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# Presence of cave bears in western Austria before the onset of the Last Glacial Maximum: new radiocarbon dates and palaeoclimatic considerations

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ABSTRACT: Tischoferhöhle and Pendling-Bärenhöhle near Kufstein, Tyrol, are among the only locations where remains of cave bear, *Ursus spelaeus*-group, were found in the western part of Austria. One sample from each site was radiocarbon-dated four decades ago to ca. 28 $^{14}$C ka BP. Here we report that attempts to date additional samples from Pendling-Bärenhöhle have failed due to the lack of collagen, casting doubts on the validity of the original measurement. We also unsuccessfully tried to date flowstone clasts embedded in the bone-bearing sediment to provide maximum constraints on the age of this sediment. Ten cave bear bones from Tischoferhöhle showing good collagen preservation were radiocarbon-dated to 31.1–39.9 $^{14}$C ka BP, again pointing towards an age underestimation by the original radiocarbon-dated sample from this site. These new dates from Tischoferhöhle are therefore currently the only reliable cave bear dates in western Austria and constrain the interval of cave occupation to 44.3–33.5 cal ka BP. We re-calibrate and re-evaluate dates of alpine cave bear samples in the context of available palaeoclimate information from the greater alpine region covering the transition into the Last Glacial Maximum, eventually leading to the demise of this megafauna. Copyright © 2014 John Wiley & Sons, Ltd.

KEYWORDS: cave bear; Eastern Alps; Inn Glacier; Last Glacial Maximum; radiocarbon dating.

## Introduction

The cave bears (*Ursus spelaeus*-group) were elements of the megafauna that occupied large areas between the Iberian Peninsula and the Urals during the Late Pleistocene. About 40 caves with remains of this animal are known from the Alps, which apparently formed a key territory in Europe. Genetic research has shown that these alpine cave bears present four different species or subspecies that were variably adapted to the mountain ecosystem. Cave bears of the *U. spelaeus eremus* and *U. spelaeus ladinicus* lines hibernated in caves from the alpine foreland up to 2800 m a.s.l. and developed progressively smaller forms with increasing altitude (Rabeder *et al.*, 2008). Available chronological data indicate that most of the alpine cave bears inhabited the caves during the Middle Würmian, from about 60 000 to 35 000 years ago.[1] This is remarkable considering the high-amplitude, millennial-scale climate swings that characterised the Middle Würmian (or Marine Isotope Stage 3 (MIS 3), e.g. North Greenland Ice Core Project members, 2004). To what extent these stadial–interstadial shifts, which are also recorded in alpine speleothems (e.g. Spötl *et al.*, 2006; Moseley *et al.*, 2014), had an impact of the cave bear populations is currently not known (cf. Bocherens *et al.*, 2011). This climatological and environmental aspect is even more interesting in the light of ancient DNA studies suggesting that isolated cave bear populations coexisted in individual alpine caves over a time span of some 15 000 years without interbreeding (Hofreiter *et al.*, 2004; Bocherens *et al.*, 2011). Starting some 40 000 years ago, the cave bears gradually disappeared from the alpine sites and around 35 000 years ago also from the lower-elevation habitats. DNA studies document a dramatic loss of genetic diversity in cave bear populations after 30 000 years before present (Stiller *et al.*, 2014) until they became finally extinct about 28 000 years before present (Pacher and Stuart, 2009; Bocherens *et al.*, 2014; Martini et al., 2014).[2] Climate deterioration towards the onset of the Last Glacial Maximum (LGM, i.e. increased continentality) and the concomitant decrease in vegetation productivity are regarded as the main cause for the extinction of these exclusively herbivorous animals (e.g. Münzel *et al.*, 2014); other causes, such as increasing competition and hunting by humans, however, are also debated (e.g. Münzel, 2011; Bocherens *et al.*, 2014; Stiller *et al.*, 2014).

In the Eastern Alps cave bear sites cluster in the central and eastern part of the Northern Calcareous Alps as well as in the karst region north of Graz (Fig. 1). No reports of cave bear findings exist from the Central Alps, the highest part of the Austrian Alps, despite the presence of caves. Surprisingly few occurrences are known from the western part of the Eastern Alps, i.e. in the provinces of Tyrol and Vorarlberg (Fig. 1). This may in part reflect the lower density of caves and the scarcity of karst plateaus compared with the regions further east.

Two cave bear sites are known from Tyrol, Tischoferhöhle and Pendling-Bärenhöhle, and a third site, Neue Laubenstein-Bärenhöhle, was only recently discovered some 20 km NNE and is currently the only alpine cave with cave bear remains in southern Germany (Darga and Rosendahl, 2001; Rosendahl and Grupe, 2001). Tischoferhöhle and Pendling-Bärenhöhle are the focus of this study, with the aims to improve the chronology of these cave bear sites and to contribute to the questions of how long these caves were used as shelters and how climate change impacted on this megafauna.

