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The cave bear fauna of the cave Schottloch (Dachstein Mountains, Austria)

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Schottloch | *Ursus spelaeus eremus* | Plateaubären | Gebirgsanpassung

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Abstract: The fossil fauna of the Schottloch was excavated and described 140 years ago. A modern analysis of the extensive material has now been carried out for the first time. The taxonomic position of the cave bear remains, the degree of mountain adaptation compared to other high alpine cave faunas and the geological period during which the cave bears used the Schottloch as wintering quarters is the main research objective of this study. It concerns numerous bones and teeth of cave bears, which could be assigned to the cave bear taxon *Ursus spelaeus eremus* Rabeder et al. 2004 on the basis of metrical and morphological criteria. The bears of the Schottloch are similar in size and evolutionary stage to the cave bears described from various other karst plateaus of the Eastern Alps, which are called »plateau bears«. The period during which these bears lived on the Dachstein plateau also corresponds to the temporal distribution of the other »plateau bears«. The feeding possibilities of the herbivorous cave bears on the large plateaus at around 2,000 m a.s.l. are discussed.

Kurzfassung: Die fossile Fauna des Schottlochs wurde vor 140 Jahren ausgegraben und beschrieben. Eine moderne Analyse des umfangreichen Materials ist nun erstmals durchgeführt worden. Die taxonomische Stellung der Höhlenbärenreste, der Grad der Gebirgsanpassung im Vergleich zu anderen hochalpinen Höhlenfaunen und der geologische Zeitraum, in dem die Höhlenbären das Schottloch als Überwinterungsquartier nutzten, ist das Hauptforschungsziel dieser Studie. Es handelt sich um zahlreiche Knochen und Zähne von Höhlenbären, die anhand metrischer und morphologischer Kriterien dem Höhlenbärentaxon *Ursus spelaeus eremus* Rabeder et al. 2004 zugeordnet werden konnten. Die Bären des Schottlochs ähneln in Größe und Evolutionsstufe den Höhlenbären, die aus verschiedenen anderen Karstplateaus der Ostalpen beschrieben wurden und als »Plateaubären« bezeichnet werden. Der Zeitraum, in dem diese Bären auf dem Dachsteinplateau lebten, entspricht auch der zeitlichen Verteilung der anderen »Plateaubären«. Die Ernährungsmöglichkeiten der pflanzenfressenden Höhlenbären auf den großen Hochebenen um 2.000 m.ü.M. werden diskutiert.

Introduction

The Dachstein Mountains are part of the Northern Calcareous Alps in Austria and are partly located in the provinces of Upper Austria, Styria and Salzburg. The highest elevation is the »Hohe Dachstein« (2,995 m), which slopes down to the south with steep walls (»Dachstein-Südwand«). To the north, northwest and east of the Dachstein peak are extensive karst plateaus, which were inhabited by cave bears in the Middle Wurmian period (60,000 to 30,000 years ago). The initially uniform karst plateau is now divided into the eastern plateau »Auf dem Stein« (verbatim: on the stone) and the northwestern plateau »Gosaustein« (verbatim: stone of Gosau). So far, only two bear caves have become known in the Dachstein area, the Schreiberwand cave in the North of the »Hoher Dachstein« at 2,250 m (Rabeder et al., 2019) and the Schottloch in the south-eastern edge of the large plateau »Auf dem Stein« at 1,980 m (**Fig. 1-2**).

Besides the recently described Schreiberwand cave (Rabeder et al., 2019) in the western part of the Dachstein Mountains, the Schottloch is another cave with cave bear remains in this area. Large quantities of cave bear bones only (skull, jaw, single teeth and bones) were recovered here in this small cave (**Fig. 3**) in 1881 and 1882 (Kraus, 1881; Döppes & Rabeder, 1997). Some of the bones exhibit bite marks indicating the presence of wolves (*Canis lupus*).

