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Cave bear occupation in Schwabenreith Cave, Austria, during the early last glacial: constraints from 230 Th/U-dated speleothems

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ABSTRACT: The cave bear was a prominent member of the Upper Pleistocene fauna in Eurasia. While breakthroughs were recently achieved with respect to its phylogeny using ancient DNA techniques, it is still challenging to date cave bear fossils beyond the radiocarbon age range. Without an accurate and precise chronological framework, however, key questions regarding the palaeoecology cannot be addressed, such as the extent to which large climate swings during the last glacial affected the habitat and possibly even conditioned the final extinction of this mammal. Key to constraining the age of cave bear fossils older than the lower limit of radiocarbon dating is to date interlayered speleothems using ²³⁰Th/U. Here we report new results from one such site in the Eastern European Alps (Schwabenreith Cave), which yielded the highest density of bones of cave bear (*Ursus spelaeus eremus*). Although dating of the flowstones overlying this fossiliferous succession was partly compromised by diagenetic alteration, the ²³⁰Th/U dates indicate that the bear hibernated in this cave after about 113 ka and before about 109 ka. This time interval coincides with the equivalent of Greenland Stadial 25, suggesting possible climate control on the cave bear's habitat and behaviour.

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KEYWORDS: cave bear; early last glacial; Eastern Alps; speleothem; ²³⁰Th/U dating.

Introduction

The cave bear (*Ursus spelaeus*) was a prominent member of the Late Pleistocene megafauna. Sediments of numerous caves in western and eastern Eurasia preserve bones and teeth of this mammal, which became extinct in mid-Europe 28–24k cal a BP (Pacher and Stuart, 2009; Baca *et al.*, 2016; Mackiewicz *et al.*, 2017; Terlato *et al.*, 2019).

Three main 'types' of Late Pleistocene cave bears have been identified based on palaeogenetic and morphological analyses: *U. spelaeus sensu stricto* (*sensu lato*), *U. ingressus* and *U. kudarensis* (Hofreiter *et al.*, 2004a; Knapp, 2019), the latter only found in the Caucasus and further east. Based on morphological features, some studies split *U. spelaeus* (*sensu lato*) into the subspecies *U. s. spelaeus*, *U. s. eremus* and *U. s. ladinicus* (Rabeder *et al.*, 2004; Rabeder and Hofreiter, 2004). This classification is partially supported by palaeogenetic analyses (Hofreiter *et al.*, 2002, 2004a; Dabney *et al.*, 2013; Stiller *et al.*, 2014), but the discussion is not yet fully resolved (Knapp *et al.*, 2009; Knapp, 2019).

An area of high density of cave bear fossils are the Alps, and in particular the Northern Calcareous Alps, where about 45 caves are known in which this animal hibernated and died (Fig. 1). Thanks to several decades of palaeontological research including numerous excavations, several of these sites are well documented (e.g. Döppes and Rabeder, 1997; Rabeder and Frischauf, 2016). A fascinating aspect of this

research is that *U. s. eremus* and *U. ingressus* coexisted in mountain caves only about 10 km apart for about 15 000 years during Marine Isotope Stage (MIS) 3, without hybridization and interactions (Hofreiter *et al.*, 2004b). These and other findings hinge on accurate and precise chronological data which have traditionally been almost exclusively based on radiocarbon. Recent dating campaigns have shown, however, that some of the earlier published radiocarbon data of Alpine cave bear remains were too young (e.g. Spötl *et al.*, 2014, 2018). In addition, there is a serious lack of reliable geochronological data of cave bear fossils before the lower limit of radiocarbon dating, i.e. older than about 45–50k cal a BP. This is unfortunate because several Alpine sites revealed bones, whose radiocarbon analyses yielded infinite ages (Pacher and Stuart, 2009; Spötl *et al.*, 2018; Döppes *et al.*, 2019).

Dating bones and teeth using techniques other than radiocarbon is challenging given the open-system behaviour of bones with respect to U-series isotopes, precluding routine ²³⁰Th/U dating of bone material (Pike *et al.*, 2002; Sambridge *et al.*, 2012). Likewise, luminescence dating of clastic sediments, in which these fossils are commonly embedded, is associated with fundamental issues, including incomplete bleaching and possible reworking (e.g. Munroe *et al.*, 2016), unless deposited near the cave entrance (e.g. Henshilwood *et al.*, 2011).

An alternative geochronological approach involves ²³⁰Th/U dating of speleothems stratigraphically intercalated with fossils and/or fossiliferous clastic sediments. This technique is both accurate and precise and is not limited to the last 50 ka. The key requirements are that the carbonate samples are

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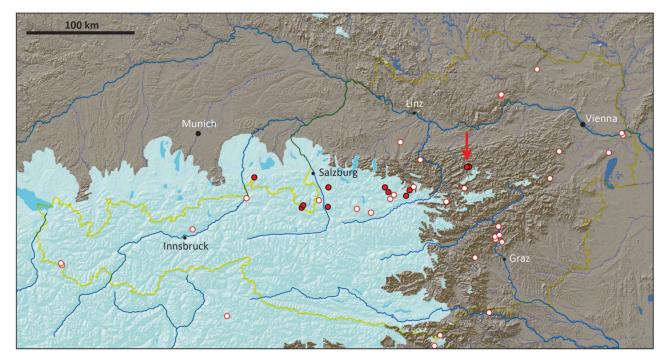