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[1]Unless otherwise noted ages given in this paper are quoted in calendar years before the year 1950 AD.

[2]The radiocarbon dates quoted in these and all other publications listed in the present paper were consistently re-calibrated using INTCAL13 (Reimer *et al.*, 2013).

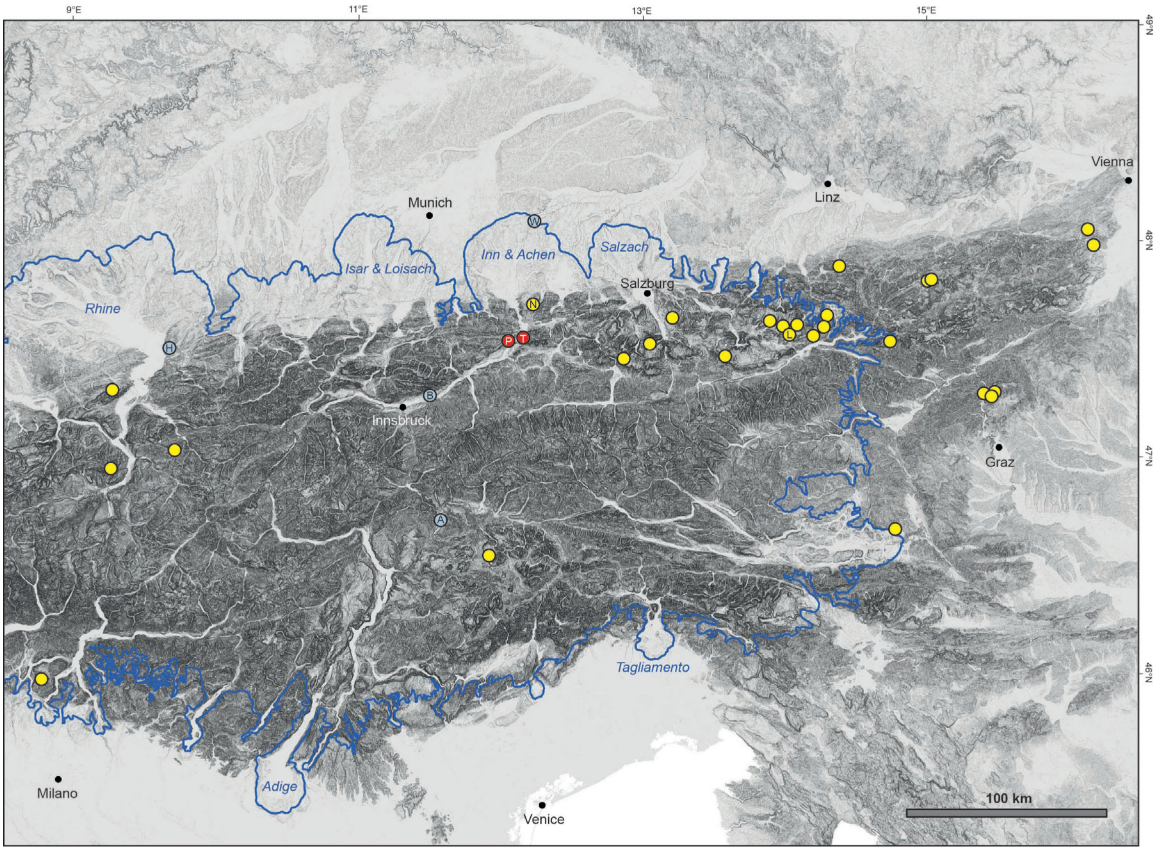


**Figure 1.** Important cave bear caves in the eastern segment of the Alps (yellow circles), location of the studied cave sites, Tischoferhöhle (T) and Pendling-Bärenhöhle (P), as well as other caves mentioned in the text: Liegloch (L) and Neue Laubenstein-Bärenhöhle (N). Light blue circles mark other important Pleistocene sites mentioned in the paper: Baumkirchen and Mils (B), Hochwart (H), Albeins (A), Wasserburg (W). The maximum extent of the LGM ice stream network is delineated by the solid blue line (after Ehlers and Gibbard, 2004) and major palaeoglacier lobes are labelled in italics.

