfassung: Die Radiokohlenstoffdatierung ist im Allgemeinen die erste Wahl zur Altersbestimmung von organischem Material. In Höhlen sind die Skelettreste von Tieren oder Menschen oft die einzigen erhaltenen datierbaren Funde. Routinemäßig wird für die Radiokohlenstoffdatierung Kollagen aus Knochen extrahiert, da es nicht ohne weiteres Kohlenstoff mit seiner Umgebung austauscht. Allerdings kann sich auch Kollagen zersetzen und ist manchmal gar nicht oder nur unzureichend erhalten. Neben der Altersbestimmung sind die Ernährungsgewohnheiten von besonderem Interesse und werden anhand der stabilen Isotope von Kohlenstoff ($\delta^{13}C$) und Stickstoff ($\delta^{15}N$) rekonstruiert. Wir beschreiben die Radiokohlenstoffdatierung und die Analyse mit stabilen Isotopen von Höhlenbärenresten aus den österreichischen Alpen, aus Franken (Deutschland) und fossilen Funden einer Fundstelle bei Bobenheim-Roxheim (Deutschland), aber auch das informative Potential einer erfolgreichen Anwendung der Methoden. Wir wollen das Wissen schärfen, worauf man achten muss, um zuverlässige Altersbestimmungen von Höhlenbären und anderem Knochenmaterial zu erhalten. Darüber hinaus stellen wir zwei weitere wissenschaftliche Methoden, die Lumineszenzdatierung und die Dendroökologie, als weitere Möglichkeiten vor, Informationen über Fundorte, deren Chronologie und klimatische Bedingungen offenzulegen.

Introduction

This research focuses on cave bear remains from the Austrian Alps and the foothills of the Franconian Alb, Germany. However, cave bear bones and teeth are not only found in caves, as the name suggests, but also at open air sites in the lowlands, such as Bobenheim-Roxheim in the Upper Rhine Graben. After determining the distinct species of the bear remains, usually radiocarbon dating is applied (DÖPPES et al., 2016; ROSSI et al., 2018; DÖPPES et al., 2019). When dealing with radiocarbon ages, a closer look at the radiocarbon section of this paper will be helpful as this provides hints on how radiocarbon data should be presented or interpreted.

For in situ finds, some other methods can also be of value when aiming to understand the complete context of the bear remains, including food resources and environmental conditions. For example, differences between the results of Optically-Stimulated Luminescence dating (OSL) of the sediments in which the cave bears are found and the radiocarbon age of their bones and teeth may indicate that the finds are relocated. To be able to reconstruct the climatic conditions in which the animals lived, it is useful to apply dendroecology, which offers data in annual resolution. OSL dating and dendroecology are shortly described to show their potential and for the interested reader who would like to gain more insights into the caves directly but also the environmental conditions of the past. Here, we devote only a short paragraph to this method in order to achieve completeness and to show how important it is to link several methods for a reliable chronological perspective.

More information about the life of bears can be revealed from the bones or teeth by determining their stable isotope values of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$). Here, $\delta^{13}C$ can help to differentiate among plant food sources, because this value varies significantly between C3 and C4 plants. The trophic level of the food resource is then marked by $\delta^{15}N$. Because the heavier isotope (^{15}N) accumulates along food chains, fish have — for instance — higher $\delta^{15}N$ values than fruit. Methods such as strontium isotope analysis ($^{87}Sr/^{86}Sr$; not described in this article) may indicate whether the cave bears moved along large distances or remained rather stationary throughout their lifetime.

In this article, the focus lies on radiocarbon (^{14}C) and stable isotope analysis $\delta^{15}N$ and $\delta^{13}C$ as these methods are applied most often. The study starts with describing the sites where the cave bear remains were found, followed by a presentation of the methods applied — radiocarbon and stable isotope ($\delta^{13}C$ and $\delta^{15}N$).

The results section will present data on cave bear remains from mountainous regions and compare them to samples from the Rhine valley. Different possibilities to present the data are shown which in consequence allow answering various questions in relation to cave bear remains.

Material and sites

Bone and teeth samples of cave bears from several caves in the Austrian Alps, the Franconian Alb, but also from the German Upper Rhine-Graben in Bobenheim Roxheim (**Fig. 1**) were sampled for radiocarbon dating and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis. Here we introduce recently conducted radiocarbon measurements and stable isotope data, which were determined on the same collagen for better comparison of the data. The samples originated from recent excavations or from museum and private collections.

Austrian Alps

Almost all caves in the Austrian Alps lie at about 2,000 m above sea level (asl). The only exception with an altitude of 1,600 m is the Brettstein cave in the Totes Gebirge. All sites in Austria are of interest for cave bear evolution. Among them, the Potentialschacht is a newly discovered site and the easternmost high Alpine cave bear site in Austria.

Brettstein cave

The Brettstein cave system (Untere Brettsteinbärenhöhle) with 13 entrances is located at 1,660 m asl on the karst plateau of Totes Gebirge (Styria). Its total known length is 5,420 m (Spelix 2019) with an elevation difference of 218 m. The year of the discovery is unknown. The first map of the cave was produced in 1929. New parts of the cave were found in 1938, 1967 and from 1996 to 2001. Palaeontological excavations took place from 1994 to 1997. The presence of the faunal remains and their radiocarbon dates (s. below) suggest that the plateau was still ice-free about 26,500 years ago (DÖPPES et al., 2016; DÖPPES et al., 2019). The Brettstein cave yielded remains of two cave bear species *U. sp. eremus* and *U. sp. ladinicus*. The four teeth samples presented here were taken during excavation campaigns from 1994 to 1997 and are stored at the Department of Palaeontology at the University of Vienna.

Salzofen

Like the Brettstein cave, the Salzofen is part of Totes Gebirge and lies around 2,005 m asl. The cave system with shafts and halls has a main entrance and two secondary entries. It was found in 1924 and has a known length of 3588 m with an elevation difference of 124 m. Excavations began in the same year and continued until 1964. The faunal remains are dominated by cave bear and cave lion (GOTSCHIM, 2019; KÖNIG, 2019). There are signs that this cave was also used by humans as shelter while hunting. First ^{14}C results of six samples from four different sites (DÖPPES et al., 1997; DÖPPES, 2000) seem to point to two different periods: Some date to around 32,800 years BP and others are older than 49,000 years BP, beyond the age range of the radiocarbon method. The four bone samples (2 phalanges and 2 metacarpals) from Ursus sp. eremus used in this study were taken during an older campaign and are stored at the Natural History Museum in Vienna.

Hennenkopf cave

The Hennenhopf cave (Äußere Hennenkopfhöhle) is situated at 2,073 m asl on a vegetation-free plateau called »Steinernes Meer« near the town of Saalfelden am Steinernen Meer (CECH et al., 1997; DÖPPES et al., 2022). Its total length as known today is

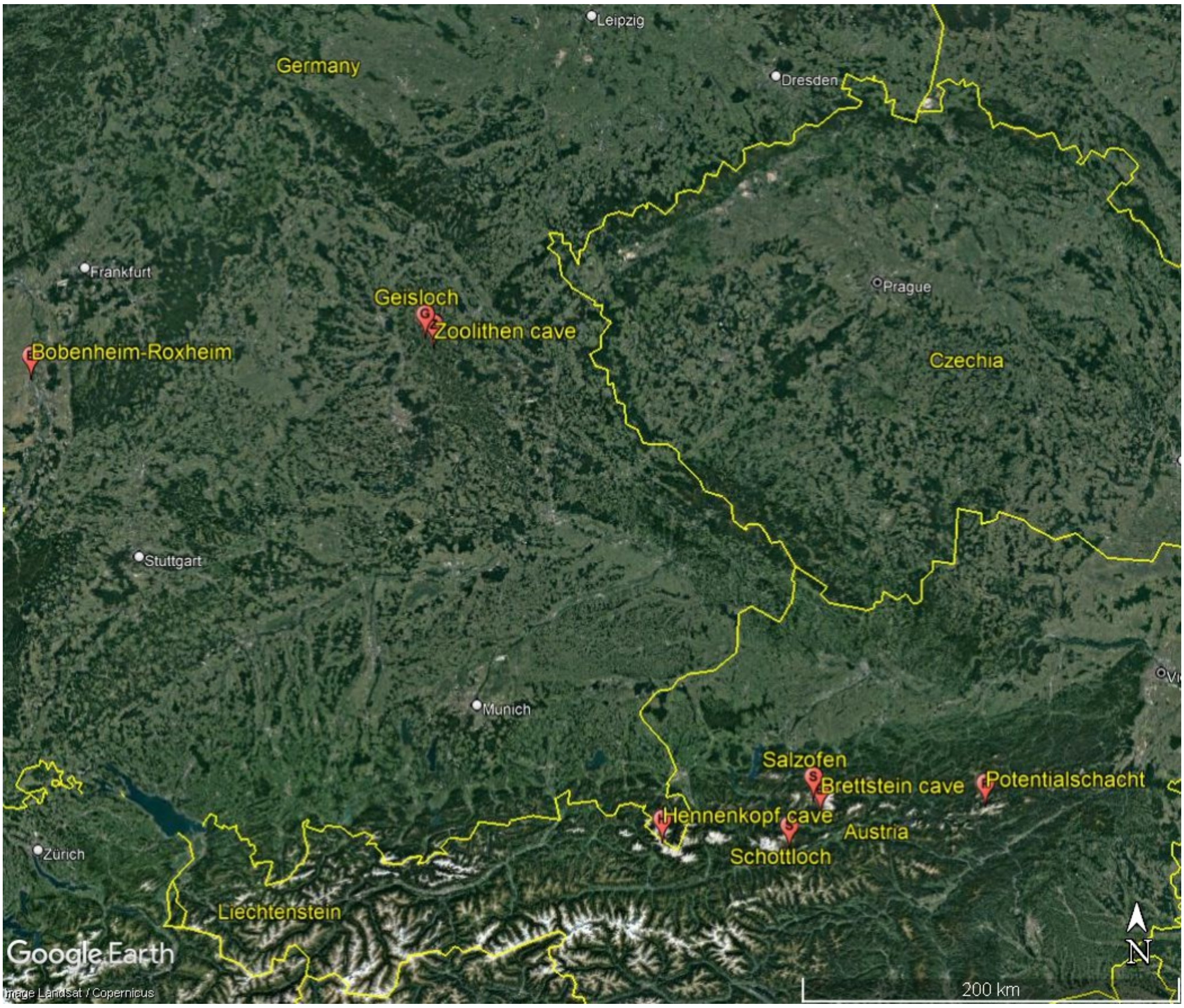

Fig. 1: Map of sample locations of cave bear remains analyzed in this study. Picture taken from Google Earth Pro. | **Abb. 1**: Karte der Fundorte mit den in dieser Studie untersuchten Höhlenbärenresten. Das Bild stammt von Google Earth Pro.

3,976 m with an elevation difference of 177 m. It was discovered only in 1942 as the entrance of this cave is quite hidden. The cave bear remains were recovered between 1986 and 1991 and are stored at the Natural History Museum in Vienna. Until now, there were no unambiguous radiometric age determinations of the bear remains. The samples of this study include two basal phalanges and fragments of a left ulna and a right radius assigned to the small-sized cave bear of the species *U. sp. eremus*.

Schottloch

This cave is located in the southeastern part of the Dachstein karst plateau near Liezen (Styria) at an elevation of 1,980 m asl. A rather low entrance height (1 m) leads into a small, but high hall (> 2 m) where most cave bear remains (only fragments) were found. The cave has a known length of 32 m. Compared to bear remains from other sites, such as the Ramesch cave (Ramesch-Knochenhöhle) and the Salzofen, the specimens from the Schottloch appear to have been smaller in size (Rabeder, 1997). The three bones investigated in this study include fragments of a left radius, a femur and a pelvis. They were recovered during an old campaign from 1880 and 1881, whose finds are stored at the Natural History Museum in Vienna.

Potentialschacht

The Potentialschacht is a shaft cave in the Hochschwab massif near St. Ilgen (Styria). The cave entrance lies at 2,070 m asl on a karst plateau. The known length is 2,329 m with an elevation difference of 107 m. The cave consists of a sequence of shafts and canyons and is difficult to access. The cave was explored by members of the Speleological Society of Vienna and Lower Austria from 2005 to 2019 (Plan & Baron, 2021). Remains of juvenile cave bears were found at secondary sites in a mixture of clay and debris in different locations. The animals probably entered the cave through openings that are blocked today. Using aDNA analysis, it was found that these bears belong to the species *U. spelaeus eremus* (Kavcik-Graumann et al., 2022). Two fragments of a humerus and a rib from bear cubs were collected during a recent expedition. The cave bear material is stored at the Natural History Museum in Vienna.