The cave was already well known to the local population at least in the previous century. The first scientific inspection and description was made by F. Kraus (1881), who engaged the mountain guide K. Fischer and an assistant for two excavation campaigns in 1881 and 1882. This work in the Schottloch was the oldest palaeontological excavation in a high alpine bear cave and revealed well-preserved cave bear remains listed by Kraus (1881). Further collections of cave bear bones were made by J. Schadler (1920) in the course of prospecting the cave for a fertilisation campaign (Ehrenberg, 1962). It was not until 1977 that the cave was surveyed and mapped by members of the Landesverein für Höhlenkunde in Oberösterreich (Upper Austrian Cave Society, s. Döppes & Rabeder, 1997). A preliminary report on the new data from the Schottloch was given at the International Cave Bear Symposium in Golling, Salzburg (Kavcik-Graumann et al., 2022).

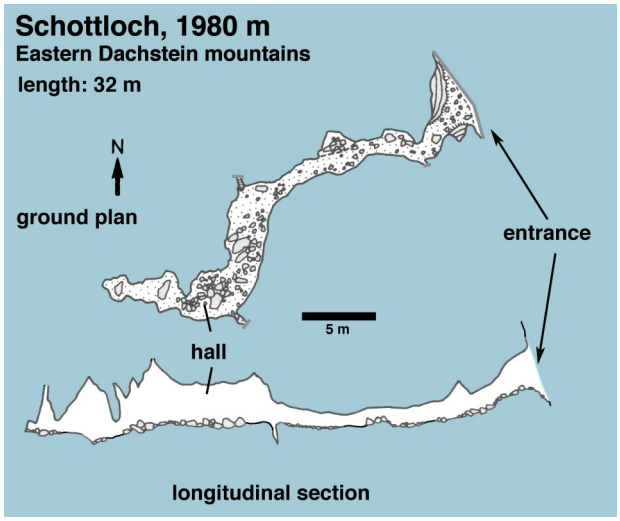

Fig. 1: Ground plan and longitudinal section of the bear cave »Schottloch« at the southern edge of the plateau »Auf dem Stein« after Döppes & Rabeder, 1997: 225. | **Abb. 1**: Grundriss und Längsschnitt der Bärenhöhle »Schottloch« am Südrand des Plateaus »Auf dem Stein« nach Döppes & Rabeder, 1997: 225.

Basics

Community: Haus im Ennstal, Polit. District: Liezen, Styria. Austrian cave register no.: 1544/10. Geographic location: longitude 13°46' E, latitude 47°27'39" N, altitude 1,980 m.