## *Study sites*

Pendling-Bärenhöhle, also known as Rauberloch, Austrian cave cadastre No. 1266/21, is a 12-m-long half-cave, which opens at 1485 m a.s.l. near the crest of Pendling, a saddle-like mountain (1563 m a.s.l.) on the northern side of the Inn Valley south-west of Kufstein (Fig. 1). This mountain was submerged by ice during the climax of the Upper Würmian (LGM), when the ice from the Central Alps filled the Inn Valley and spread across the lower Inn Valley towards Bavaria (van Husen, 1987) reaching a maximum thickness of ca. 190 m above the summit of Pendling (Fig. 1). During a first (emergency) excavation in 1971, a series of bone fragments and teeth were collected and one bone – probably from a cave bear – was radiocarbon-dated to 28 370 ± 905 BP (Kneußl, 1972). Clastic sediments were examined, and the results were reported by Kneußl and Mangelsdorf (1979). A second excavation performed in 2011 resulted in several bone fragments, but only few bones and teeth allowed an unequivocal identification (including cave bear and brown bear). An attempt to date one of these cave bear bones using radiocarbon failed due to the lack of collagen (Frischauf *et al.*, 2012). This result prompted a re-investigation of Kneußl's original collection of bones and teeth, which is stored in the repository of the local history museum in Kufstein.

Tischoferhöhle, Austrian cave cadastre No. 1312/1, is also a half-cave, albeit considerably larger than Pendling-Bärenhöhle, and opens above the gorge of the Sparchenbach at 594 m a.s.l. east of Kufstein (Fig. 1). The entrance is 23 m wide and 9 m high and the cave floor ascends for 41 m towards the inner end. The cave sediment-fill was nearly completely removed during the 1906 excavation led by Schlosser (1909). The clastic sediments reached a thickness of up to 3 m, were locally disturbed and revealed the following stratigraphy (from base to top; Schlosser, 1909): (i) a basal pocket of well-rounded cobbles of dolomite was found in one place in the central part of the cave and was interpreted as a fluvial deposit formed at a time when the stream (Sparchenbach) still reached the cave entrance. Today the cave entrance is located 77 m above the stream. (ii) Loamy sediment up to 3 m thick constituted the main sediment unit and consisted of pea-sized, angular and weathered dolomite clasts embedded in a silty–sandy matrix. These clasts were attributed to weathering (frost shattering) of the cave ceiling, which is composed of Upper Triassic dolomite (Hauptdolomite Formation). The loamy unit contained abundant bones of cave bear (ascribed to at least 380 individuals) and rare bones of cave lion, cave hyena, wolf, reindeer, fox, deer, ibex and chamois. No internal stratigraphy was identified during the excavation except for some banding, and part of this unit was also disturbed due to previous uncontrolled searches for bones. Originally dated by one cave bear bone to 27 875 ± 485 BP (Kneußl, 1973), more recent analyses on a cave lion bone (Burger *et al.*, 2004) and three projectiles made of bone and antler (Bolus and Conrad, 2006) resulted in ages, which are invariably older. (iii) The third unit consisted of grey clay interpreted as a deposit of glacial meltwater. This fine-grained sediment was 10–20 cm thick, thinned from the interior towards the entrance of the cave and lacked fossil remains. (iv) Overlying this clay was a cultural layer which yielded human and animal bones and various artefacts and ceramic fragments dated to the transition between the early and middle Bronze Age (Harb, 2002).

 

(v) The youngest stratigraphic unit was only preserved in the inner parts of the cave and consisted of a thin layer of partly dehydrated moonmilk, a porous variety of speleothem.

## Methods

We selected five bones (astragalus) and one tooth of cave bear from Kneußl's original collection from Pendling-Bärenhöhle plus two cave bear bone fragments from the 2011 excavation for radiocarbon dating. A small amount (tens of milligrams) was drilled from the interior of each bone fragment and the root of the tooth (p4inf) using a dental drill.

For Tischoferhöhle all the sediment from the loamy layer was excavated by Schlosser (1909) without recording the internal stratigraphic position of the fossils. To constrain the chronology of this former sediment layer and hence the occupation history of the cave site we randomly selected ten cave bear bones from the extensive collection of M. Schlosser stored in the local history museum in Kufstein and prepared samples for radiocarbon dating by cutting aliquots (2–3 g) from these bones using a diamond-coated saw.