Franconia, Germany

Geisloch

This cave at 475 m asl near Oberfellendorf has developed in Upper Jurassic (Malm) carbonates and is situated in a dolomitized reef. It has a large central hall with irregular branching passages (total length 750 m). The 5 m long shaft entrance and a small chamber have been known since 1788. The large central hall with the site »Knochenkammer« was discovered in 1968. Some paleontological investigations were carried out in 1981 but no excavation has taken place (Heller, 1981).

Two different bone layers are described, on the cave floor where the bones are spread unsystematically and below the flowstone layer. The bone sample mentioned here was directly collected from the site »Knochenkammer« under the flowstone in 2020. In total, five bone samples were dated the first time, but only one had enough collagen preserved for analysis.

Zoolithen cave

The Zoolithen cave is a natural karst cave near Ebermannstadt and lies around 455 m asl (Rosendahl, 2001; Hilpert et al., 2005). It extends over 1,000 m and is the oldest known cave in Franconia (found in 1602). Based on remains from this cave, Johann Christian Rosenmüller described the species of *Ursus spelaeus* for the first time in 1794. Bones and teeth of over 800 bears were recovered from this cave. Bone finds from this cave site can be found in numerous museums in the world. In 1971, new parts were discovered. Morphological analysis of the premolars of the cave bears revealed that the various small chambers were filled at different times (Rabeder, 1983). The bone sample mentioned in this study, which consists of a part of the left zygomatic arch, was recovered at the time of the new discoveries and is stored as the collection Reis at the Reiss-Engelhorn-Museen in Mannheim.

Rhine valley

Fossil finds from the Upper Rhine Graben come from a gravel pit in Bobenheim-Roxheim (today Silbersee), an old arm of the Rhine. The finds were acquired before 1984 by Klaus Reis from Deidesheim (Rhineland-Palatinate, Germany). Nowadays, the application of modern technologies such as »suction dredging« unfortunately fragments or even destroys faunal remains. Accordingly, it is no longer possible to find complete skulls or other bones in gravel pits, as Klaus Reis did in the 1950s. The material has been stored in the Reiss-Engelhorn-Museen (rem) in Mannheim in the collection Reis since 2020. In addition to the cave bear (*Ursus ingressus*) find from Bobenheim-Roxheim, bones of large mammals (cave lion, cave hyena, reindeer, giant deer, steppe bison, and woolly rhinoceros) were sampled for stabile isotope analysis to compare to the cave bear data. All samples from Bobenheim-Roxheim are from the petrous bone, the densest bone of the mammals. Some faunal elements (cave lion, European moose) have also been palaeogenetically studied (Stanton et al., 2020; Dussex et al., 2020).

Methods

Radiocarbon dating

Radiocarbon is a method that uses the only radioactive carbon isotope, ^{14}C, with a half-life of 5,730 years for dating organic and inorganic materials containing carbon (Bronk Ramsey, 2008). The datable age range covers the last 50,000 years with variable temporal resolution depending on the presence of calibration plateaus. When dating bones, laboratories aim at extracting the collagen, which does not exchange carbon with its environment over time. The bone mineral phase or bone apatite on the other hand readily exchanges carbon with its surrounding which then leads to erroneous ages if the foreign carbon cannot be removed. The sample preparation to extract the collagen consists of removal of the bone apatite using diluted hydrochloric acid (HCl) followed by an alkaline/base step with diluted sodiumhydroxide (NaOH) to remove soluble humic acids as these also can shift the age towards younger or older ages depending on their origin. However, as NaOH tends to extract CO_2 from the surrounding air, another acid step is needed to remove the modern contamination. The remaining material is then gelatinized at 60 °C for 20 hours before macroscopic fragments are removed with an Ezee-FilterTM (Elkay). The collagen in its now liquid phase is then further cleaned in an ultrafiltration step that removes proteins of smaller masses (< 30kDa) and broken chains of amino acids. The sample is then frozen in a freezer for two days before it is finally freeze-dried to end up as fluffy material that is easy to handle (Brown, 1988; Lindauer et al., 2015). To be able to detect any contamination occurring during the sample preparation, a so-called process-blank sample is run with the samples to be dated. In our case, we use bone samples from horses that were killed in the 30-year war (1,618–1,648 AD) where the exact date is known, in this case September 1644. As this is close to or at the edge of a plateau region, it is quite comfortable to see contamination with either younger material or older material. In general, samples that weigh 1–2 g are sufficient. Less material can become problematic, because often hardly 1% of the original material is collagen. A reliable measurement in the accelerator ideally uses / is based on 1 mg of elemental carbon, which requires 4–7 mg of collagen, depending on the carbon content, to be combusted.

The sample is combusted into gaseous CO_2 in an elemental analyzer (VarioMicro elementar, Lindauer & Kromer, 2013). The CO_2 gas is fed into a glass tube (»reactor«) filled with iron powder as catalyst (on which the carbon settles) where the reaction (in this case reduction) to elemental carbon takes place at a temperature of 575 °C (Lindauer & Kromer, 2013). Thereafter the sample is pressed into a target and measured in an accelerator mass spectrometer, in this case of the type MICADAS (MIni CArbon DAting System) as described in (Kromer et al., 2013). The measurement results are fractionation corrected, which takes into account any mass-dependent shifts between the ^{12}C, ^{13}C (the two stable carbon isotopes) and the ^{14}C isotope that occur either in the sample itself, during combustion, graphitization or due to processes during ionization and acceleration in the AMS. The measurement is adjusted to the worldwide used oxalic

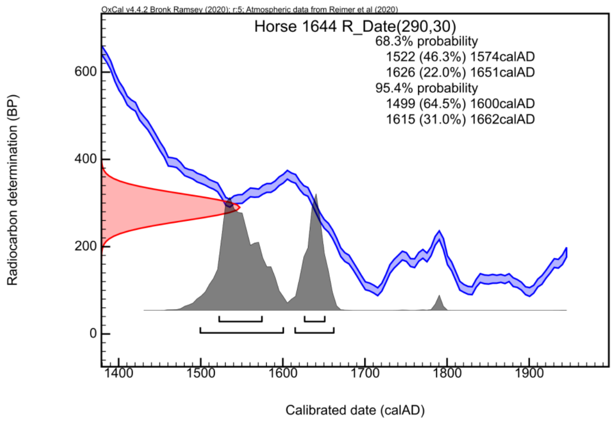

Fig. 2: Red bell curve: Measured radiocarbon age of 290 ± 30 ^{14}C yrs BP calibrated with OxCal 4.4 and the IntCal20 dataset. Grey shaded areas/peaks: Calibrated calendar ages using the one-sigma (68%) and two-sigma (95%) probability of the ^{14}C age and calibration curve. Note that the known age of death of the horse is AD 1,644, which lies in the peak region of the smaller probability and shows that relying on the major peak would result in the wrong age range. | **Abb. 2**: Rote Glockenkurve: Gemessenes Radiokarbonalter von 290 ± 30 ^{14}C Jahren BP, kalibriert mit OxCal 4.4 und dem IntCal20-Datensatz. Grau schattierte Bereiche/Spitzen: Kalibrierte Kalenderalter unter Verwendung der Ein-Sigma- (68 %) und Zwei-Sigma-Wahrscheinlichkeit (95 %) des ^{14}C -Alters und der Kalibrierungskurve. Man beachte, dass das bekannte Sterbealter des Pferdes 1.644 n. Chr. ist, was im Bereich der kleineren Wahrscheinlichkeit liegt und zeigt, dass eine Beschränkung auf die große Spitze zu einem falschen Altersbereich führen würde.

acid II standard and contains also blank measurements of samples too old to still contain ^{14}C as well as e.g. IAEA standards of known ^{14}C content or process blanks. The measurement results given in »years BP« need to be calibrated to refer to calendar ages instead of ^{14}C-ages. When presenting radiocarbon data, it is standard to include laboratory codes, in our case »MAMS + Number«, sample name, material used (e.g. bone, charcoal, etc.), uncalibrated ages (hence measurement results) in »yrs BP« or »^{14}C yrs BP«, calibrated ages either in »cal BC/AD/BCE/CE« or in »cal BP« (Millard, 2016). It must always be mentioned which program (in our case usually Oxcal) was used with which calibration dataset (e.g. IntCal13 or latest IntCal20). This way, it is possible to reconstruct data and recalibrate them in the future when new calibration datasets, sites or samples will be available. The calibration procedure of one ^{14}C-age often results in several probabilities of calendar age ranges as seen in the calibration graph in **Fig. 2**. This example — the above mentioned horse bones — was chosen, although being much younger than the cave bear age range, to describe the effect of extracting single probabilities. Remember that the horse was killed in 1644 AD, a calendar age that (in this example) does not lie in the calibrated age range with the highest probability. Excluding this age range just by selecting the highest probability range would result in an erronious date. Therefore, it is only possible to exclude certain ranges when other (not ^{14}C) chronological information is present (which must be proven!). Otherwise when using ^{14}C alone, the complete age ranges must be given when presenting radiocarbon data. Using a certain age range only also

Labcode MAMS	Sample	Pretreatment	^{14}C age yrs BP	$\delta^{13}C_{AMS}$ ‰
39641	Resin NK34	no	30,958 ± 203	-30.8
32881	Ovibos NK34 Bobenheim-Roxheim	solvents, collagen extraction with ultrafiltration	50,007 ± 854	-21.1

Tab. 1: Measurement of untreated, scratched-off conservation substance (»resin«) and of bone sample pretreated with solvents prior to collagen extraction to monitor differences in ages of the two components. The δ^{13}C value in this case is only of limited use as it was not measured with an isotope ratio mass spectrometer (IRMS) but in the AMS system to correct for fractionation during measurement. The ages are not calibrated. | **Tab. 1**: Messung der unbehandelten, abgekratzten Konservierungssubstanz (»Harz«) und der vor der Kollagenextraktion mit Lösungsmitteln vorbehandelten Knochenprobe, um die Altersunterschiede der beiden Komponenten zu überwachen. Der δ^{13}C-Wert ist in diesem Fall nur bedingt aussagekräftig, da er nicht mit einem Isotopenverhältnis-Massenspektrometer (IRMS), sondern mit dem AMS-System gemessen wurde, um die Fraktionierung während der Messung zu korrigieren. Die Altersangaben sind nicht kalibriert.

reduces the probability of really presenting the true age as the notation »68 % (1 sigma)« or »95 % (2 sigma)« only refers to the complete range respectively.

Samples from collections

The material for investigations is not always given to the laboratory from excavations directly. Earlier finds are often stored either in museums or in private collections. In some cases, skeletal remains have been conserved with substances that may contain significant amounts of carbon. This can prove difficult when it comes to radiocarbon dating. Whenever known, information on the conservation substances used should be reported to the radiocarbon lab, so that the sample preparation can be adjusted. Otherwise, a variety of solvents has to be used for removing the unknown substances to be on the safe side (Bruhn, 2001). However, these solvents generally also contain significant amounts of carbon. Here, the fact that the solvents evaporate easily before being absorbed by the samples is advantageous. This study also dated the preservative applied to one sample in order to monitor if incomplete removal of the substance would shift the age. There are two possibilities: If the preservative consists mainly of petrochemically derived substances it will be fairly old as petrochemicals are completely depleted of radiocarbon. When mixed with younger additives, the preservative becomes increasingly younger. In case the conservation substance has a biological origin, such as glue derived from animal bones, it is much younger or even of modern age compared to the sample being dated and would shift the age to significantly younger ages. It should be mentioned that it is easier to shift an age towards younger ages than to further deplete it of radiocarbon. **Tab. 1** shows an example from Bobenheim-Roxheim (collection Reis) where the sample had been conserved with an unknown substance. Fortunately, the preservative could be scratched off the bone and was visible as a kind of shiny glue. It is unknown, however, if the substance soaked into the bone, which still makes an adequate pretreatment necessary in addition to surface removal. In this case, the conservation agent was a mixture of petrochemically derived compounds with modern admixtures. Resulting in an age of 20,000 years younger than the bone sample itself, incomplete removal would have shifted the age of the bone sample to younger ages. When sending samples to radiocarbon laboratories it is therefore important to mention any possibility of conservation substances involved. The more information given — ideally the substance named — the more reliable the final data will be. An important factor to determine the quality of the bone data is the collagen yield and, even more important, the atomic ratio of carbon to nitrogen (C/N) in the collagen received after sample preparation. Both values are determined during the combustion step in the elemental analyzer that not only combusts the sample to CO_2, but also determines the amounts of carbon and nitrogen in the sample. It is common practice to report only data where the C/N ratio lies within a certain range, namely 2.9–3.6 (DeNiro, 1985). In the radiocarbon laboratory of the Curt-Engelhorn-Centre Archaeometry (CEZA), Mannheim, samples with a collagen yield below 0.5 % are not measured as these samples often produced erroneous ages, even when the C/N ratio lies within acceptable ranges.