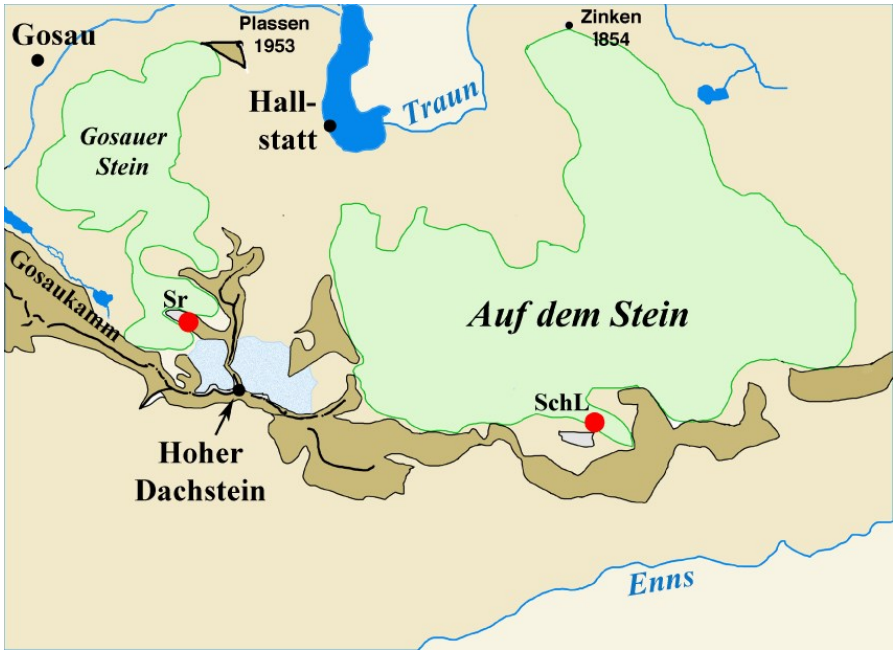

Fig. 2: Geographic location of the karst plateaus »Auf dem Stein« and »Gosauer Stein« in the Dachstein Mountains, with position of the bear caves Schreiberwand cave (Sr) and Schottloch (SchL). Map sketch by G. Rabeder and N. Kavcik-Graumann. | **Abb. 2**: Geographische Lage der Karstplateaus »Auf dem Stein« und »Gosauer Stein« im Dachsteingebirge mit der Lage der Bärenhöhlen Schreiberwandhöhle (Sr) und Schottloch (SchL). Kartenskizze von G. Rabeder und N. Kavcik-Graumann.

Material

The fossil material from the Schottloch kept in the collections of the Natural History Museum in Vienna under the inventory number »NHMW2019/0012«: 3 crania and 14 cranial fragments, 5 mandibles and 12 mandible fragments, 6 sternal and 15 costal fragments, 6 scapula and 17 pelvic fragments, 135 long bones, 35 autopodia, 128 metapodia, 18 phalanges, 10 bacula, 4 patellae. A small amount of bear remains from the Schottloch are in the collections of the Oberösterreichisches Landesmuseum in Linz: 4 fragments of juvenile bones as well as 13 fragments of adult animals (6 vertebral fragments, one fragment each of humerus, radius and femur, 1 metacarpal as well as 3 fragmenta indet.). A total of over 500 determinable bone elements are available. A total of 30 canines, 24 premolars, 94 molars and 128 metapodials were usable for the metrical and morphological recording as well as the statistical evaluation. The number of recovered incisors (7 specimens) is too small for a valid statement.

Methods

The quantities of the individual molars and metapodials are only partially useable for statistical statements, because of the relatively small numbers per tooth category. The total number of completely preserved molars and metapodials allows reliable information about the average dimensions of the extremities and teeth. The taxonomic affiliation can be concluded from the proportions of the dentition and metapodial values (LDH index, **Fig. 4**). Another taxonomic criterion is the evolution level of the premolars and molars (p4/4 index, m2 inf. enthypoconid, Rabeder et al., 2008). Because only four P4 sup. are preserved in the material, only the morphological index of the p4 inf. (p4 inf. index) is used here. For the chronological determination of the bear remains, 20 bone samples were taken and sent to the Curt-Engelhorn-Centre Archaeometry (CEZA) in Mannheim (Germany). The radiocarbon dating was performed by AMS (Accelerator Mass Spectrometer) on collagen extracted from bone material (Kromer et al., 2013).

Results

Metric of canines, sex index

The canines show a relatively large sex dimorphism index (sdi = male values / female values x 100) i.e. that the metric mean values of the male and the female individuals diverge relatively strongly (**Tab. 1**). In the scatter plot (**Fig. 3**), the separation of larger (male) and smaller (female) specimens is very clear.

Metric of cheek teeth and metapodia

The cheek teeth from the Schottloch are on average about 8 % smaller than the corresponding teeth of the standard fauna of *Ursus ingressus* from the Gamssulzen cave (see **Tab. 2**, Rabeder, 1995; 1999), but the metapodials are only about 5 % shorter than in the corresponding bones from the Gamssulzen cave (see **Tab. 3**, Withalm, 2001).

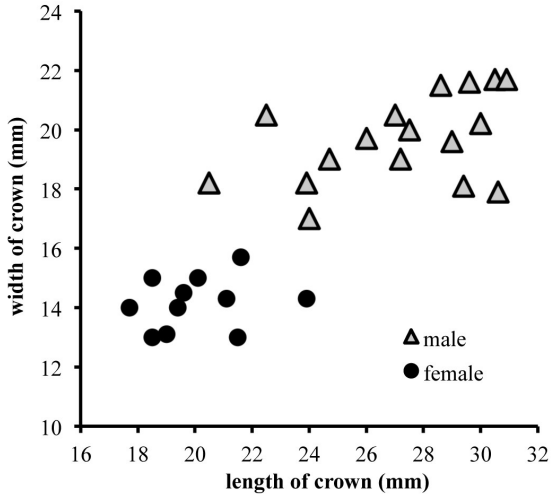

Fig. 3: Scatter plot of length and width values of cave bear canine crowns from the Schottloch (Dachstein Mountains). | **Abb. 3**: Streudiagramm der Längen- und Breitenwerte von Höhlenbären-Eckzähnen aus dem Schottloch (Dachsteingebirge).