Following tests of whole bone nitrogen content, collagen extraction was done on those samples with sufficiently high nitrogen using the ultrafiltration method (Brown *et al.*, 1988) with Vivaspin® filter cleaning following Bronk Ramsey *et al.* (2004). Samples yielding sufficient collagen were combusted to carbon dioxide and processed to graphite using the zinc reduction method (Slota *et al.*, 1987) and analysed using acceleration mass spectrometry (AMS) at the $^{14}$CHRONO Centre, Queen's University Belfast. Latton mammoth bone (Lewis *et al.*, 2006) provided by F. Brock, Oxford University, was used for the background correction for samples UBA-25118 and UBA-25124-126, whereas anthrocite was used for the other samples. Ages were calculated according to Stuiver and Polach (1977) using the AMS-measured $^{13}C/^{12}C$, which accounts for both natural and machine isotope fractionation. The reported error in the age is multiplied by 1.3 based on reproducibility of bone standards and includes long-term variability in the background. For asymmetrical standard deviations the larger value is reported. Ages were calibrated using INTCAL13 (Reimer *et al.*, 2013) and the Calib 7.0 software (Stuiver *et al.*, 2013). Calibrated ages are reported with one standard deviation (1$\sigma$). Stable isotopes ($\delta^{13}C$ and $\delta^{15}N$), % carbon and % nitrogen were measured on a Delta V Advantage with Flash elemental analyser. Reproducibity for ultrafiltered bone collagen is 0.22‰ for $\delta^{13}C$ and 0.15‰ for $\delta^{15}N$. Carbon and nitrogen ratios are reported as atomic values ($C/N_a$).

We also examined flowstone fragments of Kneußl's collection from Pendling-Bärenhöhle, and performed MC-ICP-MS $^{230}Th/U$ dating at the Max Planck Institute for Chemistry (Mainz, Germany) on three of them to provide (maximum) age constraints on the age of the sediment fill. Methods of sample preparation and analytical details are described elsewhere (Scholz *et al.*, 2014).

## Results

### *Pendling-Bärenhöhle*

All bone samples and the tooth specimen showed very low nitrogen contents (Table 1) suggesting insufficient preservation of collagen. According to van Klinken (1999) and Brock *et al.* (2012), a minimum content of 0.7% N is required for a reliable radiocarbon measurement of the collagen fraction of bones, which is clearly not the case for these samples.

Analyses of the flowstone fragments showed low U concentrations (0.08–0.13 p.p.m.) and variably high detrital $^{232}Th$ contents (10–163 p.p.b.), which is also reflected by the brownish colour of the calcite. Calculation of $^{230}Th/U$ ages was impossible because all samples showed ($^{230}Th/^{238}U$) and ($^{234}U/^{238}U$) activity ratios exceeding secular equilibrium (Table 2). This either points to a post-depositional opening of the U-series decay system, to a very high detrital contamination or to a combination of both. The fact that these flowstone pieces were embedded in moist, loamy sediment makes diagenesis, and hence an opening of the U-series isotope system, likely.

### *Tischoferhöhle*

All test samples showed good collagen preservation with N values between 2.2 and 4.1% and $C/N_a$ ratios between 3.2 and 3.3 (Table 3). Radiocarbon values range from

**Table 1.** Results of collagen extraction of bone and tooth samples from Pendling-Bärenhöhle. RAUB1–8 are from the original collection of W. Kneußl, partly depicted by Kneußl and Mangelsdorf (1979).

| Sample no. | Laboratory no. | N (%) | Remarks |
|---|---|---|---|
| RAUB1 | UBA-23262 | 0.06 | Cave bear bone (astragalus), excavation 1971 |
| RAUB2 | UBA-23263 | 0.04 | Cave bear bone (astragalus), excavation 1971 |
| RAUB3 | UBA-23264 | 0.07 | Cave bear bone (astragalus), excavation 1971 |
| RAUB4 | UBA-23265 | 0.07 | Cave bear bone (astragalus), excavation 1971 |
| RAUB7 | UBA-23266 | 0.05 | Cave bear bone (astragalus), excavation 1971 |
| RAUB8 | UBA-23427 | 0.18 | Cave bear tooth (p4inf), excavation 1971; No. 15 in Fig. 12 of Kneußl and Mangelsdorf (1979) |
| HAM1 | UBA-23267 | 0.06 | Cave bear bone (hamatum), excavation 2011 |
| TRIQ1 | UBA-23268 | 0.06 | Cave bear bone (triquetrum), excavation 2011 |

**Table 2.** $^{230}Th/U$ dating results of three flowstone clasts from the original collection of W. Kneußl from Pendling-Bärenhöhle. RL 12 are two subsamples from the same fragment.