Stable isotopes

In addition to radiocarbon dating, the organic component of bones (collagen) may also be used for dietary reconstructions. Collagen is a protein and contains carbon and nitrogen, whose stable isotope compositions relate to the foodstuffs or forage that the human or animal consumed. The isotopic signals vary along trophic chains due to isotope fractionation that occurs in metabolic processes (Krajcarz et al., 2016). Sample preparation for stable isotope analysis on bone is similar to the collagen extraction for radiocarbon dating. The main difference is that ultrafiltration is usually omitted. However, bone collagen that is prepared for radiocarbon dating can also be used for stable isotope analysis and does not require additional sample material. At the stable isotope facilities at CEZA, samples are analyzed as triplicates. The material is combusted in a vario PYRO cube CNSOH elemental analyzer (Elementar) and the N2 and CO_2 gases transferred to a precisION isotope ratio mass spectrometer (IRMS, Elementar/Isoprime) for isotope analysis. In addition to the samples, each run includes several international and in-house standard materials for data normation and quality control. The $\delta^{13}C$ values are adjusted to the Vienna Pee Dee Belemnite standard (V-PDB) and the $\delta^{15}N$ values to Ambient Inhalable Reservoir (AIR). Deviations from these standards are given in ‰.

Carbon isotope values ($\delta^{13}C$)

The primary reason of variation of the stable isotope composition of carbon is isotope fractionation that occurs in plants at the base of foodwebs. It causes C3 plants — that prevail among the European vegetation — to have remarkably lower $\delta^{13}C$ values than C4 plants such as maize, sugarcane or millet, which are adjusted to drier and warmer environmental conditions (Cerling et al., 1997) and are not expected to be noteworthy food sources of cave bears in Europe during the Pleistocene. Much slighter variation occurs among C3 plants due to variation in humidity (Diefendorf et al., 2010; Kohn, 2010) or vegetation cover (canopy effect) (Drucker et al., 2008). Especially in the context of exploring isotopic variation of $\delta^{13}C$ values of cave bear collagen, the influences of altitude, latitude and longitude are considered (Krajcarz et al., 2016). However, relations are rather marginal and point to complex, in detail often hardly resolvable and explainable relations. Finally, carbon isotope values also increase slightly along food chains so that the $\delta^{13}C$ values rise by 0.8 to 1.3 ‰ with each trophic level leading to higher values in carnivores than in herbivores (Bocherens & Drucker, 2003).

Nitrogen isotope values ($\delta^{15}N$)

Plants take up nitrogen directly from the soil, in which the isotope composition depends on the microbial activity. Comparatively low values are found in acidic soils or pioneering vegetation (Krajcarz et al., 2016), whereas well-developed soils, the addition of animal dung, resp. manuring in agricultural economic systems (Bogaard et al., 2007; Fraser et al., 2011), arid climates or saline soils lead to higher $\delta^{15}N$ values. Stable nitrogen isotopes also fractionate along food chains, which leads to an increase of the $\delta^{15}N$ of bone collagen by 3 to 5 ‰ with each trophic level, so that tissues of carnivores have higher $\delta^{15}N$ values than those of herbivores (Lee-Thorp, 2008; Grupe et al., 2015). Bone collagen of infant mammals or dentine, that forms during infancy and remains afterwards unchanged, usually also exhibits higher $\delta^{15}N$ values than tissues that are formed later in life (Jenkins et al., 2001). This isotopic enrichment is caused by the so-called suckling effect, because isotopic fractionation during metabolic processes in a mother's body leads to increased $\delta^{15}N$ and $\delta^{13}C$ values in breastmilk so that suckling infants appear to be one trophic level above their mothers.

Stable isotopes and cave bear remains

Hervé Bocherens and colleagues carried out significant pioneering stable isotope research on cave-bear remains (Krajcarz et al., 2016; Bocherens, 2019). Hibernation discriminates bears from other mammals and is also considered to influence the stable isotope composition of their bone collagen as it causes changes in the metabolism of the amino acids (Krajcarz et al., 2016). During hibernation, bears re-absorb the nitrogen-containing waste, which should lead to an increase of $\delta^{15}N$ comparable to an extra trophic level. Similarly, $\delta^{13}C$ can change when the bears use their fat stores while not eating. As fat has lower $\delta^{13}C$ values than the tissues of the brain, muscles and metabolic organs, bear tissues that form during hibernation may exhibit depleted $\delta^{13}C$ values. This effect might be seen mostly in juvenile bears whereas the signal in adult bears can still be dominated by diet-related values. Indeed, e.g. cave bears from sites in the Ach Valley of the Swabian Jura exhibit significantly lower $\delta^{15}N$ and $\delta^{13}C$ values than other species, including herbivores and brown bears (Münzel et al., 2011). This observation suggests, that despite a possible hibernation effect and constant remodeling, the isotopic signatures of adult bears reflect primarily dietary habits. Research that focusses on the reconstruction of dietary niches should use bone collagen of adult animals, as samples of infantile animals or tooth dentine may be influenced by the suckling effect (Krajcarz et al., 2016; Bocherens, 2019). Krajcarz et al. (2016) suggested data adjustments to correct for the suckling effect in tooth dentin or altitude effects on the isotopic composition of bone collagen. These approaches should, however, be applied with caution as the extent of the suckling effect depends on the type of tooth analyzed and the position of the sample within the tooth. The altitude of a site effects its vegetation, humidity and other environmental parameters, but does not have any direct influence on the isotopic data itself.

Additional methods

Optically stimulated luminescence dating (OSL)

OSL dating aims at directly dating the sediment layer or rather when it was accumulated (Wagner, 1998). The luminescence signal is built when minerals such as quartz and potassium feldspar — the most commonly used minerals in OSL — store the energy from radioactive decay in the mineral itself but also from the surrounding. This energy is stored as long as the mineral is not exposed to light or elevated temperatures. In the laboratory (dark laboratory with subdued red light) the sample is measured using stimulation of distinct wavelengths as each mineral then emits light at another, characteristic wavelength. For example, quartz is stimulated in blue or in green wavelengths and emits in the ultraviolet wavelength range, potassium feldspar (K-feldspar) is stimulated in infrared and emits in blue. The amount of light then emitted is a measure for the energy stored in the crystal of this mineral. With an additional measurement of the radioactivity of the sample itself but also of surrounding material one receives information about the energy per unit time (in this case per year). When comparing the energy stored in the mineral and the radioactivity, hence energy available per unit time, it is possible to assign an age to the sample. Different characteristics of the minerals such as the faster bleaching ability of quartz compared to K-feldspar can also be used to determine incomplete bleaching processes and therefore gain information about the sedimentary processes. In this case, a minimum age would be the result. If ages of quartz and feldspar overlap, both minerals were exposed to sunlight, resp. daylight for a long enough time and accumulated in the cave due to aeolian transport. Sampling and dating each stratigraphic layer of a sediment profile provides the most robust results. Such a strategy may detect age inversions due to bioturbation, slope slumps, landslides or other causes.

For OSL, the datable age range routinely reaches 200,000 years. Using special equipment such as cooled infrared detection photomultipliers, age determination can exceed this limit by several 100,000 years. Using this method, the age of the sediment layer of the Homo heidelbergensis was determined to 684,000 years (Wagner et al., 2010). In caves, OSL can be challenging as the source of the sediment might be difficult to determine, but nevertheless, it directly dates the sediment layer itself which cannot be done with other methods (Jacobs et al., 2011; Guerin et al., 2012).

Dendroecology

Dendroecology is a discipline closely linked to dendrochronology (DC). In dendroecology (DE) tree-rings are used to elucidate e.g. woodland succession and composition, treeline dynamics, ecotone development and to quantify spatiotemporal environmental changes. However, how can DE help to reconstruct environmental conditions, if tree borders are usually below the cave bear sites? Tree- and timberlines are changing with environment and therefore pine trees can grow at varying altitudes depending on temperature and climate. Ancient trees are usually found in gravel pits and peat bogs or as timber at archaeological sites. Although not directly linked, such wood samples can help to reconstruct the microclimate of their area. When linked to other datasets, like microfossils or isotopes they may also contribute to exploring climate conditions on a continental scale. In addition, charcoal fragments are often found in various types of sediments and are commonly used for paleo-ecological studies to elucidate woodland development on a local scale and paleoenvironmental reconstruction in general. Moreover, when applied to charcoals, DC (and its sub-disciplines) can provide new information complementing the data obtained from wood species analysis. This combined approach may enhance existing records leading to a better understanding of the past environment (Damblon & Haesaerts, 2011; Ferme & Villalba, 2011; Cichocki et al., 2014). While these results enhanced the interpretation of on- and off-site records, anthracology can stand alone providing new insight in the development and creation of landscapes.

The determination of the widths of the tree rings is the first step. Tree rings are wider when the environmental conditions are favorable for the specific tree species. For this purpose, annual tree rings (or if possible, even early wood and late wood of the same year) are measured in 2-3 directions of a wood disc to make sure missing or incomplete rings are also found. The occurrence and spatiotemporal distribution of different species, comparable to pollen analysis, is also a marker of climatic conditions and commonly used for environmental reconstructions. Species such as oak, alder, ash or elm indicate relatively warm conditions, whereas pine, juniper and fir trees are growing in cooler climates. Additional observations of morphological and anatomical features like insect boreholes, fungal strains, traumatic resin ducts and growth abnormalities are further valuable indicators to elucidate past environmental and ecological settings (Marguerie & Hunot, 2007).

Cellulose extracted from tree rings, can be used for several kinds of analyses. Radiocarbon dating is probably most often applied. Ideally, cellulose of several single tree rings of adjacent years is used in order to reduce the error or even manage to reduce the age range to a single year (Kuitems et al., 2022). In addition, the cellulose can also be used for stable isotope analysis of $\delta^{13}C$, δD or D/H (ratio deuterium 2H to hydrogen 1H), and $\delta^{18}O$ to reconstruct the origin of carbon e.g. through photosynthesis ($\delta^{13}C$), water availability, precipitation ($\delta^{18}O$) and water vapour (δD)

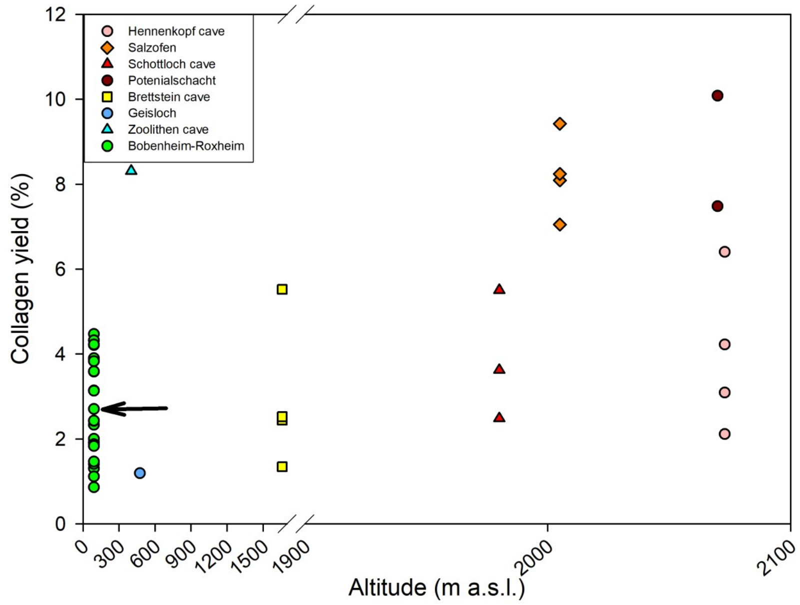

Fig. 3: Collagen yields according to site and altitudes. Apart from Bobenheim-Roxheim, all data represent cave bear remains. The arrow marks the cave bear sample from Bobenheim-Roxheim. Here, the presentation of several species shows the variability within a single location. | **Abb. 3**: Kollagenausbeute je nach Fundort und Höhenlage. Mit Ausnahme von Bobenheim-Roxheim handelt es sich bei allen Daten um Höhlenbärenreste. Der Pfeil markiert die Höhlenbärenprobe aus Bobenheim-Roxheim. Die Darstellung mehrerer Arten zeigt hier die Variabilität innerhalb einer Fundstelle.