Figure 1. Map showing cave bear sites in Austria and neighbouring countries (red circles) as well as the location of Schwabenreith Cave (arrow). Sites where *Ursus spelaeus eremus* was identified are shown by solid red dots. The extent of the Alpine ice sheet during MIS 2 is shown for reference in light blue. Source map: Geological Survey of Austria. [Color figure can be viewed at wileyonlinelibrary.com].

sufficiently clean (i.e. low detrital 232 Th) and have not undergone post-depositional alteration. 230 Th/U dating of speleothems has been successfully applied to constrain the age of a variety of cave fossils (e.g. Lari et al., 2015; Stinnesbeck et al., 2017) as well as prehistoric cave art (e.g. Hoffmann et al., 2016; Dublyansky et al., 2018). Unfortunately, speleothems interbedded with cave bear remains are rare in Alpine caves, partly probably due to the cool and dry climate of the last glacial period during which cave bears took shelter in these sites. One cave, however, Schwabenreith Cave in eastern Austria, stands out in this respect. This site not only revealed the highest density of well-preserved cave bear bones in the Alps (Döppes and Rabeder, 1997), but also excavations have shown that parts of this cave preserve sediment successions, where the fossiliferous cave sediments are both under- and overlain by speleothems. This renders Schwabenreith Cave a special location, and the aim of the present study was to use state-of-the-art ²³⁰Th/U dating to tightly constrain the timing of cave bear occupation at this site.

Study site

Schwabenreith Cave (Austrian cave register no. 1823/32) is located in Lunz am See in the north-western part of Lower Austria. This single-entrance cave opens at 959 m a.s.l., consists of two near-horizontal passages and has a total length of 134 m (Fig. 2; Hartmann and Hartmann, 1985).

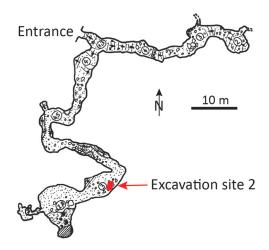
Excavations were conducted at two locations within the cave between 1990 and 1996 (Fladerer, 1992) and in 2015. Of particular interest is excavation site 2, which revealed the following general stratigraphy (from top to bottom; Pacher, 2000; Fig. 2):

- A couple of subhorizontal flowstone layers, each up to a several centimetres thick, partly interbedded with loam.
- Loam (about 1 m thick) containing abundant cave bear fossils as well as angular bedrock fragments, but lacking an internal stratigraphy.

- Light grey, unfossiliferous and partly laminated sandy loam in which large bedrock blocks are embedded.
- An older speleothem generation consisting of a few stalagmites, including a 50-cm-tall specimen, resting on bedrock.

Detailed studies of the taphonomy were conducted on 18525 bones and 1796 teeth of cave bear. In total, 16011 of these bones were found at excavation site 2 (Pacher, 2000), where bones of adult bears (65.2%) outnumber those of juvenile (31.4%) and newly born individuals (3.4%). The bear fossils, which belong solely to *U. s. eremus* (Rabeder *et al.*, 2008), generally lack bite marks. No other animals known from other bear caves in the Northern Calcareous Alps (e.g. cave lion) were found in this cave. The skeletons are complete, and there is no evidence of significant post-mortem re-deposition (Pacher, 2000), nor of the presence of humans inside the cave during prehistoric times.

Initial attempts to constrain the age of these cave bear sediments included radiocarbon and 230Th/U dating. An uncalibrated accelerator mass spectrometry (AMS) radiocarbon analysis of a cave bear bone from excavation site 3, located at the end of the eastern gallery of the cave, yielded an age of $52.5 + 1.9/-2.5k^{-14}C$ a BP (VERA 0061 – Pacher, 2000). In a later review, Pacher and Stuart (2009: table 3) excluded this date from their compilation. Recently, Döppes et al. (2016, 2018) reported seven AMS radiocarbon analyses. Five of them ranged from as young as 34.0 ± 0.2 to 48.3 ± 0.9 k ¹⁴C a BP and two were reported as >49k ¹⁴C a BP. Previous ²³⁰Th/U analyses of calcite speleothems were performed by alpha-spectrometry. Two samples from the older speleothem generation underlying the bone-bearing sediments from excavation site 2 yielded ages of 112 ± 5 and 116 ± 5 ka, while a flowstone sample above the bone-bearing sediments (whose precise location, however, is unclear - Pacher, 2000) gave 78 + 30/-23 ka (Döppes and Rabeder, 1997; note that the uncertainties of these alpha spectrometric ²³⁰Th/U analyses are reported at the 1 sigma level).



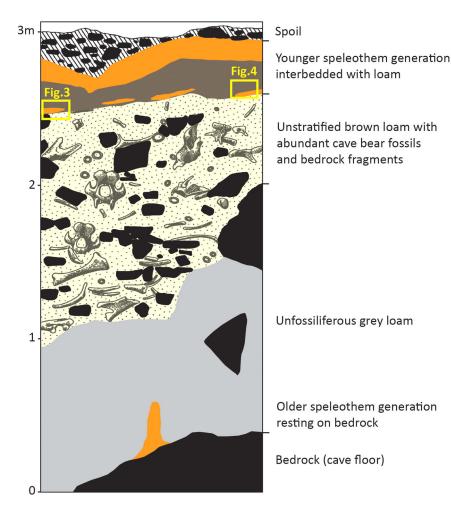


Figure 2. Plan view of Schwabenreith Cave and location of excavation site 2 (after Hartmann and Hartmann, 1985). The lower panel shows the stratigraphic overview section of excavation site 2 (simplified after Döppes and Rabeder, 1997). Speleothems are shown in orange. The approximate position of the profiles sampled for this study are shown by yellow rectangles. [Color figure can be viewed at wileyonlinelibrary.com].