| Sample no. | $^{238}U$ ($\mu g\,g^{-1}$) | $^{232}Th$ ($ng\,g^{-1}$) | ($^{234}U/^{238}U$) | ($^{230}Th/^{238}U$) | Age corrected |
|---|---|---|---|---|---|
| RL 2 | $0.1256 \pm 0.0008$ | $158.3 \pm 1.8$ | $1.147 \pm 0.037$ | $1.361 \pm 0.091$ | Out of range |
| RL 3 | $0.0914 \pm 0.0006$ | $162.5 \pm 2.0$ | $1.26 \pm 0.11$ | $1.40 \pm 0.18$ | Out of range |
| RL 12-1 | $0.0776 \pm 0.0005$ | $9.69 \pm 0.13$ | $1.0176 \pm 0.0026$ | $1.026 \pm 0.012$ | Out of range |
| RL 12-2 | $0.0774 \pm 0.0005$ | $18.75 \pm 0.22$ | $1.0169 \pm 0.0030$ | $1.059 \pm 0.010$ | Out of range |

 

**Table 3.** Radiocarbon dates of bones from Tischoferhöhle near Kufstein, unless otherwise noted. Sample Ti1B was analysed in duplicate. Calibration was accomplished using Calib 7.0 and INTCAL13.

| Sample no. | Laboratory no. | Sample description | Whole bone (% N) | $C/N_a$ | $\delta^{13}C_{VPDB}$ (‰) | $\delta^{15}N_{AIR}$ (‰) | Age ($^{14}C$ a BP) | Calibrated age (cal a BP) (1σ range) | Remarks |
|---|---|---|---|---|---|---|---|---|---|
| Ti1B | UBA-25535 | Fragment of a right lower jaw (mandibula dex) | 2.23 | 3.26 | −21.0 | 2.5 | 39 934 ± 902 | 42 898–44 347 | This study |
| Ti1B_2 | UBA-25535 | Duplicate | | | | | 39 724 ± 772 | 42 824–44 077 | This study |
| Ti3 | UBA-25118 | Fragment of a lumbar vertebra (vertebra lumbalis) | 2.70 | 3.21 | −21.4 | 4.5 | 31 138 ± 539 | 34 561–35 601 | This study |
| Ti6 | UBA-25121 | Fragment of a penis bone (baculum) | 2.45 | 3.19 | −21.1 | 3.2 | 32 586 ± 743 | 35 757–37 673 | This study |
| Ti9 | UBA-25124 | Right metacarpal bone of the first finger ray (metacarpale 1 dex) | 3.58 | 3.19 | −20.8 | 3.3 | 34 458 ± 807 | 38 050–40 003 | This study |
| Ti10 | UBA-25125 | Left metacarpal bone of the first finger ray (metacarpale 1 sin) | 2.22 | 3.17 | −20.4 | 1.7 | 36 002 ± 1001 | 39 620–41 551 | This study |
| Ti11 | UBA-25126 | Left metacarpal bone of first toe ray (metatarsale 1 sin) | 3.86 | 3.16 | −21.2 | 2.8 | 31 515 ± 564 | 34 864–35 971 | This study |
| Ti2 | UBA-25536 | Fragment of a right lower jaw (mandible dex) | 3.81 | 3.24 | −20.6 | 2.2 | 34 409 ± 454 | 38 461–39 444 | This study |
| Ti4 | UBA-25537 | Vertebra of the neck (vertebra cervicalis) | 2.77 | 3.26 | −21.1 | 2.3 | 32 824 ± 377 | 36 312–37 443 | This study |
| Ti14 | UBA-25538 | Juvenile metapodial bone | 3.40 | 3.23 | −20.8 | 1.1 | 32 201 ± 350 | 35 686–36 445 | This study |
| Ti16 | UBA-25539 | Left metacarpal bone of fifth finger ray (metacarpale 5 sin) | 2.74 | 3.26 | −21.3 | 3.5 | 32 680 ± 431 | 36 119–37 347 | This study |
| | Hv-5441 | Cave bear bone indet. | N/A | | | | 27 875 ± 485 | 31 237–32 319 | Kneußl (1973) |
| | Hv-4850 | Cave bear bone indet. | N/A | | | | 28 370 ± 905 | 31 441–33 258 | Kneußl (1972); Pendling-Bärenhöhle |
| Ku | KIA16510 | Cave lion, pelvis fragment | N/A | | | | 31 890 ± 300 | 35 474–36 130 | Burger *et al.* (2004) |
| T 139 | KIA19543 | Arrow tip made of bone | N/A | | | | 32 010 +510/–480 | 35 305–36 416 | Bolus and Conrad (2006) |
| T 143 | KIA19544 | Arrow tip made of bone | N/A | | | | 31 530 +210/–200 | 35 136–35 652 | Bolus and Conrad (2006) |
| T 137 | KIA19545 | Arrow tip made of antler | N/A | | | | 29 500 ± 200 | 33 532–33 883 | Bolus and Conrad (2006) |

31 138 ± 539 to 39 934 ± 902 BP. One sample was analysed twice and the results are consistent (Table 3).