(McCarroll & Loader, 2004). Annual growth rings of trees can serve as high-resolution archives for climate and ecological information. Here it is important to focus on latewood, which is more independent of the influence of carbohydrate mobilization in metabolic reactions during early plant growth and thus, of variation from previous years. Moreover, annually resolved isotope chronologies from latewood cellulose are successfully used for dating wood from unknown ages (e.g. Loader et al., 2019; Domínguez-Delmás, 2020).

Results and discussion

In the following paragraphs, we discuss the outcomes of different analytical methods, ways of data presentation and combining them. For comparison, we include stable isotope data from the literature that are uncorrected regarding altitude or bone/tooth type (Kneussl, 1972; Kneussl, 1973; Blant et al., 2010; Bocherens et al., 2011; Münzel et al., 2011; Spötl et al., 2014; Döppes et al., 2016, Krajcarz et al., 2016; Döppes et al., 2019). This allows to evaluate the new data in the context of other sites with respect to age range, diet and climate. The caves mentioned in these publications and used for comparison of ^{14}C, $\delta^{13}C$ and $\delta^{15}N$ are Tischofer cave, Ramesch cave, Gamssulzen cave, and Winden cave in Austria as well as Nietoperzowa cave and Perspektywiczna cave in Poland. In some publications, only ^{14}C or stable isotope data were available, but not both. Therefore, data from the following caves were used for comparison of ^{14}C data: Schwabenreith cave, Herdengel cave, Schreiberwand cave, Bärenfalle, Schlenken cave (Schlenken-Durchgangshöhle), Brettstein cave older data (Döppes, 2000; Pacher, 2003) from Austria, Conturines cave from Italy, and Herkova cave from Slovenia. A smaller list of different caves was added and contained only stable isotope data: Geißenklösterle cave and Hohle Fels cave from Germany (Swabian Jura) as well as Medvedia cave in Slovenia. Of course, these datasets are not complete as they do not refer to all publications available on this topic, but nevertheless, they provide a good overview.

Radiocarbon dating

All radiocarbon ages were calibrated to ages cal BP with Oxcal 4.4 (Ramsey, 1995) and the IntCal20 dataset (Reimer et al., 2020). In a first step, the yields of the collagen extraction provide some additional information on the quality of the collagen itself. The collagen preservation is directly linked to the storage conditions of the soil surrounding the bones and therefore differences in collagen yield might point to differences in soil chemistry. **Fig. 3** illustrates that there is no clear relation between collagen yields of cave bear bones and the altitude of the sites investigated. Despite sites in lower lying landscapes such as Franconia are underrepresented, collagen preservation seems to be slightly better at sites in higher altitudes, probably due to lower temperatures as well as less humic acids and bacteria in the soil. At Bobenheim-Roxheim, the collagen yield of the cave bear bone fell into the variation of other species, such as *Mammuthus trogontherii*, *Megaloceros*, *Bison priscus*, *Bos primigenius* and few specimens of *Dama sp.*, *Rangifer tarandus*, *Crocuta crocuta spelaea*, *Panthera spelaea*, *Stephanorhinus sp.* Apart from the two teeth of *Mammuthus* (M3) only petrous bone was used for this site.

Radiocarbon data can also be helpful to determine the duration of the use of a cave, even though the subsample analyzed may not cover the complete age range it. The ages presented here (**Tab. 2**, see appendix) cover a range from around 30,000 years to beyond the radiocarbon age limit of 50,000 years uncalibrated. The oldest data originate from the Hennenkopf cave (four samples from 44,000 years BP until over 50,000 years BP, MAMS 43821-4). The results of adult cave bears from the Salzofen (MAMS 43825-8, 36,000–46,100 years BP) and the Schottloch (MAMS 43829-31, 34,000–45,000 years BP) originate from similar cave elevations but comprise different age ranges

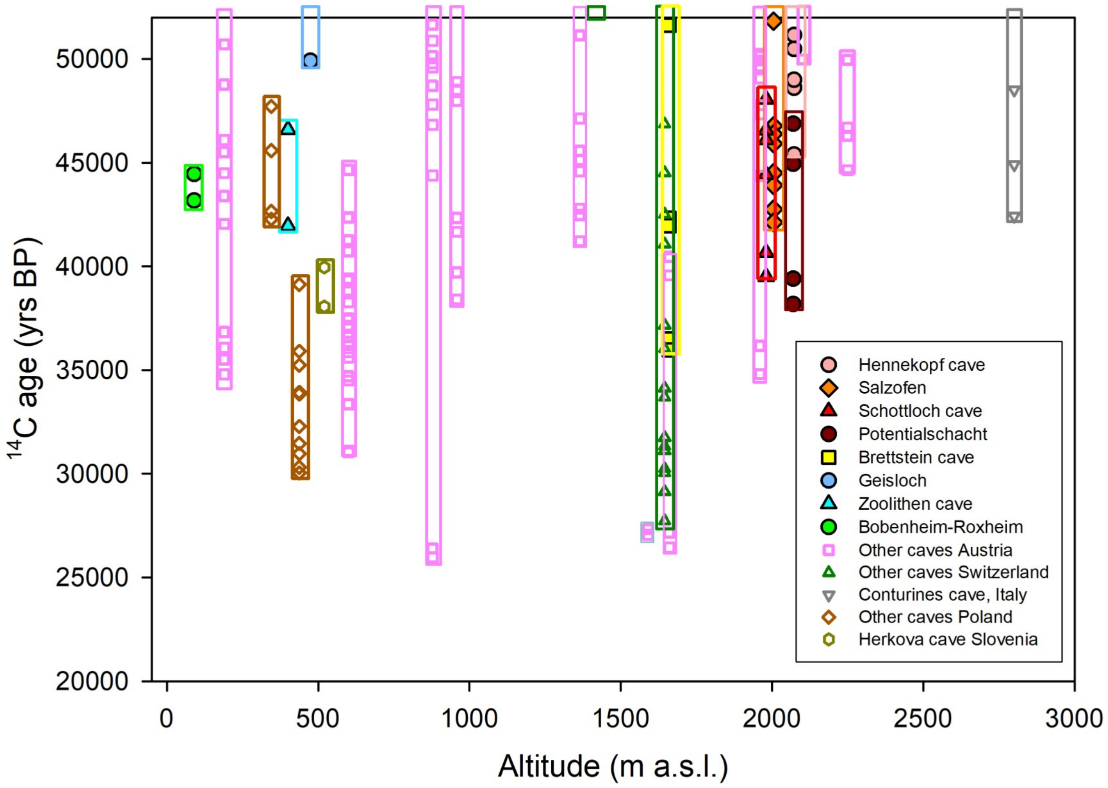

Fig. 4: Uncalibrated radiocarbon ages plotted as a function of altitude of the caves. Ages older than 50,000 years are beyond the datable range of the method and usually reported as »>49,000«. The respective symbols are surrounded by bars to indicate duration but kept to differentiate between the colours. Here, we present them with a larger error to visualize that some of the ages extend beyond the age limit. Unfilled symbols refer to data of cave bears from other publications (Blant et al., 2010; Bocherens et al., 2011; Döppes et al., 2016; Döppes et al., 2019; Kneussl, 1972, 1973; Krajcarz et al., 2016; Münzel et al., 2011; Spötl et al., 2014). | **Abb. 4**: Unkalibrierte Radiokarbonalter, aufgetragen in Abhängigkeit von der Höhe der Höhlen. Alter, die älter als 50.000 Jahre sind, liegen außerhalb des datierbaren Bereichs der Methode und werden gewöhnlich als »>49.000« angegeben. Die jeweiligen Symbole sind mit Balken überdruckt, um die Dauer anzugeben, aber mit gleicher Farbe wie die Symbole. Hier stellen wir sie mit einem größeren Fehler dar, um zu verdeutlichen, dass einige der Altersangaben über die Altersgrenze hinausgehen. Die ungefüllten Symbole beziehen sich auf Daten von Höhlenbären aus anderen Publikationen (Blant et al., 2010; Bocherens et al., 2011; Döppes et al., 2016; Döppes et al., 2019; Kneussl, 1972, 1973; Krajcarz et al., 2016; Münzel et al., 2011; Spötl et al., 2014).

with the Schottloch being contemporary to the Hennenkopf cave. The juvenile bears from the Potentialschacht (MAMS 48555-6, 33,800–43,400 years BP) fit into the age range of the Salzofen. The Brettstein cave, situated near the Salzofen, presents the largest age range of the caves with multiple samples available (MAMS 43564-7, 31,000 until beyond 50,000 years). The caves in Franconia, Geisloch (MAMS 48559, 48,000 years BP) and Zoolithen cave (MAMS 24997, 40,000 years BP) with only one data point for each seem to be contemporaneous with the Alpine sites as does the cave bear found in the Upper Rhine Graben at Bobenheim-Roxheim (MAMS 32882, 40,000 years BP). With respect to other cave bear sites, our data fit well into the general age ranges of European cave bears. The radiocarbon ages can serve several purposes when combining them with different information on the same material, which is presented in the following paragraphs.

Age versus altitude

A plot of the calibrated radiocarbon ages of the cave bear remains — showing the upper and lower age limits of all dated samples of a particular cite — indicates that in the Alpine region of Austria, earlier starting dates seem to be associated with higher altitudes (**Fig. 4**). When comparing the results to other published data from Austria and some other European countries, the data presented here fit nicely into the spectrum of their radiocarbon ages (**Fig. 4**). Keeping in mind that not all cave bear remains from the respective caves and sites were found or dated, there seems to be a tendency that caves at higher altitudes were inhabited for a shorter period.

This has a climatic indication, as the caves needed to be accessible during the time in which the bear remains accumulated. Moreover, ages from sites at lower elevation are more widespread. In the Austrian and Swiss Alps, bears lived at elevations below 2,100 m asl from beyond the radiocarbon dating limit until around 25,000 cal BP at least (according to the limited dataset of 43 samples). Therefore, it is also not surprising to find cave bear remains at sites in the Alpine Foreland such as the Geisloch, that predate the possible age range of the radiocarbon method. With only one sample, it is of course, impossible to say whether this age also marks the end of the occurrence of cave bears in the Geisloch. For Bobenheim-Roxheim, that lies between the mountain ranges of the Odenwald and Palatinate Forest in the Upper Rhine Graben, the single data point agrees with the expected age range. However, using larger datasets allows to more precisely reconstruct periods of the presence of cave bears in the surrounding of the caves and possible movements due to environmental changes, such as the growth of glaciers or favorable conditions of the habitats of cave bears.

In higher altitudes above 2,000 m asl., most caves seem to have been inhabited by cave bears until around 35,000 years cal BP (Marine Isotope Stage MIS 3) which coincides with the start of a phase of increasing glaciation during the Würmian Glacial (Ivy-Ochs et al., 2008; Auer et al., 2014). This is accompanied by a reduction of plant growth and decrease of the climatic timberline. Swiss sediment records indicate that during MIS 3 the lowlands of Switzerland were ice-free, although environmental conditions were unstable and rather cool (Ivy-Ochs et al., 2008; Heiri et al., 2014). An interstadial at around 45,000 years is recorded with an expansion e.g. of open Picea forests in Switzerland (Ivy-Ochs et al., 2008). By 30,000 years, the Alpine glaciers had reached the mountain front as demonstrated by the outwash deposits. Large valley glaciers formed from the outflow of the main accumulation areas in the higher Alps, significantly reducing the variety of plants available for cave bears and other herbivores. Local effects can vary and would need to be investigated for a more detailed interpretation. The weight of the ice shield significantly depressed the lithosphere, which rose again during deglaciation and melting, a process that still continues until today.