Canini	crown length	crown width	number	length stand.	with stand.
female	20.55	14.35	13	97.27	93.40
male	26.90	19.53	17	101.70	99.49
total	24.15	17.28	30	101.05	104.79
sexdimorphism index	130.88	136.13		104.55	106.52
sex index			43.33		

Tab. 1: Mean values of the length and width measurements of the canine tooth crowns of the cave bears from the Schottloch (Dachstein Mountains). | **Tab. 1**: Mittelwerte der Längen- und Breitenmaße der Eckzähne der Höhlenbären aus dem Schottloch (Dachsteingebirge).

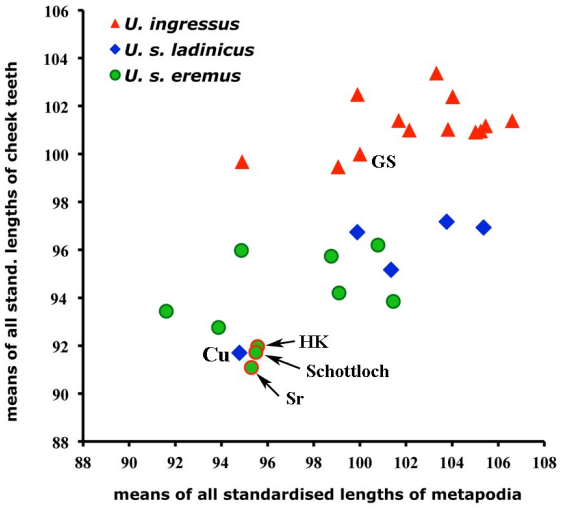

Fig. 4: LDH diagram of cave bear faunas of the Alpine Late Pleistocene. Abbr.: Cu = Conturines cave (Rabeder, 1991), GS = Gamssulzen cave (standard fauna, Rabeder, 1995; 1999), HK = Hennenkopf cave (Döppes et al., 2023), Sr = Schreiberwand cave (Rabeder et al., 2019). | **Abb. 4**: LDH-Diagramm der Höhlenbärenfaunen des alpinen Spätpleistozäns. Abkürzungen: Cu = Conturines-Höhle (Rabeder, 1991), GS = Gamssulzenhöhle (Standardfauna, Rabeder, 1995; 1999), HK = Hennenkopfhöhle (Döppes et al., 2023), Sr = Schreiberwandhöhle (Rabeder et al., 2019).

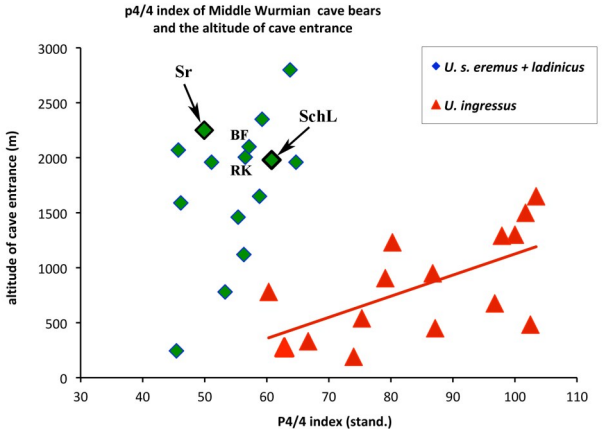

Fig. 5: Morphological index of the fourth premolars (p4/4 index) of alpine cave bear faunas in correlation to the altitude of the cave entrances. Abbreviations: BF = Bärenfalle, RK = Ramesch-Knochenhöhle, SchL = Schottloch, Sr = Schreiberwandhöhle. | **Abb. 5**: Morphologischer Index der vierten Prämolaren (p4/4-Index) alpiner Höhlenbärenfaunen in Korrelation mit der Höhenlage der Höhleneingänge. Abkürzungen: BF = Bärenfalle, RK = Ramesch-Knochenhöhle, SchL = Schottloch, Sr = Schreiberwandhöhle.