## Discussion

### *Pendling-Bärenhöhle: re-assessment of published radiocarbon date*

Our failure to radiocarbon-date bone and tooth samples from Pendling-Bärenhöhle is in line with a previous analysis of a cave bear bone (astragalus) from the 2011 excavation, which also lacked collagen (Frischauf *et al.*, 2012). The fact that eight bones and one tooth yielded uniformly very low N contents casts serious doubts on the original radiocarbon date published by Kneußl (1972). This measurement was performed in the early days of radiocarbon dating (by the former $^{14}C$ laboratory in Hanover, Germany). This sample was prepared following the Longin method, without filtration, only by separating the humic acid fraction using base treatment (M. Geyh, written communication, 2014). We therefore regard this date as probably too young and conclude that no reliable chronological data are available from this site.

### *Tischoferhöhle: evaluation of published and new radiocarbon dates*

The calibrated ages range from 42 898–44 325 to 33 532–33 883 cal a BP and fall within the published ages of *U. spelaeus* from the Alps (Fig. 2). The Tischoferhöhle ages overlap with those from Neue Laubenstein-Bärenhöhle 20 km to the north (Fig. 1; 45 106–46 153, 42 844–43 582, 40 931–41 571 cal a BP; Darga and Rosendahl, 2001; Rosendahl and Grupe, 2001). The original $^{14}C$ date of a cave bear bone from Tischoferhöhle, however, is significantly younger: 27 875 ± 485 BP (Kneußl, 1973) or 31 237–32 319 cal a BP. This date was determined in the same laboratory and using the same technique as the specimen from Pendling-Bärenhöhle, and hence we regard it as less reliable than the new dates and as probably too young. Burger *et al.* (2004) published a radiocarbon date of a cave lion bone from Tischoferhöhle, which falls within the younger end of our *U. spelaeus* age spectrum (Table 3; Fig. 2). Schlosser (1909) found eight projectiles made of bone and antler which belong to the Mladeč type (Aurignacian). Radiocarbon dates from two of these points (made of bone) also fall within the younger end of our *U. spelaeus* age range (Bolus and Conrad, 2006; Table 3). The third point was made of antler and yielded a slightly younger age (Table 3). The stratigraphic context of these three artefacts, however, was not explicitly reported by Schlosser (1909). Some authors assume that they were found in the thick loamy unit together with the cave bear remains (Groß, 1965), while others doubt it (Harb, 2002) and conclude that there is no archaeological evidence to suggest that cave bears were hunted in this cave (W. Sölder, personal communication, 2013). In conclusion, the 10 dates presented in the present study are the only reliable radiocarbon dates of *U. spelaeus* from Tischoferhöhle.

### *Cave bears and palaeoclimate in the Alps – some considerations*

The new dates from Tischoferhöhle show a spread of 7.5–10.0 ka (using the minimum and maximum range of individual dates, respectively) and allow us to constrain the duration of cave bear presence at this site. Figure 2 shows that this time interval during MIS 3 was characterised by five rapid warming events in Greenland, known as Greenland