With respect to the predominant vegetation during these phases, pollen records such as the paleolake record from Baumkirchen at the northern rim of the Inn valley in Austria (Barrett et al., 2018) can reveal the type of species and the timing of their appearance and decline. Barrett and co-workers found indications for an interstadial at around 35,000 years characterized by poorly developed forest stands that are dominated by several species of *Pinus*, *Alnus alnobetula*, *Salix*, *Hippophae*, *Dryas octopetala*, *Juniperus* and *Larix*. These pollen finds point to rather warm and humid conditions compared to previous periods. An earlier interstadial is recorded (41,000–38,000 years) which shows a reduced variation in trees but a well-developed grassland vegetation. These two warmer phases are embraced by two cooler and drier phases (46,000–41,000 years and 38,000–37,000 years) with low pollen input and open vegetation still including some trees such as *Pinus*, *Betula*, *Picea* (Starnberger et al., 2013; Barrett et al., 2018).

The cave bear data in this study cover these periods of increasing glaciation and reduced food resources in high altitudes. Considering that the Brettstein cave is the lowest one with 1,660 m asl while the Hennenkopf cave (2,073 m asl) and the Potentialschacht (2,070 m asl) lie at the highest altitudes, higher caves in general may show a shorter inhabitation period (Hennenkopf cave until 43,000 years ago, Potentialschacht until 37,000 years ago). Caves located in lower altitudes such as the Brettstein cave may have been better accessible due to favourable climatic conditions and food resources throughout the ages and therefore shows a longer duration with larger spread in ages of the bear remains. The Schottloch at intermediate altitude (1,980 m a.s.l.) supports this pattern. In the Late Würmian Glacial, when the ice shields reached their maximum the cave bear population apparently declines maybe due to failing adaption with respect to food resources as the plants then were covered by ice.

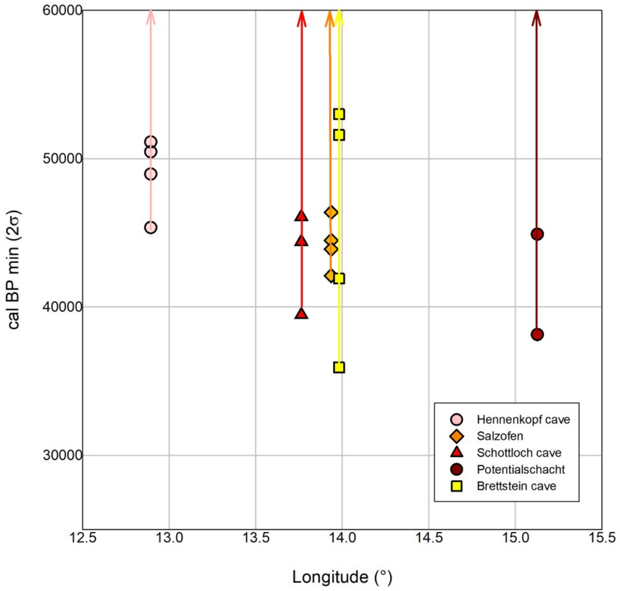

Fig. 5: Lower (younger) age limits (minimum ages) of Alpine cave bear radiocarbon dates (95% probability) plotted versus longitude of the caves to denote final stages of use of the caves by bears. Note that the upper age limits are not taken into account in this graph and that ages around 50,000 are so close to the measurement limit that they must be taken with great caution. | **Abb. 5**: Untere (jüngere) Altersgrenzen (Mindestalter) der Radiokarbondaten von alpinen Höhlenbären (95 % Wahrscheinlichkeit) aufgetragen gegen die geografische Länge der Höhlen, um die letzten Stadien der Nutzung der Höhlen durch Bären anzuzeigen. Beachten Sie, dass die oberen Altersgrenzen in dieser Grafik nicht berücksichtigt sind und dass die Altersangaben um 50.000 so nahe an der Messgrenze liegen, dass sie mit großer Vorsicht zu betrachten sind.

Age versus longitude

Movements of cave bears may also be revealed by plotting the age data versus geographic locations or coordinates. In **Fig. 5**, the lower limits (minimum ages) of the cave bear ages are plotted against longitude for the Alpine region in Austria. With respect to climate, in the western part of the Alps (Switzerland and western Austria) the glaciation was reaching lower valleys than in the Eastern part and seems to have proceeded from west to east over time. This is reflected in figure 5 where increasing values for longitude represent a direction from west to east. Even though the data are rather sparse, there is a tendency to support that caves in the eastern parts of the Austrian Alps were inhabited for a longer period than caves towards the west.

Stable isotopes

Apart from the two bear cubs from the Potentialschacht, all data represent adult bears. A thoroughly led discussion on stable isotope data from cave bears in comparison to other large mammals is presented in (Bocherens, 2019). The evaluation of the data produced in the current study builds on this earlier research.

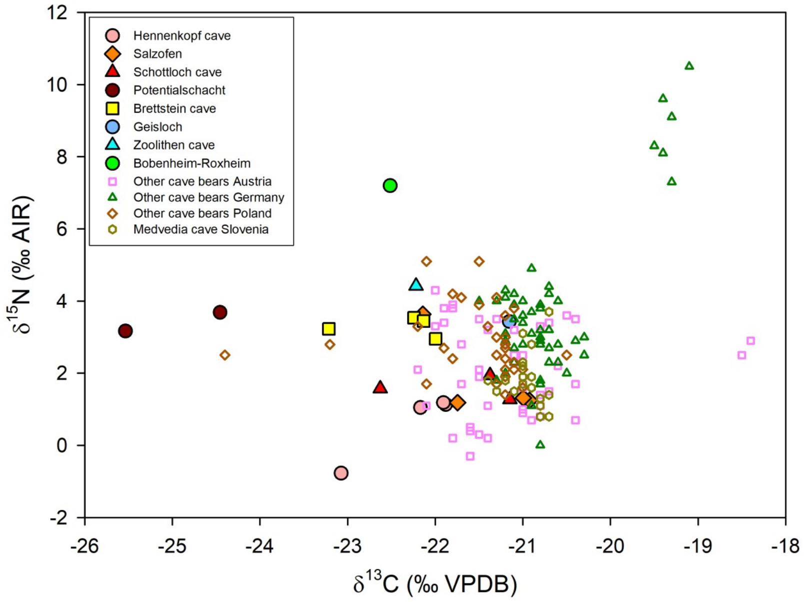

Fig. 6: Stable isotope data of cave bear bones from this study (larger symbols) in comparison to data from other publications on European cave bears (small symbols) (Blant et al., 2010; Bocherens et al., 2011; Döppes et al., 2016; Döppes et al., 2019; Kneussl, 1972, 1973; Krajcarz et al., 2016; Münzel et al., 2011; Spötl et al., 2014). | **Abb. 6**: Stabile Isotopendaten von Höhlenbärenknochen aus dieser Studie (größere Symbole) im Vergleich zu Daten aus anderen Publikationen über europäische Höhlenbären (kleine Symbole).

Combined δ^{15}N and δ^{13}C data

The carbon isotope data of the cave bear collagen varied widely between -25.5 ‰ (Potentialschacht) and -20.9 ‰ (Salzofen). The bear cubs from the Potentialschacht have significantly lower δ^{13}C values than the samples from all other sites (**Fig. 6**). Unfortunately, no data of adult bears from the Potentialschacht are available to see whether this deviation is the result of local effects such as food availability. The data of the adult bears from all other sites overlap widely with δ^{13}C values between about -23 and -21 ‰.

The δ^{15}N values ranged from -0.8 ‰ (Hennenkopf cave) to 7.2 ‰ (Bobenheim-Roxheim). The analytical values differ among the sites, whereas intra-site variation is often comparatively small (**Fig. 6**). The bear cubs from the Potentialschacht fall well into the overall range, and exhibit slightly higher values than the adult bears from the nearby Schottloch.

Bocherens et al. (2019) figure 2 presents cave bear data from previous studies in comparison to analytical values of herbivorous and carnivorous animals. The bears exhibit similar data ranges to the herbivorous mammals. The observation indicates an herbivorous diet, in contrast to an omnivorous feeding strategy as suggested in earlier investigations (Bocherens et al., 2019). Our dataset is similar to the previous results and supports this interpretation (**Fig. 6**). Overall, δ^{15}N values of between below 0 and around 4 ‰ are common for an herbivorous diet and appear too low to reflect noteworthy contributions of meat to their forage. However, the sample from Bobenheim-Roxheim shows a remarkably higher δ^{15}N level comparable to some bears from Romania discussed in Bocherens et al. (2019). This deviation might be explained by a different diet specialization. For example, graminoids and forbs as well as mushrooms often have higher δ^{15}N values than shrubs or trees. Gras or steppe plants are often characterized by higher δ^{15}N values. In addition, different parts of a plant may contribute nitrogen with different isotopic compositions. Roots can be elevated in δ^{15}N compared to leaves of the same plant. A more detailed investigation of the different plants available at the respective sites at the periods of interest would be necessary to be able to discuss the deviation more confidently.

Besides isotopic variations originating from diet, also physiological differences might be of importance. Apart from nursing, weaning and growth, especially hibernation provides an additional source of variation among cave bear data (Bocherens et al., 2019). Because the adult bears of the Hennenkopf cave and the Potentialschacht with bear cubs are found nearby and roughly at the same altitude, they can be compared. The bear cubs have higher levels of δ^{15}N than the adult bears from sites at the same altitude and a similar environment. Here, higher δ^{15}N values could be a consequence of suckling. So far, data compared between bear cubs and adult bears shows that cubs still suckling milk during hibernation show increased δ^{15}N comparable to one trophic level higher than the adult bears and depleted values of δ^{13}C values (Fig. 5 in Bocherens et al., 2019; Bocherens, 2015). In adult bones, this nursing effect should be erased due to growth and remodeling. The unusually low δ^{15}N value of one (adult) cave bear from the Hennenkopf cave that is also accompanied by a lower δ^{13}C value is rather difficult to explain. Hibernation could cause a decrease in δ^{13}C but at the same time would show an increase in δ^{15}N. Maybe this could correlate with an altitude effect as discussed in Krajcarz et al. (2016), where δ^{15}N and δ^{13}C show a tendency to decrease with increasing altitudes. Keeping in mind that the Hennenkopf cave lies at the highest altitude of the caves in the study presented here, this might be a plausible argument (**Fig. 7-8**). As many overlapping effects could contribute to the isotopic composition of carbon and nitrogen in collagen, we can for now observe differences according to sites as well as cubs and adult animals, but remain reluctant with our interpretations until a more solid database is available.