Samples and methods

All samples of this study were obtained from excavation site 2 (Fig. 2). These include cave bear bones and speleothems. All bones as well as flowstones SCHW1 to SCHW3 were obtained from the H7 side of the excavation pit (see Pacher, 2000: fig. 2, for details). One flowstone specimen was obtained from the opposite side of this pit (F4/5), and a 50-cm-tall stalagmite had already been recovered from the older speleothem generation during the main excavation at this site.

Five cave bear bones (Table 1) from the fine-grained fossiliferous layer were pre-screened for their whole bone N content. Elemental analysis of scrapes from the bone surface yielded values between 0.35 and 1.35% N. Collagen was extracted from cleaned, crushed bone samples with an

acid–base–acid treatment followed by gelatinization and ultrafiltration (Brock *et al.*, 2010) using the Vivaspin filter cleaning method introduced by Bronk Ramsey *et al.* (2004). The collagen was then freeze-dried. The dried samples were weighed into pre-combusted quartz tubes with an excess of copper oxide (CuO), sealed under vacuum and combusted to carbon dioxide (CO₂). The CO₂ was converted to graphite on an iron catalyst using the zinc reduction method (Slota *et al.*, 1987). ¹⁴C/¹²C and ¹³C/¹²C ratios were measured by AMS at ¹⁴CHRONO, Queen's University Belfast. The sample ¹⁴C/¹²C ratio was background-corrected using measurements on collagen extracted from the Latton mammoth bone (Lewis *et al.*, 2006) and normalized to the HOXII standard (SRM 4990 C; National Institute of Standards and Technology). The ¹⁴C/¹²C ratios were corrected for isotope fractionation using

Table 1. Radiocarbon dates and isotopic analysis of bones from Schwabenreith Cave as well as collagen quality control indicators (C/Na, %C and % collagen yield). %N was measured on bone scrapes before collagen extraction. All analysed bones are from excavation site 2 of Pacher (2000, including the quadrant numbers). Samples SW2146 and SW2146_2 as well as SW2147 and SW2147_CS are two aliquots of the same bone each.

Sample id	Element	Excavation quadrant	%N	Lab. code	¹⁴ C age вр	δ ¹³ C _{VPDB} (‰)	$\delta^{15}N_{AIR}~(\%)$	C/N	%C	Collagen yield (%)
SW2145	Bone fragment	F4/5	1.35	UBA- 30488	>46 113	-22.2	0.9	3.17	47.6	2.5
SW2146	Humerus	H7	1.31	UBA- 30489	>45 923	-22.5	0.9	3.17	29.3	9.3
SW2146_2	Humerus	H7	0.66	UBA- 30723	>44 013	-22.4	0.7	3.20	48.6	8.7
SW2147	Tibia	H7	0.35	UBA- 29256	Failed					
SW2147_CS	Tibia	H7	0.87	UBA- 29257	Failed					

the AMS measured $\delta^{13}C$ value, which accounts for both natural and instrumental fractionation. The radiocarbon age and one standard deviation were calculated using the Libby half-life of 5568 years following the methods of Stuiver and Polach (1977). Stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and C:N ratios were measured on a Delta V Advantage with a Flash elemental analyser. Stable isotope standards IA-R041 L-alanine, IAEA-N-2 ammonium sulphate and IAEA-CH-sucrose were analysed with the unknown samples to provide a two-point calibration. An internal fishbone collagen sample was also analysed. Reproducibility for ultrafiltered bone collagen is 0.22% for $\delta^{13}C$ and 0.15% for $\delta^{15}N$.

Speleothem samples for ²³⁰Th/U dating were obtained in 2015 from the pit at excavation site 2 and include four flowstones and one stalagmite. The former were taken from the excavated face of the pit, while the stalagmite had been recovered during the 1990–1996 campaign from the same pit. The specimens were cut and polished and subsamples for dating were obtained using a dental drill. The powders were dissolved in 7 N HNO₃, and a mixed ²³³U–²³⁶U–²²⁹Th spike (Gibert *et al.*, 2016) was added to the solution. Chemical

separation of U and Th was carried out by ion exchange chemistry (Yang *et al.*, 2015). U and Th isotope ratios were determined with a Nu Instruments multi-collector inductively coupled plasma mass spectrometer (MC-ICP-MS) at the Max Planck Institute for Chemistry, Mainz, Germany. Samples were measured by a standard-sample bracketing procedure as described by Obert *et al.* (2016). All ages were corrected for potential detrital contamination assuming a bulk Earth 232 Th/ 238 U weight ratio of 3.8 and 230 Th, 234 U and 238 U in secular equilibrium. Except for two samples (SCHW1-4 and SCHW4-1, Table 2), the correction is insignificant within error.

Results

Two of the five bone samples had collagen yields of < 1% which was insufficient for radiocarbon dating. The remaining three samples resulted in conventional ages of >44 to >46k 14 C a BP (Table 1).