LHD-diagram

»In the LHD-diagram (locomotion vs. dietary habits diagram), the average length of the metapodials (as a measure of locomotion) and the average length of the molars (as a measure of the chewing ability) are related« (Kavcik-Graumann et al., 2016). The Late Pleistocene cave bears of the Alps are classified into two distinct clusters according to the relation of metapodial length to molar length. The faunas with *Ursus ingressus* have relatively longer molars and are clearly distinguished from the faunas with *Ursus spelaeus* by this characteristic. The subspecies *U. spelaeus eremus* and *U. spelaeus ladinicus* cannot be distinguished by this feature (**Fig. 4**).

The pair of values of the Schottloch fauna lies in the cluster of *Ursus spelaeus* and very close to the points of the Schreiberwand cave (Dachstein Mountains) and the Hennenkopf cave (Steinernes Meer), but also to the Conturines cave (Dolomites). The cave bears of the four cave faunas mentioned have the smallest dimensions and correspond to the expression »high alpine small form« coined by K. Ehrenberg (1962). The relatively small dimensions are interpreted as an adaptation to life in the high mountains (Rabeder et al., 2008).

Morphology of premolars

The number of usable premolars is relatively small (**Tab. 4**), so that the significance is not high. The low frequency of highly developed types (e.g. C2, D2 or E2 in the p4 inf. as well as D, E or F in the P4 sup. speak for a relatively low evolutionary level. The p4/4 index calculated from the valence and frequency of the morphotypes (Rabeder, 1999; Frischauf & Rabeder, 2021, Frischauf et al., 2022) suggests that the bears from the Schottloch belong to the taxon *Ursus spelaeus eremus* (**Fig. 5**). From the distribution of the points in the two clusters, a positive correlation with the altitude of the cave entrances is evident: more clearly in *U. ingressus* than in *U. spelaeus*.

Element		length	width	md index
p4 inf.	mean	14.15	9.59	148.44
	standardised	92.83	92.97	74.89
	n	18	18	17
P4 sup.	mean	17.38	12.75	40.00
	standardised	86.36	89.73	15.64
	n	6	6	5
P4/4 index	value *			52.46
	n			22
m1 inf.	mean	28.06	12.60	
	standardised	92.9	86.9	
	n	15	14	
M1 sup.	mean	27.19	18.50	
	standardised	94.63	93.67	
	n	22	22	
m2 inf.	mean	27.44	16.52	211.11
	standardised	89.6	90.5	113.93
	n	18	17	9
M2 sup.	mean	42.10	21.50	338.46
	standardised	94.82	95.32	90.26
	n	22	22	13
m3 inf.	mean	23.49	17.02	
	standardised	85.23	89.05	
	n	17	17	
all cheek- teeth	mean *	91.63	91.72	
	n	118	116	
all molars	mean *	91.72	91.60	
	n	94	92	

Tab. 2: Metric (in mm) and morphodynamic indices of cheek teeth of *Ursus s. eremus* from the Schottloch. Abbr.: md index = morphodynamic index, mean* = weighted mean, value* = weighted geometric mean. | **Tab. 2**: Metrische (in mm) und morphodynamische Indizes der Backenzähne von *Ursus s. eremus* aus dem Schottloch. Abkürzungen: md index = morphodynamischer Index, Mittelwert* = gewichteter Mittelwert, Wert* = gewichtetes geometrisches Mittel.

Element	n	length	dew	PI	length stand.	dew stand.	PI stand.
Mc1	12	59.38	17.78	29.93	93.50	92.10	98.49
Mc2	19	70.80	22.52	31.74	96.07	89.00	92.47
Mc3	12	75.04	23.78	31.68	94.04	89.72	95.38
Mc4	15	79.40	26.32	33.17	94.98	94.00	99.04
Mc5	15	78.13	27.67	35.40	94.70	94.75	100.01
mt1	6	52.42	16.38	31.25	98.71	92.56	93.76
mt2	4	64.98	19.85	30.63	96.55	93.19	96.76
mt3	15	75.58	21.02	27.82	97.78	89.83	91.89
mt4	17	79.95	21.78	27.24	94.84	88.91	93.74
mt5	13	82.01	23.05	28.12	95.69	94.45	98.75
means of all*	128				95.49	91.55	95.89