Altitude versus δ^{15}N data

To monitor a possible dependency of the δ^{15}N data on altitude,

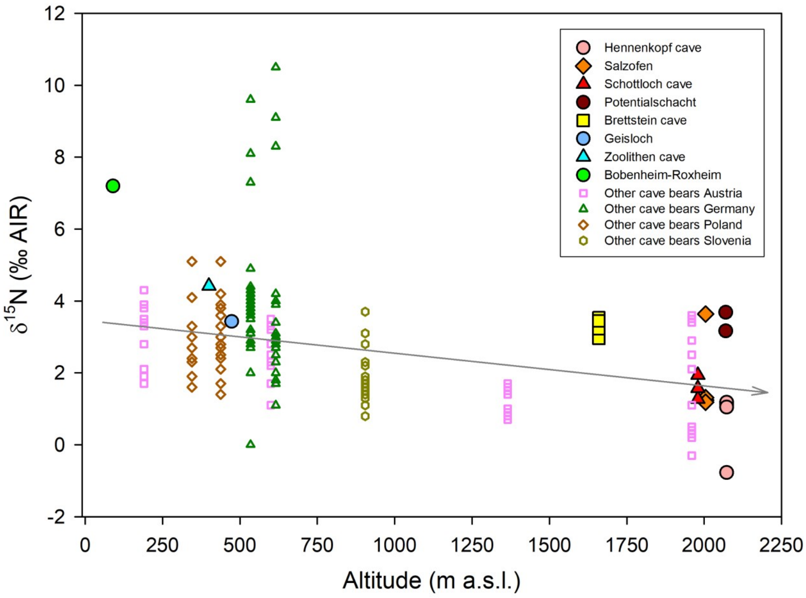

Fig. 7: Stable isotope $\delta^{15}N$ data with respect to altitude of the cave entrance. Large symbols: data from this study; small symbols: previously published data (Blant et al., 2010; Bocherens et al., 2011; Döppes et al., 2016; Döppes et al., 2019; Kneussl, 1972, 1973; Krajcarz et al., 2016; Münzel et al., 2011; Spötl et al., 2014). | **Abb. 7**: Daten zu stabilen Isotopen $\delta^{15}N$ in Abhängigkeit von der Höhe des Höhleneingangs. Große Symbole: Daten aus dieser Studie; kleine Symbole: bereits veröffentlichte Daten (Blant et al., 2010; Bocherens et al., 2011; Döppes et al., 2016; Döppes et al., 2019; Kneussl, 1972, 1973; Krajcarz et al., 2016; Münzel et al., 2011; Spötl et al., 2014).

the data of this study were plotted with those from other studies (**Fig. 7**). Values of less than 0 ‰ are regarded as unusually low.
The data distribution indicates a trend of lower $\delta^{15}N$ values with increasing altitude, which matches observations of earlier studies. The single sample from Bobenheim-Roxheim appears to be comparatively high. More data are needed to confirm the overall relevance of the tendency. An interesting observation in figure 7 is that the bear cubs from the Potentialschacht at 2,070 m asl. show remarkably higher values than the adult bears from the Hennenkopf cave at 2,073 m asl., basically at the same altitude. The difference is less than the increase in trophic level of 3–5 ‰, but might still be due to the suckling effect of the bear cubs. The data of the cubs might also represent a mixture of breastmilk and solid food after weaning. The carbon isotope data are inconclusive regarding the breastfeeding aspect (see above) and the collagen of the mother animals of the cups may still have had slightly diverging isotope compositions from those of the adult bears from the Hennenkopf cave.
The $\delta^{15}N$ value of the sample from Bobenheim-Roxheim at 90 m asl. seems to be remarkably high. However, it is the only sample from a site at such low elevation and data from the German sites of Hohle Fels cave and Geißenklösterle cave in the Swabian Jura at around 500-600 m asl exhibit similar values. A more detailed analysis of single amino acids and deuterium as suggested in Bocherens et al. (2019) might provide more evidence whether the high $\delta^{15}N$ values at the German sites may have been caused by distinct plants that grew in lower regions. Altitudinal trends in $\delta^{15}N$ might be explained with the effects of precipitation or aridity on the one hand as well as effects of temperature on the other hand. Soil development may also have had an effect, as poor soils, which prevail in rocky terrain, lead to low $\delta^{15}N$ values of the vegetation.

Altitude versus $\delta^{13}C$ data

The trend of decreasing values with increasing elevation is not as emphasized and straightforward as for the $\delta^{15}N$ data (**Fig. 8**). The cumulated data from earlier publications are somewhat inconclusive, because they tend to increase at altitudes below ~ 500 m asl and remain constant or decrease slightly with higher elevation (**Fig. 8**). Our data corresponds to the overall trends, especially regarding the samples from adult bears. However, the cubs exhibit distinctly lower values. The interpretation is not straightforward but might be due to hibernation effects that are more pronounced for cubs than for adult bears apart from possibly different plant availability. In general, the range of $\delta^{13}C$ values of ~ 8 ‰ between the highest and the lowest value (**Fig. 8**) is smaller than for $\delta^{15}N$ with roughly 14 ‰ (**Fig. 7**).
According to Krajcarz et al. (2016), the main driver for variations in $\delta^{13}C$ with altitude is air pressure and partial pressure of CO_2 in the atmosphere, which is masked by effects of air temperature, precipitation and the hydrological regime. Plant specific characteristics such as leaf thickness, canopy effect (density of leaf cover), etc. also contribute to the $\delta^{13}C$ results. Therefore, the trends observed would require a thorough analysis with respect to paleoclimate, lithology and pollen to reconstruct plant availability and environmental conditions to be able to interpret the complex dataset of $\delta^{13}C$ values. Apparently, various environmental conditions effect both, the $\delta^{13}C$ and the $\delta^{15}N$ data, and the altitude of the sites is only one aspect among them. Moreover, individual animals may have been mobile and their habitats included a range of sites at different elevations and with variously composed plant communities. All of them may have contributed to the isotopic composition of the bone collagen and are often difficult to decipher.

Stable isotope compositions versus longitude

Keeping in mind that the glaciation during the Würmian proceeded from the West, it is intriguing to plot the data versus longitude of the cave´s position. Similar to the ^{14}C ages in figure 5. Krajcarz et al. (2016) postulate a latitudinal but not a longitudinal effect for the stable isotope data. No clear trend regarding longitude is visible for stable isotopes of $\delta^{13}C$ (**Fig. 9**). At first

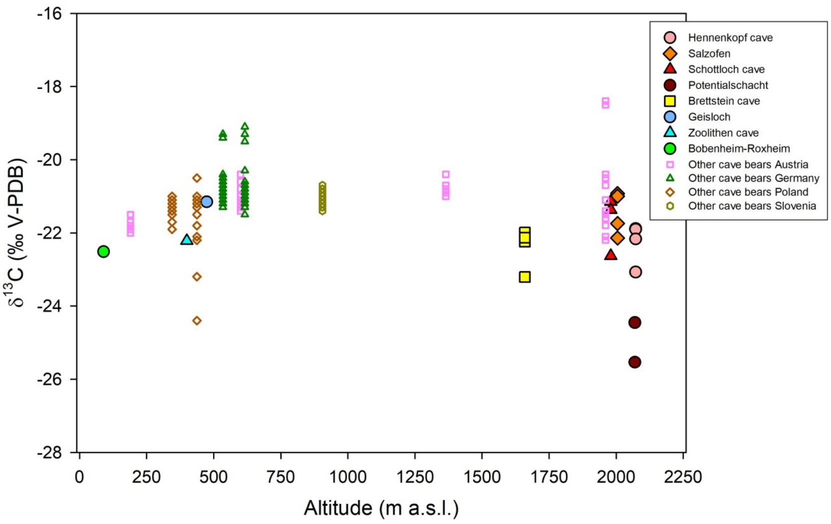

Fig. 8: Stable isotope $\delta^{13}C$ data with respect to altitude of the cave entrance. Large symbols: data from this study; small symbols: previously published data (Kneussl, 1972; Kneussl, 1973; Blant et al., 2010; Bocherens et al., 2011; Münzel et al., 2011; Spötl et al., 2014; Döppes et al., 2016; Krajcarz et al., 2016; Döppes et al., 2019). | **Abb. 8**: Daten zu stabilen Isotopen $\delta^{13}C$ in Abhängigkeit von der Höhe des Höhleneingangs. Große Symbole: Daten aus dieser Studie; kleine Symbole: bereits veröffentlichte Daten (Kneussl, 1972; Kneussl, 1973; Blant et al., 2010; Bocherens et al., 2011; Münzel et al., 2011; Spötl et al., 2014; Döppes et al., 2016; Krajcarz et al., 2016; Döppes et al., 2019).

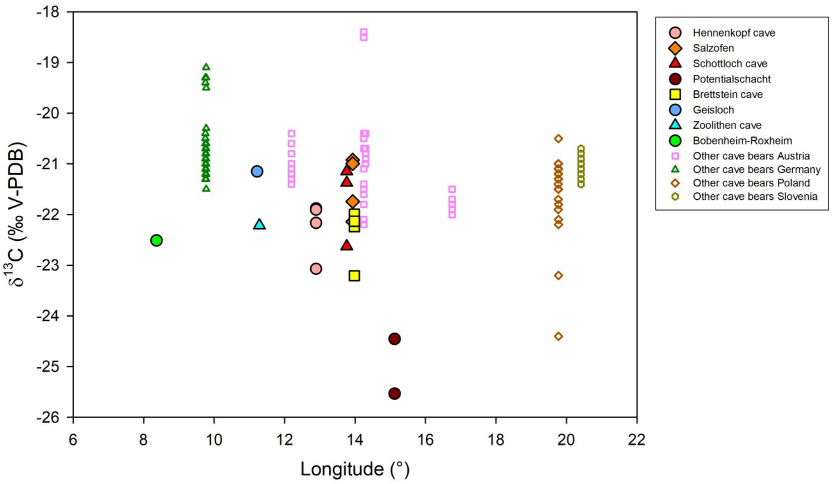

Fig. 9: Stable isotope $\delta^{13}C$ values versus longitude of the cave sites. Note that bone samples of cave bears from Germany, Poland and Slovenia were collected at lower altitudes and are already published (Kneussl, 1972; Kneussl, 1973; Blant et al., 2010; Bocherens et al., 2011; Münzel et al., 2011; Spötl et al., 2014; Döppes et al., 2016; Krajcarz et al., 2016; Döppes et al., 2019). | **Abb. 9**: Stabile $\delta^{13}C$-Werte in Abhängigkeit von der geografischen Länge der Höhlenfundstellen. Beachten Sie, dass Knochenproben von Höhlenbären aus Deutschland, Polen und Slowenien in niedrigeren Höhenlagen gesammelt und bereits veröffentlicht wurden.

sight, the data from Germany, Poland and Slovenia seem to have higher values than those of bears of this study with a general decreasing trend from lower to higher longitudes. However, the data for Germany determined in this study representing the lower longitudes only consists of a single datapoint per location and will not be representative. Apart from bear cubs of the Potentialschacht that diverge from the general pattern, the remaining data overlap with the previously published data and do not allow for a distinct interpretation. The large scatter may also be seen as disclosing no trend and therefore no dependency of $\delta^{13}C$ on longitude as suggested by Krajcarz et al. (2016).

At first sight there seems to be a trend of decreasing $\delta^{15}N$ values with increasing longitude, hence from west to east. However, taking into account that the data from Bobenheim-Roxheim, the Zoolithen cave and the Geisloch are only represented by a single datapoint, this interpretation is rather vague. The large spread in the dataset from the caves Geißenklösterle and Hohle Fels also precludes a distinct interpretation. The new $\delta^{15}N$ data presented in this study seems to show a decrease until 13° longitude and then increase again until 15° longitude. Apart from the higher $\delta^{15}N$ values of some Geißenklösterle and Hohle Fels data, all previously published data show a large scatter into which the new data fit nicely. There seems to be no well-defined correlation of longitude data to $\delta^{15}N$ and therefore the scatter maybe can be explained by local factors such as soil development and variation in specific vegetation.

Stable isotopes versus latitude

Krajcarz et al. (2016) found a correlation between $\delta^{13}C$ and latitude. Therefore, we combined our data with the previously published collection and evaluated them regarding similar trends. In figure 11, our data fit nicely into the rest of the published cave bear data. Only the bear cubs from the Potentialschacht, as seen in figure 9, diverge from the remaining data of adult bears. In contrast to Krajcarz et al. (2016) and taking into account the larger dataset from previous publications and this study we do not clearly see a correlation of $\delta^{13}C$ with latitude. The relatively low latitudinal coverage of the cave bear data over only 3° (compared to Krajcarz et al. (2016) with roughly 11°) may not cause enough isotopic variation and is

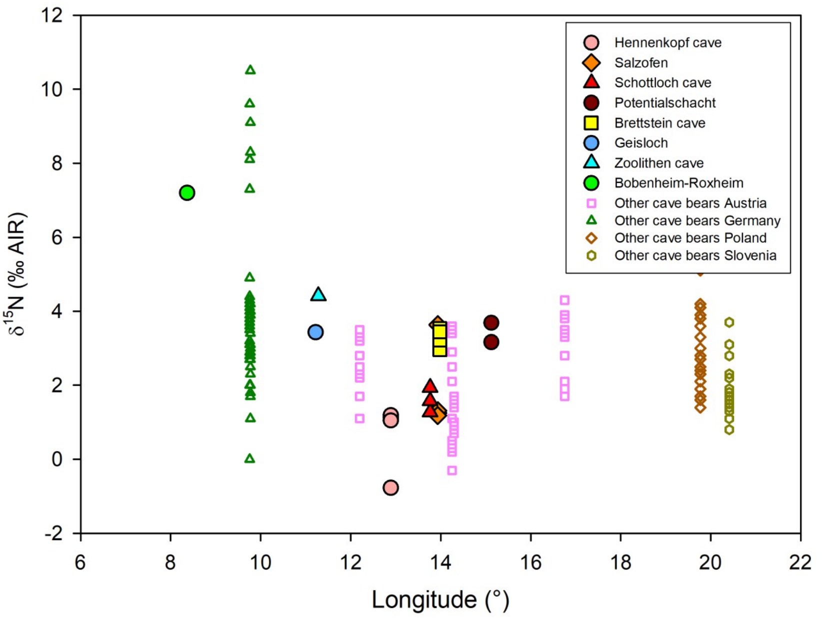

Fig. 10: Stable $\delta^{15}N$ values versus longitude of the cave sites. Note that bone samples of cave bears from Germany, Poland and Slovenia were collected at lower altitudes and are already published (KNEUSSL, 1972; KNEUSSL, 1973; BLANT et al., 2010; BOCHERENS et al., 2011; MÜNZEL et al., 2011; SPÖTL et al., 2014; DÖPPES et al., 2016; KRAJCARZ et al., 2016; DÖPPES et al., 2019). | **Abb. 10**: Stabile $\delta^{15}N$-Werte in Abhängigkeit von der geografischen Länge der Höhlenfundstellen. Beachten Sie, dass Knochenproben von Höhlenbären aus Deutschland, Polen und Slowenien in niedrigeren Höhenlagen gesammelt und bereits veröffentlicht wurden.