One of the four flowstone samples (SCHW2 – Fig. 3) lacked sufficiently clean calcite and was not further studied. Speleothem sample SCHW1 is of particular interest because

Table 2. ²³⁰Th/U dating results of speleothems from Schwabenreith Cave.

	²³⁸ U		²³² Th (ng						Age uncorr.		Age corr.	
Sample	$(\mu g \ g^{-1})$	±	g^{-1})	±	²³⁴ U/ ²³⁸ U	±	²³⁰ Th/ ²³⁸ U	±	(ka)	±	(ka)	±
SCHW1-1	0.351	0.002	15.9	0.2	1.0614	0.0022	0.7036	0.0052	118.1	1.5	116.9	1.6
SCHW1-2	0.369	0.002	29.1	0.5	1.0641	0.0022	0.5491	0.0077	80.6	1.3	78.5	1.6
SCHW1-3	0.343	0.002	7.1	0.1	1.0598	0.0013	0.5905	0.0053	88.6	1.2	88.1	1.2
SCHW1-3A	0.322	0.002	7.08	80.0	1.0582	0.0022	0.6536	0.0046	104.3	1.2	103.7	1.3
SCHW1-4	0.271	0.002	58.7	0.7	1.0657	0.0028	0.8109	0.0080	158.1	2.4	152.3	3.3
SCHW1-5	0.268	0.002	6.86	0.07	1.0577	0.0017	0.6787	0.0035	111.2	1.0	110.6	1.0
SCHW1-6	0.247	0.002	47.2	0.5	1.0589	0.0024	0.7961	0.0076	154.0	2.2	148.8	3.1
SCHW3-1	0.279	0.002	7.0	0.4	1.0597	0.0022	0.629	0.040	97.8	+ 10.1 -9.3	97.2	+ 10.0 -9.4
SCHW3-1A	0.262	0.002	14.7	0.2	1.0588	0.0023	0.6722	0.0060	110.1	1.6	108.6	1.7
SCHW3-2	0.276	0.002	5.9	0.1	1.0601	0.0017	0.551	0.006	79.9	1.2	79.3	1.2
SCHW3-3	0.2738	0.0034	17.23	0.42	1.062	0.012	0.658	0.014	105.8	4.2	104.2	4.3
SCHW3-4	0.2725	0.0036	10.64	0.12	1.065	0.013	0.6503	0.0091	102.7	3.2	101.7	3.1
SCHW4-1	0.214	0.001	18.8	0.2	1.0678	0.0023	0.5020	0.0066	71.15	0.58	68.8	1.3
SCHW4-2	0.198	0.001	6.0	0.2	1.0585	0.0013	0.3713	0.0073	47.8	1.1	47.0	1.1
SCHW4-3	0.206	0.001	6.7	0.2	1.0951	0.0015	0.3182	0.0088	38.1	1.1	37.3	1.2
SCHW4-4	0.1984	0.0025	14.57	0.16	1.076	0.012	0.4891	0.0082	67.6	1.6	65.7	1.9
SCHW5-1	0.377	0.002	4.01	0.04	1.1124	0.0019	0.7451	0.0042	118.0	1.2	117.7	1.2
SCHW5-2	0.317	0.002	1.48	0.05	1.0991	0.0017	0.653	0.013	96.7	3.1	96.6	3.1
SCHW5-3	0.349	0.002	6.02	0.06	1.1051	0.0023	0.7647	0.0040	125.4	1.3	125.0	1.3
SCHW5-4	0.250	0.002	33.4	0.4	1.1527	0.0034	0.8283	0.0066	135.7	1.8	132.5	2.1
SCHW5-5	0.243	0.002	15.1	0.2	1.0953	0.0020	0.7201	0.0058	115.9	1.5	114.4	1.7
SCHW5-6	0.3275	0.0053	2.033	0.022	1.104	0.017	0.721	0.011	113.1	4.6	112.9	4.5
SCHW5-7	0.3585	0.0021	7.98	0.11	1.0967	0.0017	0.7293	0.0052	117.2	1.5	116.6	1.5



Figure 3. Exposure at excavation face 7 H showing a flowstone layer overlying the bone-bearing cave loam succession. Speleothem sampling locations are marked. [Color figure can be viewed at wileyonlinelibrary.com].

it comprises about 10 cm of layered calcite deposited directly on a cave bear bone (Fig. 3). Seven subsamples drilled from individual calcite layers yielded highly variable 230 Th/U ages ranging from 152.3 \pm 3.3 to 78.5 \pm 1.6 ka, lacking stratigraphic order (Fig. 5A,B).

Flowstone SCHW3 was deposited above SCHW1 (Fig. 3) and comprises 4 cm of macroscopically fairly clean calcite. Five subsamples were obtained from this piece of flowstone. Two subsamples from the interior yielded 108.6 ± 1.7 and 104.2 ± 4.3 ka, consistent with a third lateral sample whose precision, however, is poor $(97 \pm 10 \text{ ka} - \text{Fig. 5C})$. A subsample closer to the lower boundary of the flowstone gave a slightly younger age $(101.7 \pm 3.1 \text{ ka})$, and a subsample taken 5 mm below the top gave $79.3 \pm 1.2 \text{ ka}$ (Fig. 5C).

Flowstone SCHW4 was obtained from the opposite side of the excavation pit, about 15 cm above the uppermost cave bear bones (Fig. 4). Four subsamples yielded stratigraphically consistent 230 Th/U ages between 68.8 ± 1.3 and 37.3 ± 1.2 ka (Fig. 5D).