Tab. 3: Measurements (in mm) and plumpness index of metapodia of *Ursus s. eremus* from the Schottloch. Abbr.: dew = distal epiphyseal width, Mc = metacarpale, mt = metatarsale, PI = plumpness index (= dew / length x 100), all* = the means are weighted. | **Tab. 3**: Maße (in mm) und Plumpheitsindex der Metapodien von *Ursus s. eremus* aus dem Schottloch. Abkürzungen: dew = distale Epiphysenbreite, Mc = Metakarpale, mt = Metatarsale, PI = Plumpheitsindex (= Tau / Länge x 100), alle* = die Mittelwerte sind gewichtet.

Morphotypes	A	A/B	A/D	B1/C1	B2	C1	C1/C2	C2	C3	D1	D1/2	D2	n
P4 sup.	2	2	1	–	–	–	–	–	–	–	–	–	5
p4 inf.	–	–	–	1	1	6	3	1	1	1	1	1	16

Morphotypes	B1/C1	B2	C1	C1/C2	C2	C3	D1	D1/2	D2	n
p4 inf.	1	1	6	3	1	1	1	1	1	16

Morphotypes	A	A/B	A/D	n
P4 sup.	2	2	1	5

Tab. 4: Frequency of morphotypes of premolars of *Ursus s. eremus* from the Schottloch (Dachstein Mountains). | **Tab. 4**: Häufigkeit der Morphotypen der Prämolaren von *Ursus s. eremus* aus dem Schottloch.

Chronology of Schottloch bears

Although the cave bear remains from the Schottloch had already been in the depot of the Natural History Museum for over 140 years, the collagen content of the bones (on average >7 %) and its quality (C:N ratios between 3.2 and 3.3 indicting well preserved collagen) is astonishingly high, so that nine ^{14}C dates could be obtained ranging from 46,000 to 35,000 years BP (before present). Calibrated, this results in a time span of about 50,000 to 37,000 years BP, while a sample suggests an age beyond the dating limit of more than 50,000 years (**Tab. 5**).

Discussion

The »Plateau Bears« have the following common features:

1. Geographic location of the bear caves: The caves are located on the karst plateaus or at the edge of the plateaus at altitudes between 1,600 m and 2,300 m (Withalm et al., 2022) and were not only visited for hibernation but also used in summer, as indicated by the numerous fossil remains of juvenile bears.
2. Taxonomic classification: The cave bears of these plateau belong to the *Ursus spelaeus* group, mostly to the subspecies *U. spelaeus eremus*. Only from two caves in the Tote Gebirge (Brieglersberg and Brettstein caves) the subspecies *Ursus s. ladinicus* has also been recorded.
3. Dimensions: All mean values of the length and width dimensions of teeth and limb bones are clearly smaller than those of the cave bears from the lower caves. K. Ehrenberg (1962) therefore called the small bears of the high altitudes the »hochalpine Kleinform des Höhlenbären« (= high alpine small form of the cave bear), the large bears of the lower altitudes the were called »normal form«, e.g. the bears from the Gamssulzen cave (1,300 m), which was later selected as the type fauna of *Ursus ingressus* (Rabeder et al., 2004, Hofreiter et al., 2004). The reduction in dimensions was interpreted as an adaptation to life in the high mountains (shorter summers = shorter feeding time, Rabeder et al., 2008).
4. Morphology of the teeth: The evolution of the dentition can be seen by the so-called p4/4 index, which is calculated from the number and shape of the additional occlusal elements of the fourth premolars. In all alpine cave faunas, the value of the p4/4 index is positively correlated with the altitude of the cave entrances: in plateau bears (*U. spelaeus* faunas) the rate of increase per altitudinal level is low, but in *U. ingressus* faunas it is very pronounced (Rabeder et al., 2008). This phenomenon can also be explained by mountain adaptation.