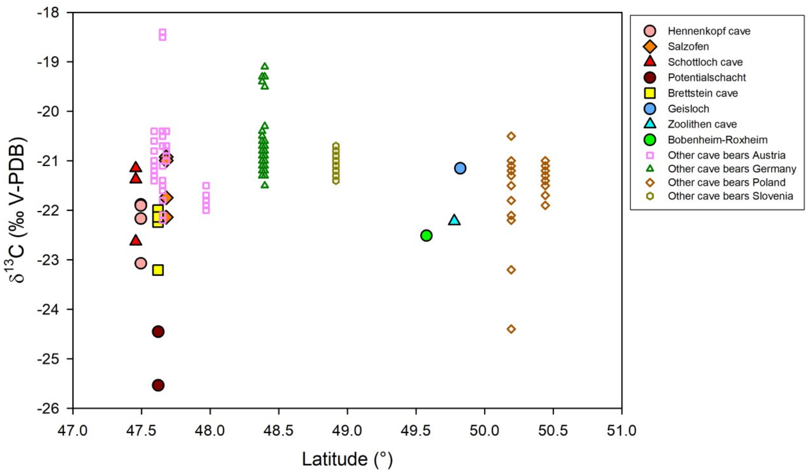

Fig. 11: Stable $\delta^{13}C$ values versus latitude of the cave bear sites. Data taken from this study (larger symbols) and earlier publications (smaller symbols: KNEUSSL, 1972; KNEUSSL, 1973; BLANT et al., 2010; BOCHERENS et al., 2011; MÜNZEL et al., 2011; SPÖTL et al., 2014; DÖPPES et al., 2016; KRAJCARZ et al., 2016; DÖPPES et al., 2019). | **Abb. 11**: Stabile $\delta^{13}C$-Werte in Abhängigkeit von der geografischen Breite der Höhlenbärenfundstellen. Ergebnisse aus dieser Studie (größere Symbole) im Vergleich zu Daten aus anderen Publikationen europäischer Höhlenbären (kleine Symbole).

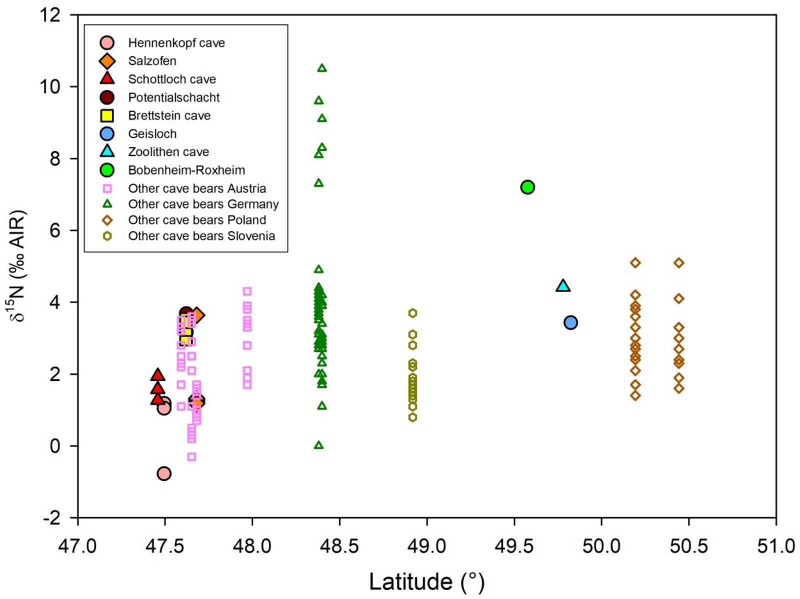

Fig. 12: Stable $\delta^{15}N$ values versus latitude of the cave bear sites. Data taken from this study (larger symbols) and earlier publications (smaller symbols) (KNEUSSL, 1972; KNEUSSL, 1973; BLANT et al., 2010; BOCHERENS et al., 2011; MÜNZEL et al., 2011; SPÖTL et al., 2014; DÖPPES et al., 2016; KRAJCARZ et al., 2016; DÖPPES et al., 2019). | **Abb. 12**: Stabile $\delta^{15}N$-Werte in Abhängigkeit von der geografischen Breite der Höhlenbärenfundstellen. Ergebnisse aus dieser Studie (größere Symbole) im Vergleich zu Daten aus anderen Publikationen europäischer Höhlenbären (kleine Symbole).

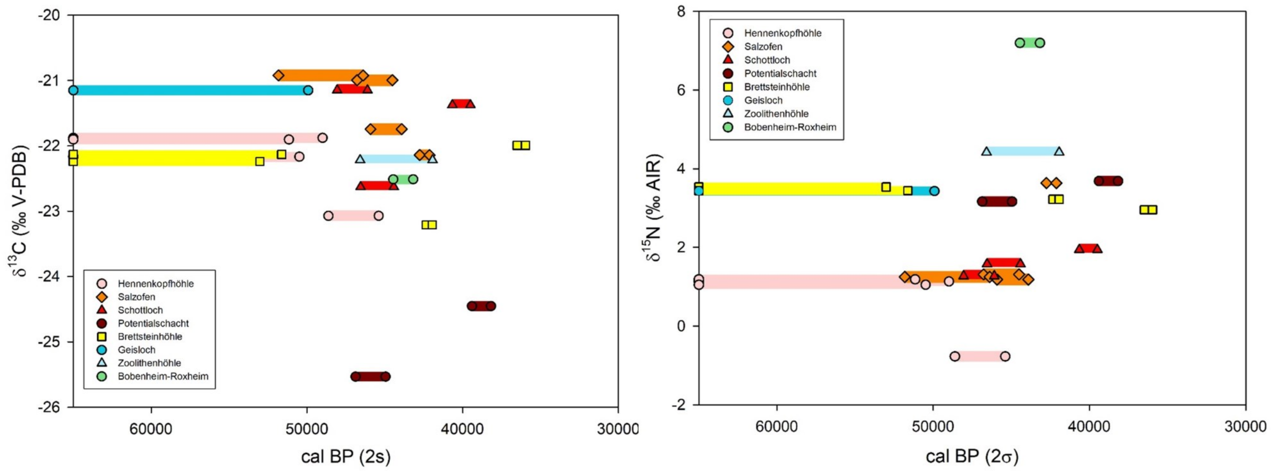

Fig. 13: Stable $\delta^{13}C$ (left) and $\delta^{15}N$ (right) values plotted versus the calibrated radiocarbon ages (95% probability) of the corresponding collagen samples extracted from cave bear remains. Note: ages over 50,000 years are too close to the age limit to be reliably calibrated and just serve to clarify the ranges in our study. | **Abb. 13**: Stabile $\delta^{13}C$- (links) und $\delta^{15}N$-Werte (rechts) dargestellt versus kalibrierte Radiokarbon-Alter (95% Wahrscheinlichkeit) der jeweiligen Kollagenproben. Alter älter als 50,000 Jahre sind zu nah am Datierungslimit um zuverlässig kalibriert werden zu können und dienen hier nur der Anschaulichkeit der Altersbereiche.

masked by all other fractionation processes. Correlating the $\delta^{15}N$ data with latitude is also not straightforward. Again, the data from German bears scatter widely. The Austrian sites seem to have a tendency towards lower $\delta^{15}N$ values than the sites in Germany, Poland and Slovenia, but overlap widely with the generally similar data ranges. The variation in the data seems rather influenced by local effects of soil composition and vegetation.

Stable isotopes in combination with radiocarbon

In combination, ^{14}C dating and stable isotope analysis can help to identify temporal changes in food availability (**Fig. 7**). As mentioned above, data close to or beyond the detection limit of radiocarbon are plotted as the youngest possible age and the age ranges are graphically extended to 60,000 cal. BC, the limit of the graph. These data are only an estimate, may even be older than visible from the graphs and have large error ranges.

The stable isotope data of the cave bear remains did not reveal any conclusive trends of variation over time that would be valid for all sites (**Fig. 7**). However, at some sites, such as Salzofen and Hennenkopf cave, $\delta^{13}C$ values appear to decrease over time. In contrast, the values from the Brettstein cave drop before 45,000 years ago and rise again afterwards until 35,000 years ago. A similar pattern may appear at the Schottloch but over a shorter time. All these observations need to be treated with caution due to the very small sample sizes at each single site.

Both kinds of isotope values of bear cubs from the Potentialschacht seem to show a trend of increase similar to the Schottloch, but at a lower level. With respect to $\delta^{15}N$, the data from most sites seem to remain constant over larger periods. The Schottloch (and the cubs of the Potentialschacht) differ slightly from this trend, as the $\delta^{15}N$ values increase over time, whereas those from the Brettstein cave decrease marginally. However, again, these observations may only be snapshots due to the very limited sample sizes and large time spans represented at each of the investigated sites. The samples from the Brettstein cave and the Salzofen revealed quite similar $\delta^{15}N$ values and exhibited comparable trends in $\delta^{13}C$ as these sites lie closely together geographically. The isotope values of the specimens from the Schottloch are only slightly shifted in comparison to the other two caves. It lies further south of the Brettstein cave and the Salzofen but still nearer to them than the other caves. Despite of this shift, the data from the Schottloch follow the trends of those from the Brettstein cave. If relatively younger samples would be available for the Salzofen, it would be interesting to see whether they would follow a similar trend of varying $\delta^{13}C$ values over time.

Conclusions

This study analyzed cave bear remains, including bones and teeth, from several caves in the Austrian Alps, Franconia in Germany as well as an open-air deposit from the Upper Rhine Graben. Apart from the methods applied — radiocarbon dating and stable isotope analysis — we introduced two other methods to reconstruct timing and environmental conditions of the sites in which the cave bear remains were found. In general, the conclusiveness of the interpretations regarding diet compositions and environmental conditions and their impact on the isotopic compositions of food sources is currently limited by the low number of available data. More data would present a more coherent and better constrained picture to reconstruct the onset and duration of the occupancy of caves by cave bears. Further data will also have implications for the environmental conditions that allowed cave bears to access the caves (ice free).

The cave bear data match those from earlier publications, which present isotope compositions of bear collagen from other sites in the Alps as well as lowlands in other countries such as Poland. The analytical results concordantly suggest a predominantly herbivorous diet. The trends seen in the datasets of this study were comparable to the trends in earlier investigations with respect to variation of stable isotope data with altitude.

Covering a period of the Würmian glaciation, it was possible to connect the dataset with other climate proxies such as pollen spectra of the Swiss and Austrian Alps. The comparison of occupation periods of the caves confirmed earlier evidence that the western Alps were more strongly influenced by glaciers moving into the lower valleys.

The site locations are distributed from Alpine altitudes to lowland localities in the Upper Rhine Graben and represent different habitats and dietary niches. Overall, the ranges of $\delta^{15}N$ and $\delta^{13}C$ values confirm previously published data. Especially the low $\delta^{15}N$ values indicate an herbivorous diet of the animals. Variation among the sites points to different environmental conditions reflected in soil development and plant communities. The single sample from Bobenheim-Roxheim in the Upper Rhine Graben, a site untypical for cave bear remains, stands out due to its high $\delta^{15}N$ value, which may point to an advanced soil development in the area. The $\delta^{13}C$ values are typical for consumers of C3 plants. The values of the Alpine sites of the Brettstein cave and Hennenkopf cave as well as a sample from the Schottloch exhibit comparatively low $\delta^{13}C$ values, which are still within the range of previous findings, but rare among them. Two collagen samples of cave bear cubs from the Potentialschacht exhibited unusually low $\delta^{13}C$ values, for which a conclusive explanation is still lacking. Their $\delta^{15}N$ values are within the overall range of the adult animals. Comparisons to samples from the Hennenkopf cave at a similar altitude may indicate a mixture of breastmilk consumption and solid food.