Stalagmite SCHW5 is composed of micritic calcite, unlike the coarser crystalline fabric of the flowstones, and was



Figure 4. Exposure at excavation face F4/5 showing flowstone layers capping the bone-bearing cave loam succession. The speleothem sampling location is marked. [Color figure can be viewed at wileyonlinelibrary.com].

characterized by seven 230 Th/U dates (Fig. 5E). Its growth commenced shortly before 132.5 ± 2.1 ka. The outermost layers are only partly preserved and yielded ages between 114.4 ± 1.7 and 112.9 ± 4.5 ka (ignoring an outlier of 96.6 ± 3.1 ka, which was taken from the same layer dated to 112.9 ± 4.5 ka at a lateral position).

Discussion

Assessment of age data

Cave bear bones from excavation site 2 yielded moderate to low N values suggesting variably low collagen preservation. Radiocarbon data of three samples with relatively high N values indicate that they are probably older than about 50k cal a BP (Cheng *et al.*, 2018).

²³⁰Th/U analyses do not date the bones directly, but allow to narrow down the time interval of cave bear occupation. Stalagmite SCHW5 beneath the unfossiliferous fine-clastic sediments formed during the Last Interglacial and Greenland Interstadial (GI)-25 (Fig. 6). The age of its outermost layers indicates that this speleothem generation was buried by fine-grained clastic sediments after about ~113 ka. This represents the maximum age (*post quem* age) of cave bear occupation at this site, but because the unfossiliferous clastic sediments are sandwiched between this older speleothem generation and the fossiliferous sediments, the latter are definitely younger than ~113 ka.

The flowstone layers capping the fossiliferous unit mark the end of clastic sedimentation and the recurrence of calcite deposition. The ages of this younger speleothem generation scatter and are not entirely internally consistent. However, they indicate that calcite deposition resumed at ~109 ka, i.e. during Gl-24 and continued, probably discontinuously, until Gl-23.1 (Fig. 6).

Given that there are about 10–15 cm of flowstone and loam between the uppermost cave bear bones, ~109 ka provides a minimum age estimate (*ante quem* age) for the stratigraphically highest cave bear bones.

Flowstone SCHW4 from the opposite excavation face is separated from the uppermost bone fossils by about 15 cm of brown loam and its basal 230 Th/U age of 68.8 ± 1.3 ka therefore provides a less stringent age constraint for the bones, but nevertheless demonstrates that the latter were deposited well before about 69 ka.

Although stratigraphically ideally situated, i.e. directly attached to a cave bear bone, flowstone SCHW1 yielded unreliable data. The unsystematic scatter of the dates suggests strongly that the calcite layers in this flowstone have not remained a closed system with respect to U and/or Th nuclides since the time of deposition. It is well known that bones show open-system behaviour (Pike et al., 2002; Sambridge et al., 2012) and these processes of bone diagenesis probably affected the calcite surrounding these bones (Millard and Hedges, 1996; Stinnesbeck et al., 2017). There is no systematic pattern, e.g. of decreasing ²³⁰Th/U ages with decreasing distance from the bone. Rather, the current data suggest that the calcite layers of SCHW1 were diagenetically affected in a complex matter, probably reflecting different degrees of permeability on a millimetre scale. The other flowstone specimens, which were not directly adjacent to bone fragments, do not show evidence of open-system behaviour.

Constraining the time of cave bear occupation

Based on our data the most likely time window when the cave bear used the interior of Schwabenreith Cave to hibernate was between ~113 and ~109 ka. These results

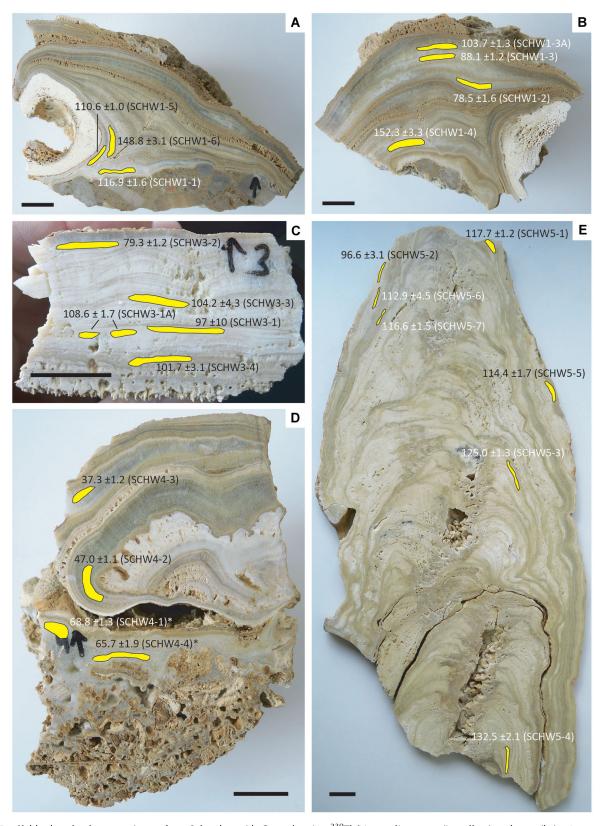


Figure 5. Slabbed speleothem specimens from Schwabenreith Cave showing 230 Th/U sampling spots (in yellow) and ages (ka) \pm 2 σ errors. (A,B) Front and rear side of flowstone SCHW1 (ca. 2-cm-thick slab), which was deposited around a cave bear bone. (C) Sample SCHW3. (D) Sample SCHW4. Two subsamples were drilled from the backside and are marked by an asterisk (*). (E) Stalagmite SCHW5. Top is up on all samples, and scale bars are 2 cm in all images. [Color figure can be viewed at wileyonlinelibrary.com].

narrow down the previously reported age range substantially, in particular the previous, very imprecise age of the upper speleothem layer $(78 + 30/-23 \text{ ka} - \text{D\"{o}ppes} \text{ and Rabeder}, 1997;$ note again that these are 1 sigma uncertainties).