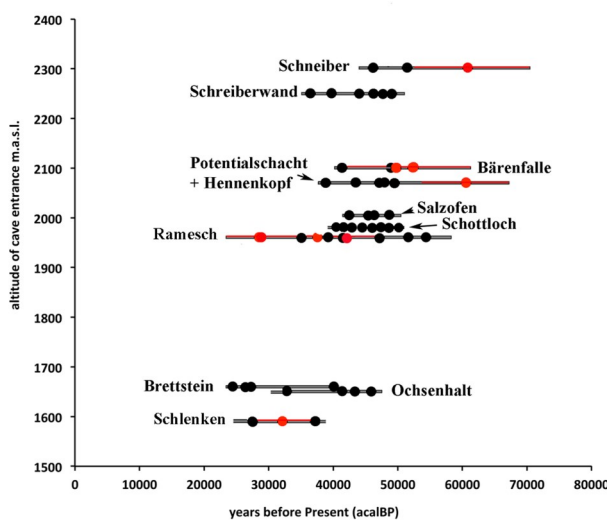

Fig. 6: Chronological data of cave bear remains (»plateau bears«, *Ursus spelaeus*) from the large bear caves of the Northern Calcareous Alps in relation to the altitude of the caves. Key to symbols: red dots and lines denote the mean values and error limits of molecular dating, black dots and lines denote the mean values and error limits (2σ _calBP) of radiocarbon dating by the AMS method. Data after Döppes et al., 2018; 2023; Frischauf et al., 2022; Kavcik-Graumann et al., 2022, Rabeder et al., 2019; Withalm et al., 2022 and this volume (Tab. 5). | **Abb. 6**: Chronologische Daten von Höhlenbärenresten (»Plateaubären«, *Ursus spelaeus*) aus den großen Bärenhöhlen der Nördlichen Kalkalpen in Abhängigkeit von der Höhenlage der Höhlen. Symbole: Rote Punkte und Linien bezeichnen die Mittelwerte und Fehlergrenzen der molekularen Datierung, schwarze Punkte und Linien bezeichnen die Mittelwerte und Fehlergrenzen (2σ _calBP) der Radiokohlenstoffdatierung nach der AMS-Methode. Daten nach Döppes et al., 2018; 2023; Frischauf et al., 2022; Kavcik-Graumann et al., 2022, Rabeder et al., 2019; Withalm et al., 2022 und dieser Artikel (Tab. 5).

5. Chronological range: ^{14}C dates of the bear remains from the Schottloch cover a period of 37,000 to 50,000 years and beyond (**Tab. 5**) and thus lie within the time range of the other »plateau bear« ages determined so far (**Fig. 6**). The period during which the »plateau bears« inhabited the karst plateaus of the Northern Calcareous Alps corresponds to almost the entire Middle Wurmian, also called the »Alpine Cave Bear Era« (Döppes et al., 2018). This era started 60,000 years ago and ended about 24,000 years ago.

The vegetation on the karst plateaus in the alpine cave bear period

Today, the karst plateaus of the Northern Calcareous Alps are largely free of vegetation or covered by a sparse alpine vegeta-

MAMS	sample name	bone element	^{14}C age	error ±	δ^{13}C	2σ calBP	2σ calBP mean	error ±	C:N	C (%)	collagene (%)
43830	SchL-9	femur	34,905	262	-20.5	40,656-39,497	40,081	301	3.3	32.3	3.6
55697	SchL-13	pelvis	36,500	230	-22.8	41,899-41,117	41,495	204	3.3	38.1	7.7
55694	SchL-8	ulna	39,360	310	-24.0	43,119-42,475	42,794	173	3.3	31.3	8.3
43831	SchL-15	pelvis	42,740	650	-23.0	46,555-44,414	45,372	545	3.2	22.3	2.5
55695	SchL-12	radius juv.	41,720	400	-20.8	45,291-43,963	44,577	316	3.2	39.6	7.6
43829	SchL-2	radius	44,760	398	-19.1	48,051-46,096	47,081	522	3.2	28.4	5.5
55693	SchL-1	tibia	45,210	580	-21.5	48,803-46,134	47,539	685	3.2	42.6	12.7
55692	SchL-11	ulna juv.	46,150	670	-25.3	50,506-46,859	48,683	942	3.2	45.1	11.8
55701	SchL-7	ulna	> 54,000	–	–	–	> 49,000	–	3.2	38.1	8.0

Tab. 5: Radiocarbon data of cave bear bones of *Ursus s. eremus* from the Schottloch calibrated in Oxcal. | **Tab. 5**: Radiokarbondaten von Höhlenbärenknochen von *Ursus s. eremus* aus dem Schottloch, nach Oxcal kalibriert.