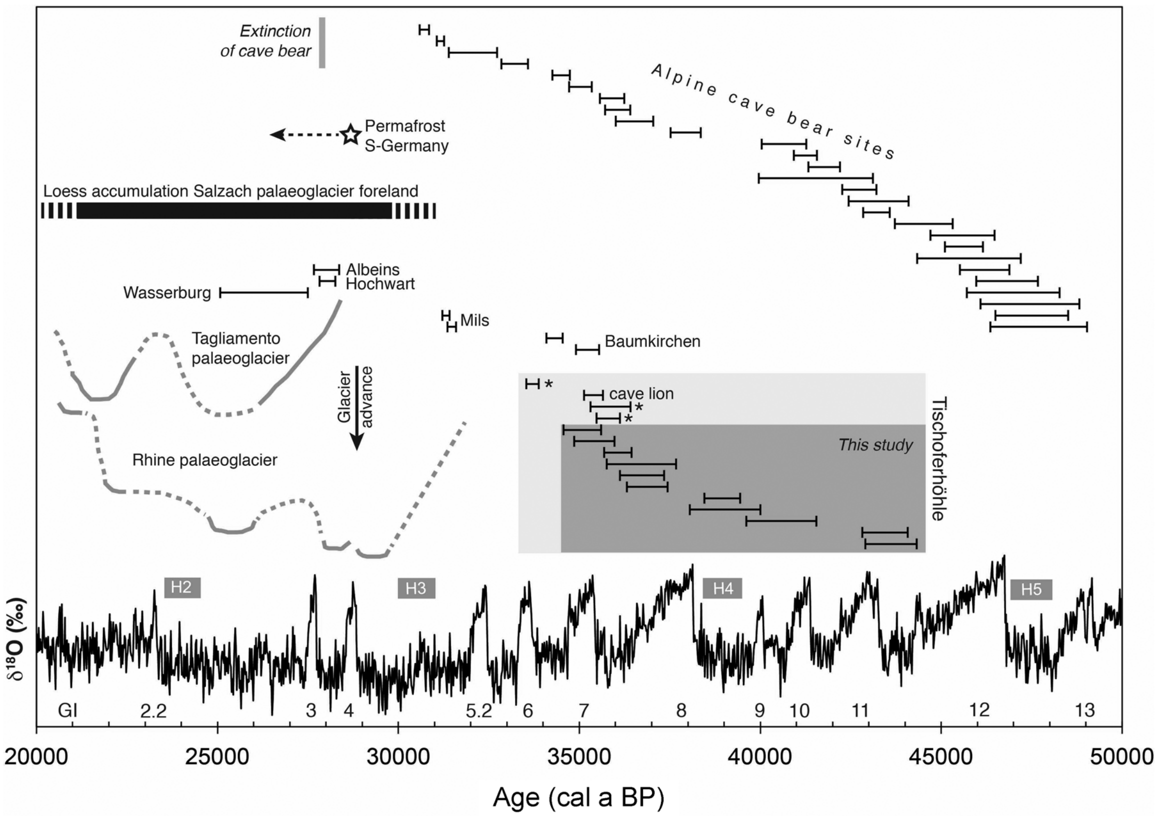


**Figure 2.** Time chart showing ages of cave bear fossils and other chronological information from western Austria and surrounding areas before and during the Last Glacial Maximum compared with the Greenland isotope curve (GICC05 time scale (Svensson *et al.*, 2008), converted to BP; Greenland interstadials (GI) are numbered according to Rasmussen *et al.*, 2014). All published radiocarbon data were re-calibrated using INTCAL13 and are shown with their 1$\sigma$ uncertainties. Radiocarbon dates of alpine cave bear sites are from Pacher and Stuart (2009), using their list of reliable dates and excluding those that go beyond the calibration range. Cave bear data from Tischoferhöhle are highlighted and include a cave lion sample (Burger *et al.*, 2004) and three projectiles (Bolus and Conrad (2006), marked by an asterisk, but whose stratigraphic context is doubtful. The vertical grey line marks the timing of extinction of *U. spelaeus* in Europe (Pacher and Stuart, 2009; Münzel, 2011; Bocherens *et al.*, 2014). Heinrich events H5–H2 are shown by horizontal grey bars (timing from Wang *et al.*, 2001). For further details see text.

Interstadials (GI) 11–7, separated by stadials, including Heinrich 4. Equivalents of GI 11, 9 and 7 have been very recently identified in the Eastern Alps by the abrupt increase in the oxygen isotopic composition of speleothems (Moseley *et al.*, 2014). The detailed structure of these Dansgaard–Oeschger events is strikingly similar between Greenland and the Alps and the U-series dating of the speleothems largely confirms the current GICC05 chronology. Hence, it appears justified to use the iconic Greenland isotope curve as a reliable template of the millennial-scale climate evolution in central Europe for most of the last glacial period (cf. Boch *et al.*, 2011).