The older speleothem generation is not directly overlain by the cave bear-bearing sediments, but by sterile and partly laminated light grey sandy silts and clays. Although no direct age constraints of this sediment layer are available, its thickness of about 1 m suggests that some time had passed between the deposition of the speleothems beneath and that of the fossiliferous sediments above, not considering possible hiatuses. The top age of stalagmite

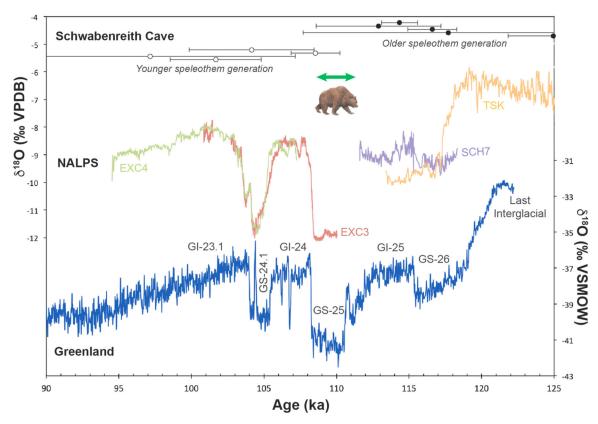


Figure 6. Proxy records for the time interval between the end of the Last Interglacial and 90 ka BP. The NorthGRIP Greenland oxygen isotope record is shown on the modelext timescale (Wolff *et al.*, 2010) with Greenland stadials (GS) and interstadials (GI) labelled according to Rasmussen *et al.* (2014). Speleothems from the Alps (EXC4, EXC3 and SCH7) are part of the NALPS record (Boch *et al.*, 2011), TSK is from Meyer *et al.* (2009 – note that this record is offset by +2‰). Top: age constraints of the older and younger speleothem generation in Schwabenreith Cave (individual 230 Th/U ages including 2 σ uncertainties) and the most likely time interval of cave bear occupation at this site (green double arrow) are indicated. [Color figure can be viewed at wileyonlinelibrary.com].

SCHW5 (~113 ka) therefore probably overestimates the maximum age of the fossil-bearing layer.

Palaeoclimatic considerations

The time window indicated by the new ²³⁰Th/U dates falls into the early part of the last glacial period. Oxygen isotope data of precisely dated stalagmites from caves in the Western and Eastern Alps (Boch *et al.*, 2011) mimic the high-magnitude changes in oxygen isotopes recorded in the ice of Greenland (North Greenland Ice Core Project Members, 2004) and demonstrate rapid large swings between stadial and interstadial climate states in the Alps. These changes had a major impact on the regional vegetation with boreal forests during major interstadials (e.g. GI-23.1) and only sparse tree stands during the intervening stadials in the foothills of the northern Alps, i.e. close to the studied cave (e.g. Drescher-Schneider, 2000; Oeggl and Unterfrauner, 2000).

Calcite deposition at Schwabenreith Cave occurred during the preceding Last Interglacial and continued, possibly interrupted by hiatuses, until the first interstadial (GI-25) at~113 ka (Fig. 6). Chemical sedimentation gave way to fine-grained clastics. Their light-grey colour, their lack of fossils and lack of interbedded speleothems imply a cold and hostile climate and episodes of cave flooding giving rise to partly laminated silts and clays. The light colour indicates a reduced influx of soil-derived organic matter into this cave gallery, reflecting reduced (open?) vegetation above the cave. Low temperatures inside the cave gave rise to frost shattering and explain the presence of large angular bedrock blocks embedded in this basal sediment, which probably represent breakdown from the ceiling (Fladerer, 1992). Given the ²³⁰Th/U age constraints, these sterile fine-grained sediments

were probably deposited during the early part of GS-25, which was a prominent stadial lasting for about 2 ka (Fig. 6). The onset of the younger speleothem generation records a significant improvement in the soil and vegetation conditions above the cave, probably due to a warmer and more humid climate. This coincided with the start of interstadial GI-24 and continued into GI-23.1, which was the most pronounced (forested) interstadial in the Alps during the last glacial period (Drescher-Schneider, 2000).

Given these age constraints, the most likely time window when *U. s. eremus* occupied the cave is the equivalent of GS-25, which lasted from 111.6 to 108.3 ka according the NALPS dataset (Boch *et al.*, 2011), consistent within error with the NGRIP_{modelext} ice core chronology (Wolff *et al.*, 2010).