Fig. 7: The karst plateau »Auf dem Stein« in the eastern Dachstein Mountains, view from the Gjaidalm to SE, is today overgrown with elements of the subalpine and alpine vegetation stages. The red arrow marks the location of the bear cave Schottloch. | **Abb. 7**: Das Karstplateau »Auf dem Stein« im östlichen Dachsteingebirge mit Blick von der Gjaidalm nach Südosten, auf dem heute Pflanzen der subalpinen und alpinen Vegetationsstufe wachsen. Der rote Pfeil markiert die Lage der Höhle Schottloch.

tion that would not meet the demands of large herbivores such as cave bears. The higher parts of the plateaus (above 2,000 m) belong to the alpine or nival vegetation zone: they are free of trees and covered with dwarf shrubs and cushion plants or are completely free of vegetation. The lower areas (around 1,600 to 2,000 m) belong to the subalpine vegetation stage, which are characterized by coniferous forests: larches, spruces and scots pines, sometimes also stone pines, as well as dwarf shrub heaths form sparse forests with a species-rich herbaceous flora and grasses; deciduous trees are absent. For all three vegetation stages it is true that today there would be far too little food available for the cave bears, because the leaf food (foliage) is not available. This would only be the case in the next lower zone, the montane vegetation zone. The upper limit of the montane zone, called »beech limit«, lies today at an altitude of 1,200 to 1,400 m, as about 800 m lower than the cave entrance of the Schottloch, from which it can be concluded that the summer temperatures during the cave bear period were about 5-6 °C higher than today.

Conclusion

The cave bear data points from the Schottloch lie within the clusters of alpine *Ursus spelaeus* faunas in both the LDH-diagram (**Fig. 4**) and the P4/4 index diagram (**Fig. 5**). A clear assignment to *U. spelaeus eremus* or *U. s. ladinicus* is morphologically not possible, because the decisive index of the m2 inf. (enthypoconid index) could not be calculated due to the small number of m2 inf. The extensive agreement in the P4/4 index with the faunas from Ramesch-Knochenhöhle and Bärenfalle (**Fig. 5**) speaks for the affiliation to *Ursus spelaeus eremus*, because DNA analyses are available from both faunas, which revealed *U. s. eremus*.

Taxonomy, chronology and diet of the so called »plateau bears«

On all large karst plateaus of the Northern Calcareous Alps there are caves where fossil remains of cave bear have been found. From the numerous chronometric, morphological and genetic data, it is clear that these bears inhabited these plateaus during the same geological period, the Alpine »Middle Wurmian« (ca. 65 to 30 ka BP) and can all be assigned to the same cave-bear taxon *Ursus spelaeus eremus* or the closely related *Ursus spelaeus ladinicus*, while all remains of *Ursus ingressus* originate from lower situated caves (**Fig. 4-5**). The cave bears that inhabited these karst plateaus in the Late Pleistocene were called »plateau bears« (Withalm et al., 2022) and the bears of the Schottloch are among them. The two taxa *U. ingressus* and *U. s. eremus* inhabited the Alps at about the same time. From the stable isotope values (^{13}C and ^{15}N), the abrasion pattern of the teeth and the 3D-morphology of the jaws, it can be concluded that the

diet of these cave bears was almost exclusively herbivorous. From the low ^{13}C values and the 3D geometry of the mandible (van Heteren et al., 2016), it could even be assumed that the diet of the cave bears consisted mainly of herbs and leaves of deciduous trees. »It can be concluded that the deciduous forest border (beech fir border) was at least 1,000 m higher in the »Alpine Cave Bear Era« than today. The average summer temperature was probably 6-8 °C higher than today« (Döppes et al., 2023).

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