Several radiocarbon dates of Tischoferhöhle cave bears fall within stadials (Fig. 2). However, we regard the present data set as too limited to draw firm conclusions about a possible climate bias in the occupation history of this cave. Given the current combined analytical and calibration uncertainties all dates can be reconciled with both stadial and interstadial climate states when 2$\sigma$ uncertainties are considered (not to mention the inherent uncertainty associated with the current Greenland ice-core timescale, GICC05–Svensson *et al.*, 2008). Provided our data are broadly representative of the age spectrum represented by the loamy layer in Tischoferhöhle, this site was last visited by cave bears during GI 7. Only a few well-dated occurrences of cave bear are known from the Alps that are younger (Pacher and Stuart, 2009; Fig. 2) and the last specimen, from Lieglloch in Totes Gebirge (Styria – Fig. 1), dates to 26 390 ± 110 BP or 30 594–30 847 cal a BP. This coincides with a fundamental transition in the environment in and around the Alps, i.e. the onset of the LGM, also known as the Upper Würmian (Chaline and Jerz, 1984). Figure 2 provides a compilation of palaeoclimatically relevant data from western Austria and nearby regions before and during the LGM. This graph shows that the last occurrence of cave bears in the Alps coincided with the onset of major glaciofluvial aggradation in the alpine valleys, reflecting a lowering of the equilibrium line altitude in response to climate cooling. The onset of this massive increase in glaciofluvial sediment supply to the main valleys is dated to ca. 31.5 cal ka BP at Mils near Baumkirchen in the central Inn Valley (Spötl *et al.*, 2013), where a former palaeolake had existed during MIS 3 (Figs 1 and 2), which silted up and was buried beneath thick glaciofluvial gravel. This phase of strong glaciofluvial aggradation continued until ca. 28 cal ka BP, constrained by a mammoth tooth embedded in proglacial gravel at Hochwart near Bregenz south of Lake Constance (De Graaff, 1992) and wood fragments in proglacial gravel at Albeins south of Brixen, South Tyrol (Fliri, 1988). Soon after, the equilibrium line altitude dropped to a record low position and the central alpine ice expanded across is previous proglacial outwash sediments onto the alpine foreland and eventually formed prominent piedmont glacier lobes (Fig. 1). The two radiocarbon dates from Hochwart and Albeins constrain the onset of this maximum advance to post-28 cal ka BP, consistent with an unfortunately imprecise radiocarbon date from the terminus of the Inn palaeoglacier at Wasserburg (Habbe *et al.*, 1996) as well as with the rather well documented first advance of the south alpine Tagliamento palaeoglacier onto the Venetian Plain (Monegato *et al.*, 2007, updated using INTCAL13). There is still some discrepancy in the chronology of advances and retreats of individual glaciers, e.g. between Rhine (reviewed by Heiri *et al.*, 2014) and Tagliamento palaeoglacier (Fig. 2), which may hold promising insights into climate gradients during the LGM.

The transition into the LGM was also marked by a strong increase in the sedimentation rate of aeolian dust (loess) along the fringe of the Alps and along major river valleys, such as the Danube in Lower Austria. Loess accumulation commenced ca. 30 ka ago in the foreland of the Salzach palaeoglacier (Starnberger *et al.*, 2011) and the bulk of the LGM loess in the central Danube valley at Krems was deposited after ca. 31 ka (Lomax *et al.*, 2014). The high sedimentation rate and the lack of soil formation suggest periglacial conditions and a drastic loss of vegetation at that time (cf. Heiri *et al.*, 2014).

To summarize, evidence from the Alps points to a strong increase in continentality and a concomitant decrease in vegetation density along the northern side of the Alps starting about 31 cal ka BP. Heinrich 3, which occurred at that time (Wang *et al.*, 2001), may have significantly contributed to this climate deterioration. By analogy with detailed studies of Heinrich 0 (Younger Dryas) these massive ice-rafting events gave rise to very cold winters and hence an increase in seasonality and continentality characterised in the circum-Atlantic realm (e.g. Broecker, 2006). Data from Zoolithenhöhle, a cave site on the Franconian Alb, support this picture of strong winter cooling. The presence of cryogenically formed speleothems dated to $28.8 \pm 0.3$ ka by U–Th (Richter *et al.*, 2014) strongly implies that the cave chambers that were previously used by hibernating cave bears during MIS 3 (Pacher and Stuart, 2009) were permafrozen by ca. 29 ka (Fig. 2).

## *Concluding remarks*

Observations from various palaeoclimate archives imply a possible link between climate and the gradual disappearance of cave bear populations from inner alpine sites between ca. 35 cal ka BP (Tischoferhöhle) and ca. 31 cal ka BP (Liegloch). Note, however, that this megafauna was well adapted to harsh climate conditions during the last glacial period. Data from this study, for example, demonstrate that cave bears occupied Tischoferhöhle during Heinrich 4, ca. 39 ka ago, and data compiled by Pacher and Stuart (2009) suggest – within the uncertainty of the calibrated radiocarbon dates – the uninterrupted presence of cave bears in alpine caves also during Heinrich 5 (Fig. 2). High-resolution chronology studies of stratigraphically well-constrained cave bear fossils across key climate intervals such as Heinrich events combined with multi-proxy studies are clearly needed to better understand the impact of rapid climate changes and climate extremes on alpine cave bear populations and their ecosystem. Future research will, we hope, also shed light on the role of humans in the reduction of this megafauna and its final extinction ca. 28 cal ka ago – a question that has received increasing attention lately (Pacher and Stuart, 2009; Münzel, 2011; Bocherens *et al.*, 2014; Stiller *et al.*, 2014). Available archaeological data from alpine cave sites provide only little insight into this question, even though the presence of Palaeolithic hunters is known from several alpine sites (e.g. Bächler, 1940; Döppes and Rabeder, 1997; Le Tensorer, 1998; Urban, 2000).

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*Abbreviations.* AMS, acceleration mass spectrometry; GI, Greenland Interstadial; LGM, Last Glacial Maximum; MIS, Marine Isotope Stage.

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