Despite some scatter, this new age assignment is – to our knowledge – the chronologically best constrained one for a local cave bear population in the early last glacial period, not only in the greater Alpine realm, but probably also elsewhere in Europe. Interestingly, the speleothem ages in conjunction with the sediment characteristics (in particular the abundance of angular bedrock fragments in the fossiliferous sediments, probably derived from frost-shattering of the cave ceiling – Fig. 2) show that the cave bear used this shelter during a stadial. This suggests a direct or indirect climate control on the cave bear's habitat and behaviour. However, chronologically better constrained studies of other cave sites are required to firmly address this ecological aspect.

Conclusions

Speleothems offer a promising approach to significantly improve the chronological framework of cave bear sites. Here we used ²³⁰Th/U dating of speleothems to bracket the age of the presence of *U. s. eremus* in Schwabenreith Cave, one of the richest and best preserved such sites in the European Alps. This approach is possible at this site because the fossiliferous sediment layer is sandwiched between two speleothem generations. Our study shows that multiple dates of individual speleothem samples are required to check the internal stratigraphy. Samples immediately adjacent to bones should be avoided because they may show strongly biased ages due to open-system behaviour. The results of this study indicate that *U. s. eremus* was present in Schwabenreith Cave during the equivalent of GS-25, a cold and dry interval which lasted from 112 to 108 ka.

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Abbreviations. AMS, accelerator mass spectrometry; GI, Greenland Interstadial; GS, Greenland Stadial; MC-ICP-MS, multi-collector inductively coupled plasma mass spectrometry; MIS, Marine Isotope Stage.

References

- North Greenland Ice Core Project Members. 2004. High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature* **431**: 147–151.
- Baca M, Popović D, Stefaniak K, et al. 2016. Retreat and extinction of the Late Pleistocene cave bear (*Ursus spelaeus* sensu lato). *The Science of Nature* **103**: 92.
- Boch R, Cheng H, Spötl C, et al. 2011. NALPS: a precisely dated European climate record 120–60 ka. Climate of the Past 7: 1247–1259.
- Brock F, Higham T, Ditchfield P, et al. 2010. Current pretreatment methods for AMS radiocarbon dating at the Oxford Radiocarbon Accelerator Unit (ORAU). Radiocarbon 52: 103–112.
- Bronk Ramsey C, Higham T, Bowles A, et al. 2004. Improvements to the pretreatment of bone at Oxford. Radiocarbon 46: 155–163.
- Cheng H, Edwards RL, Southon J, et al. 2018. Atmospheric ¹⁴C/¹²C changes during the last glacial period from Hulu Cave. *Science* **362**: 1293–1297.
- Dabney J, Knapp M, Glocke I, et al. 2013. Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. Proceedings of the National Academy of Sciences of the United States of America 110: 15758–15763.
- Döppes D, Pacher M, Rabeder G, et al. 2016. Unexpected! New AMS dating from Austrian cave bear sites. Cranium 33: 26–30.
- Döppes D, Rabeder G. 1997. Pliozäne und pleistozäne Faunen Österreichs. Mitteilungen der Kommision für Quartärforschung der sterreichischen Akademie der Wissenschaften 10: 1–411.
- Döppes D, Rabeder G, Frischauf C, et al. 2019. Extinction pattern of Alpine cave bears new data and climatological interpretation. *Historical Biology* **31**: 422–428.
- Drescher-Schneider R. 2000. Die Vegetations- und Klimaentwicklung im Riß/Würm-Interglazial und im Früh- und Mittelwürm in der Umgebung von Mondsee. Ergebnisse der pollenanalytischen Untersuchungen. Mitteilungen der Kommision für Quartärforschung der Österreichischen Akademie der Wissenschaften 12: 39–92.
- Dublyansky Y, Moseley GE, Lyakhnitsky Y, et al. 2018. Late Palaeolithic cave art and permafrost in the Southern Ural. Scientific Reports 8: 12080.
- Fladerer FA. 1992. Erste Grabungsergebnisse von der Schwabenreithhöhle bei Lunz am See (Niederösterreich). *Die Höhle* **43**: 84–92.
- Gibert L, Scott GR, Scholz D, et al. 2016. Chronology for the Cueva Victoria fossil site (SE Spain): evidence for Early Pleistocene Afrolberian dispersals. *Journal of Human Evolution* **90**: 183–197.