Correlations with altitude, longitude, latitude and age of the sites were only partly conclusive. While some trends appear to be present in aspects, such as the relation between $\delta^{15}N$ and altitude or age of the samples, the isotopic composition of the bone collagen rather reflects site-specific environmental conditions and food compositions that cannot be completely resolved. This study highlights the possibilities of combining several methods and data exploration in order to reveal regional and temporal trends. Combining stable isotope and radiocarbon data from the same samples has been used for the first time and provides an informative additional tool to standard analysis of altitude dependence, genetic information on species and also dietary and environmental reconstructions. In the framework of interdisciplinary evaluation, it is then possible to find a clearer picture of cave bear habitats and lifestyle.

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C14 Labcode	MA Analysis number	Sample name	Country	Site	Altitude [m]	Latitude	Longitude	Species	Skeletal element	Collagen yield [%]	C^{14} yrs BP	C:N	$\delta^{15}N$ [‰ AIR]	$\delta^{13}C$ [‰ VPDB]
MAMS 43821	MA-197286	HK 607	A	Hennenkopf cave	2073	47°29'43.06"	12°53'41.75"	*Ursus spelaeus eremus*	phb	4.22	48,436 ± 1273	3.2	1.13 ± 0.05	-21.88 ± 0.03
MAMS 43822	MA-197287	HK 622	A	Hennenkopf cave	2073	47°29'43.06"	12°53'41.75"	*Ursus spelaeus eremus*	phb1	6.40	51,794 ± 1927	3.3	1.18 ± 0.03	-21.90 ± 0.02
MAMS 43823	MA-197288	HK 606	A	Hennenkopf cave	2073	47°29'43.06"	12°53'41.75"	*Ursus spelaeus eremus*	ulna dist, sin	3.09	50,538 ± 1659	3.2	1.05 ± 0.01	-22.17 ± 0.03
MAMS 43824	MA-197289	HK 612	A	Hennenkopf cave	2073	47°29'43.06"	12°53'41.75"	*Ursus spelaeus eremus*	rad dist, dex	2.11	44,469 ± 794	3.3	-0.78 ± 0.04	-23.07 ± 0.07
MAMS 43825	MA-197290	SO 473	A	Salzofen	2005	47°40'51.45"	13°56'9.25"	*Ursus spelaeus eremus*	mc IV prox	8.09	38,391 ± 386	3.3	3.64 ± 0.03	-22.14 ± 0.02
MAMS 43826	MA-197291	SO 475	A	Salzofen	2005	47°40'51.45"	13°56'9.25"	*Ursus spelaeus eremus*	ph II	8.24	46,104 ± 970	3.2	1.25 ± 0.02	-20.92 ± 0.03
MAMS 43827	MA-197292	SO 478	A	Salzofen	2005	47°40'51.45"	13°56'9.25"	*Ursus spelaeus eremus*	phb	7.05	42,941 ± 664	3.2	1.31 ± 0.03	-21.00 ± 0.04
MAMS 43828	MA-197293	SO 486	A	Salzofen	2005	47°40'51.45"	13°56'9.25"	*Ursus spelaeus eremus*	mc IV prox dex	9.42	41,991 ± 596	3.2	1.18 ± 0.02	-21.74 ± 0.09
MAMS 43829	MA-197294	SchL 2	A	Schottloch	1980	47°27'31.35"	13°45'48.39"	cave bear	rad prox sin	5.50	44,768 ± 398	3.2	1.27 ± 0.02	-21.15 ± 0.05
MAMS 43830	MA-197295	SchL 9	A	Schottloch	1980	47°27'31.35"	13°45'48.39"	cave bear	fem dist	3.62	34,905 ± 262	3.3	1.93 ± 0.07	-21.37 ± 0.07
MAMS 43831	MA-197296	SchL 15	A	Schottloch	1980	47°27'31.35"	13°45'48.39"	cave bear	pelvis f	2.48	42,747 ± 648	3.3	1.57 ± 0.04	-22.63 ± 0.03
MAMS 48555	MA-205377	PS 2	A	Potenzialschacht	2070	47°37' 20.41"	15° 7'35.68"	*Ursus spelaeus eremus*	hum f juvenil	7.48	33,803 ± 150	3.3	3.68 ± 0.02	-24.45 ± 0.01
MAMS 48556	MA-205378	PS 6	A	Potenzialschacht	2070	47°37' 20.41"	15° 7'35.68"	*Ursus spelaeus eremus*	rib f juvenil	10.08	43,470 ± 46	3.2	3.16 ± 0.04	-25.54 ± 0.01
MAMS 48559	MA-205381	Geis 3	D	Geisloch	474	49°49' 25"	11° 13' 33"	*Ursus cf. deningeroides/ ingressus*	ulna	1.19	48,772 ± 861	3.3	3.43 ± 0.04	-21.15 ± 0.1
MAMS 48564	MA-205386	BS 192-3	A	Brettstein cave	1660	47°37'15.29"	13°58'53.45"	*Ursus s. eremus* and *Ursus s. ladinicus*	M1 sup	1.34	31,873 ± 118	3.3	2.95 ± 0.01	-22.00 ± 0.01
MAMS 48565	MA-205387	BS 35-1	A	Brettstein cave	1660	47°37'15.29"	13°58'53.45"	*Ursus s. eremus* and *Ursus s. ladinicus*	m1 inf	2.44	>49,000	3.2	3.53 ± 0.05	-22.24 ± 0.04
MAMS 48566	MA-205388	BS 78-6	A	Brettstein cave	1660	47°37'15.29"	13°58'53.45"	*Ursus s. eremus* and *Ursus s. ladinicus*	m1 inf	2.52	37,626 ± 195	3.3	3.22 ± 0.02	-23.21 ± 0.05
MAMS 48567	MA-205389	BS 40-12	A	Brettstein cave	1660	47°37'15.29"	13°58'53.45"	*Ursus s. eremus* and *Ursus s. ladinicus*	m1 inf	5.52	>49,000	3.2	3.44 ± 0.04	-22.13 ± 0.05
MAMS 24997	MA-153782	NK 38	A	Zoolithen cave	400	49° 46' 45,6"	11° 16' 58,3"	*Ursus spelaeus* and *Ursus s. ladinicus*	zygomatic arch sin	8.31	39,935 ± 1489	3.3	4.42 ± 0.04	-22.22 ± 0.05
MAMS 32882	MA-176486	NK 39	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Ursus ingressus*	petrosa	2.70	40,837 ± 331	3.3	7.20 ± 0.05	-22.51 ± 0.06
MAMS 32877	MA-176481	NK 26	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Panthera spelaea*	petrosa sin	3.14	28,249 ± 105	3.2	8.87 ± 0.03	-18.38 ± 0.04
MAMS 32878	MA-176482	NK 30	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Crocuta crocuta spelaea*	petrosa sin	1.91	46,756 ± 551	3.3	10.27 ± 0.07	-21.69 ± 0.04
MAMS 36748	MA-193108	NK 4	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Mammuthus trogontherii*	m3 inf sin	0.86	41,192 ± 392	3.3	8.95 ± 0.06	-21.13 ± 0.01
MAMS 36754	MA-183114	NK 23	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Mammuthus trogontherii*	M3 sup sin	2.00	44,051 ± 547	3.4	11.8 ± 0.01	-20.68 ± 0.05
MAMS 45196	MA-200967	NK 472	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Rangifer tarandus*	petrosa sin	1.87	29,754 ± 241	3.3	5.24 ± 0.05	-19.61 ± 0.01

MAMS 45823	MA-201802	NK 1441	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Dama*	petrosa dex	3.58	44,628 ± 442	3.3	6.41 ± 0.06	-21.60 ± 0.09
MAMS 45822	MA-201801	NK 1442	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Dama*	petrosa sin	3.86	47,584 ± 616	3.3	8.02 ± 0.05	-22.53 ± 0.06
MAMS 36746	MA-183106	NK 1	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Megaloceros*	petrosa dex	3.90	41,510 ± 429	3.2	7.95 ± 0.03	-19.78 ± 0.01
MAMS 39483	MA-190549	NK 54	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Megaloceros*	petrosa sin	3.1	36,707 ± 224	3.3	5.43 ± 0.01	-20.40 ± 0.03
MAMS 39484	MA-190460	NK 55	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Megaloceros*	petrosa dex	4.5	41,437 ± 382	3.3	6.03 ± 0.03	-20.65 ± 0.03
MAMS 39486	MA-190462	NK 57	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Megaloceros*	petrosa sin	4.3	43,201 ± 420	3.2	6.73 ± 0.04	-20.53 ± 0.09
MAMS 39488	MA-190464	NK 59	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Megaloceros*	petrosa sin	4.2	41,842 ± 346	3.3	6.07 ± 0.05	-20.57 ± 0.01
MAMS 39485	MA-190461	NK 56	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Stephanorhinus sp.*	Mandibula	3.6	42,485 ± 387	3.3	5.32 ± 0.05	-20.18 ± 0.01
MAMS 39493	MA-190469	NK 64	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Bison priscus*	petrosa dex	4.2	39,075 ± 283	3.3	7.44 ± 0.05	-19.92 ± 0.03
MAMS 39498	MA-190474	NK 65	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Bison priscus*	petrosa sin	1.8	40,101 ± 301	3.4	9.74 ± 0.04	-20.80 ± 0.13
MAMS 39499	MA-190475	NK 67	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Bison priscus*	petrosa sin	1.3	41,472 ± 360	3.4	8.36 ± 0.04	-20.59 ± 0.05
MAMS 39495	MA-190471	NK 68	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Bison priscus*	petrosa	1.41	39,423 ± 289	3.4	9.67 ± 0.01	-21.17 ± 0.03
MAMS 39496	MA-190472	NK 69	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Bison priscus*	petrosa	2.33	39,486 ± 283	3.3	5.32 ± 0.01	-20.67 ± 0.03
MAMS 39500	MA-190476	NK 70	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Bison priscus*	petrosa sin	2.42	44,280 ± 467	3.4	5.79 ± 0.04	-20.76 ± 0.04
MAMS 39497	MA-190473	NK 72	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Bison priscus*	petrosa	1.1	38,632 ± 264	3.4	5.79 ± 0.04	-20.79 ± 0.01
MAMS 39501	MA-190477	NK 71	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Bos primigenius*	petrosa sin	1.5	42,619 ± 391	3.4	7.14 ± 0.05	-21.24 ± 0.03
MAMS 32880	MA-176484	NK 32	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Bos primigenius*	petrosa	2.43	44,772 ± 465	3.2	4.82 ± 0.02	-20.12 ± 0.06
MAMS 45827	MA-201806	NK 1437	D	Bobenheim-Roxheim	90	49°34'36.3"	8°22'10.7"	*Mammuthus sp.*	petrosa sin	3.83	42,269 ± 346	3.3	6.20 ± 0.01	-21.75 ± 0.09

Tab. 2: Dataset of new radiocarbon and stable isotope ($\delta^{15}N$, $\delta^{13}C$) measurements on cave bears (all sites Austria, Germany) and contemporaneous mammals (Bobenheim-Roxheim, Germany) determined at CEZA Mannheim presented in this study. Abbreviations: phb = phalanx basal, rad = radius, mc = metacarpale, fem = femur, hum = humerus, M1, m1, M3, m3 = molars. | **Tab. 2**: Datensatz neuer Radiokarbon- und stabile Isotopen ($\delta^{15}N$, $\delta^{13}C$) Messungen an Höhlenbären (all Fundstellen in Deutschland und Österreich) sowie zeitgenössischen Säugetieren (Bobenheim-Roxheim, Deutschland), die an der CEZA Mannheim gemessen und in dieser Studie vorgestellt wurden. Abkürzungen: phb = Phalanx basalis, rad = Radius, mc = Metacarpale, fem = Femur, hum = Humerus, M1, m1, M3, m3 = Molaren.