- Hartmann H, Hartmann W 1985. *Die Höhlen Niederösterreichs*. Vol. 3, Wiss. Beihefte Die Höhle 30: Vienna (Verb. Österr. Höhlenforscher).
- Henshilwood CS, d'Errico F, vanNiekerk KL, et al. 2011. A 100,000-yearold ochre-processing workshop at Blombos Cave, South Africa. Science 334: 219–222.
- Hoffmann DL, Pike AWG, García-Diez M, et al. 2016. Methods for Useries dating of CaCO₃ crusts associated with Palaeolithic cave art and application to Iberian sites. *Quaternary Geochronology* **36**: 104–119.
- Hofreiter M, Capelli C, Krings M, et al. 2002. Ancient DNA analyses reveal high mitochondrial DNA sequence diversity and parallel morphological evolution of Late Pleistocene cave bears. *Molecular Biology and Evolution* **19**: 1244–1250.
- Hofreiter M, Rabeder G, Jaenicke-Després V, et al. 2004b. Evidence for reproductive isolation between cave bear populations. Current Biology 14: 40–43.
- Hofreiter M, Serre D, Rohland N, et al. 2004a. Lack of phylogeography in European mammals before the last glaciation. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 12963–12968.
- Knapp M. 2019. From a molecules' perspective contributions of ancient DNA research to understanding cave bear biology. *Historical Biology* 31: 442–447.
- Knapp M, Rohland N, Weinstock J, et al. 2009. First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. *Molecular Ecology* **18**: 1225–1238.
- Lari M, Di Vincenzo F, Borsato A, et al. 2015. The Neanderthal in the karst: first dating, morphometric, and paleogenetic data on the fossil skeleton from Altamura (Italy). *Journal of Human Evolution* 82: 88–94.
- Mackiewicz P, Baca M, Popović D, et al. 2017. Estimating the extinction time of two cave bears, *Ursus spelaeus* and *U. ingressus*. *Acta Zoologica Cracoviensia* **60**: 1–14.
- Lewis SG, Maddy D, Buckingham C, et al. 2006. Pleistocene fluvial sediments, palaeontology and archaeology of the upper River Thames at Latton, Wiltshire, England . *Journal of Quaternary Science* 21: 181–205.
- Millard AR, Hedges REM. 1996. A diffusion–adsorption model of uranium uptake by archaeological bone. *Geochimica et Cosmochimica Acta* **60**: 2139–2152.
- Munroe JS, Perzan ZM, Amidon WH. 2016. Cave sediments constrain the latest Pleistocene advance of the Laurentide Ice Sheet in the Champlain Valley, Vermont, USA. *Journal of Quaternary Science* 31: 893–904
- Obert JC, Scholz D, Felis T, et al. 2016. ²³⁰Th/U dating of Last Interglacial brain corals from Bonaire (southern Caribbean) using bulk and theca wall material. *Geochimica et Cosmochimica Acta* **178**: 20–40.
- Oeggl K, Unterfrauner H. 2000. Die Pflanzenreste des Riss/Würm-Interglazials und des Würmglazials von Mondsee. Mitteilungen der Kommision für Quartärforschung der Österreichischen Akademie der Wissenschaften 12: 93–121.
- Pacher M. 2000. Taphonomische Untersuchungen der Höhlenbären-Fundstellen in der Schwabenreith-Höhle bei Lunz am See (Niederösterreich). *Beiträge zur Paläontologie* **25**: 11–85.
- Pacher M, Stuart AJ. 2009. Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). *Boreas* **38**: 189–206.
- Pike AWG, Hedges REM, vanCalsteren P. 2002. U-series dating of bone using the diffusion–adsorption model. *Geochimica et Cosmochimica Acta* 66: 4273–4286.
- Rabeder G, Debeljak I, Hofreiter M, et al. 2008. Morphological responses of cave bears (Ursus spelaeus group) to high-alpine habitats. Höhle **59**: 59–72.
- Rabeder, G, Frischauf, C. 2016. Fossile Bären in Höhlen. In *Höhlen und Karst in Österreich*, Spötl C, Plan L, Christian E (eds). Oberösterreichisches Landesmuseum: Linz; 183–198.
- Rabeder G, Hofreiter M. 2004. Der neue Stammbaum der alpinen Höhlenbären. *Höhle* 55: 58–77.
- Rabeder G, Hofreiter M, Nagel D, et al. 2004. New taxa of alpine cave bears (Ursidae, Carnivora). *Cahiers scientifiques* **2**: 49–67.

- Sambridge M, Grün R, Eggins S. 2012. U-series dating of bone in an open system: the diffusion–adsorption-decay model. *Quaternary Geochronology* **9**: 42–53.
- Rasmussen SO, Bigler M, Blockley S, et al. 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quaternary Science Reviews* **106**: 14–28.
- Slota PJ Jr, Jull AJT, Linick TW, et al. 1987. Preparation of small samples for 14C accelerator targets by catalytic reduction of CO. *Radiocarbon* **29**: 303–306.
- Spötl C, Reimer PJ, Rabeder G, et al. 2014. Presence of cave bears in western Austria before the onset of the Last Glacial Maximum: new radiocarbon dates and palaeoclimatic considerations. *Journal of Quaternary Science* **29**: 760–766.
- Spötl C, Reimer PJ, Rabeder G, *et al.* 2018. Radiocarbon constraints on the age of the world's highest-elevation cave-bear population, Conturines Cave (Dolomites, Northern Italy). *Radiocarbon* **60**: 299–307.

- Stiller M, Molak M, Prost S, et al. 2014. Mitochondrial DNA diversity and evolution of the Pleistocene cave bear complex. *Quaternary International* **339–340**: 224–231.
- Stinnesbeck W, Becker J, Hering F, et al. 2017. The earliest settlers of Mesoamerica date back to the Late Pleistocene. *PLoS One* 12: e0183345.
- Stuiver M, Polach HA. 1977. Reporting of C-14 data discussion. *Radiocarbon* **19**: 355–363.
- Terlato G, Bocherens H, Romandini M, et al. 2019. Chronological and isotopic data support a revision for the timing of cave bear extinction in Mediterranean Europe. *Historical Biology* **31**: 474–484.
- Wolff EW, Chappellaz J, Blunier T, et al. 2010. Millennial-scale variability during the last glacial: the ice core record. *Quaternary Science Reviews* **29**: 2828–2838.
- Yang Q, Scholz D, Jochum KP, *et al.* 2015. Lead isotope variability in speleothems A promising new proxy for hydrological change? First results from a stalagmite from western Germany. *Chemical Geology* **396**: 143–151.