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The fossil bear remains from the Hennenkopf Cave (Steinernes Meer, province Salzburg, Austria)

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Abstract: The Hennenkopf Cave (Äußere Hennenkopfhöhle, 2,073 m a.s.l.) is located on a karst plateau named Steinernes Meer (Salzburg, Austria) which lacks a noteworthy vegetation above 1,800 m in the present time. The fossil material of the excavation from 1986 to 1991 – which is kept at the Natural History Museum in Vienna – mainly consists of isolated teeth and small bones that can be assigned to a small-sized cave bear. The chaotic stratification of the cave bear remains indicates that the cave bear remains were transported from an overlying cave section that has now disappeared. The morphological analyses of the molars show an assignment to *Ursus spelaeus eremus* Rabeder et al., 2004. Newly analysed ^{14}C dates now show that cave bears of the species *U. s. eremus* inhabited the Hennenkopf Cave in the same period as the other high-Alpine bear caves in the immediate vicinity, but also on other karst plateaus of the Northern Calcareous Alps (Nördliche Kalkalpen). Due to the extreme location of the cave in an environment that is today almost free of vegetation, these finds are impressive witnesses of a once very warm climate that allowed a lush vegetation cover at altitudes around 2,000 m above sea level.

Kurzfassung: Die Äußere Hennenkopfhöhle (2.073 m ü.d.M.) liegt auf dem Karstplateau Steinernes Meer (Salzburg, Österreich), das oberhalb von 1.800 m keine nennenswerte Vegetation mehr aufweist. Das fossile Material aus den Grabungen von 1986 bis 1991, das im Naturhistorischen Museum in Wien aufbewahrt wird, besteht hauptsächlich aus einzelnen Zähnen und kleinen Knochen, die einem kleinwüchsigen Höhlenbären zugeordnet werden können. Die chaotische Ablagerung der Fossilien deutet darauf hin, dass die Höhlenbärenreste aus einem darüber liegenden Höhlenabschnitt, der heute verschwunden ist, stammen und hierher transportiert worden sind. Die morphologischen Analysen der Backenzähne zeigen eine Zuordnung zu *Ursus spelaeus eremus* Rabeder et al., 2004. Neue ^{14}C-Daten zeigen nun, dass die Hennenkopfhöhle im gleichen Zeitraum von Bären der Art *Ursus s. eremus* bewohnt war wie die hochalpinen Bärenhöhlen auf den anderen Karstplateaus der Nördlichen Kalkalpen. Aufgrund der extremen Lage der Höhle in einer Umgebung, die heute fast frei von Vegetation ist, sind diese Funde eindrucksvolle Zeugen eines einst sehr warmen Klimas, das eine üppige Vegetationsdecke in Höhen um 2.000 m ü.d.M. ermöglicht hat.

Introduction

The Hennenkopf Cave (Äußere Hennenkopfhöhle, symbol: HK) is located in the Steinernes Meer, a karstic high plateau some 8 km NE of the town of Saalfelden (Salzburg, Austria) at an altitude of 2,073 m a.s.l. (**Fig. 1-2**). The cave lies close to the Austrian-German border, only two kilometres away from the cave bear sites at Schneiber Caves on Bavarian territory (Stockhammer, 2020). The Hennenkopf Cave has several entrances, which are located northeast of the mountain peak Schindelköpfe (2,356 m) in the western part of the plateau.

The main entrance (entrance 1, **Fig. 3**) opens into a rocky valley of the karst plateau adjacent to the marked path but is rather difficult to locate visually. From the wide, northeast-facing main entrance, the cave descends a few meters to the southwest into the spacious cavern »Czoernighalle« (Czoernig Hall). From its bottom, a passage turns to the south. After some 20 m, the cave becomes very narrow due to the build-up of a snow cone, from large amounts of snow precipitating into the cave through a daylight shaft (entrance 4, **Fig. 4**).

Passing the snow cone, the passage leads to an icy corridor descending steeply down to the west, named »Eisrutsche« (Ice Slide). This passage leads to the main part of the cave consisting of numerous large, lower-lying cave chambers and galleries. To reach the fossil bone site, however, the Ice Slide has to be crossed toward the south and after a narrow stretch and a short climb over a rock step one gets into the »Bärengang« (Bear Gallery). Here numerous remains of cave bears on a secondary deposit in a small shaft and in a low gallery were recovered (Cech et al., 1997; Oßwald, 2001).

Basics

Community: Saalfelden, Polit. District: Zell am See, Salzburg, Austrian cave register no.: 1331/4. Geographic location: Longitude 12°53'32.037, latitude 47°29'44.625, altitude 2,073 m.

Background

Speleological research history

Walter Freiherr von Czoernig-Czernhausen discovered the Hennenkopf Cave in 1942. He reached a spacious hall, the so-called »Czoernighalle« (**Fig. 4**). Klappacher and Knapczyk (1977) gave a first description of the cave. Günther Göttlinger and Christof Gropp (HFG Nuremberg) rediscovered the cave on August 13, 1984 and identified it as Hennenkopf Cave by a sign left by Czoernig-Czernhausen with his name and the corresponding year. A sand siphon was excavated and in the following years, several large parts of the main corridors were discovered. The cave bear remains were found on the surface of the sediment in a side passage near the entrance. When only a few narrow canyons remained unexplored in 1995, the research trips to the Hennenkopf Cave were concluded. The total surveyed length of the cave is 3,976 m with a height difference of 177 m (Oßwald, 2001).

Scientific excavations

In 1984, during the rediscovery of the cave a passage, which held fragments of animal bones and teeth on the surface of the sediment, was explored close to the main entrance. Since the narrow gallery (Bear Gallery) was almost entirely blocked by ice, its fossil findings can be considered untouched by human activity. Samples submitted to the University of Erlangen were identified as teeth of cave or brown bears. In 1985, the Karst and Cave Department of the Natural History Museum Vienna finally identified the remnants as fossil cave bear remains.

After a reconnaissance tour to the cave in June 1986 Karl Mais from the Karst and Cave Department started an excavation campaign in the Bear Gallery in September 1986 (**Fig. 5**).

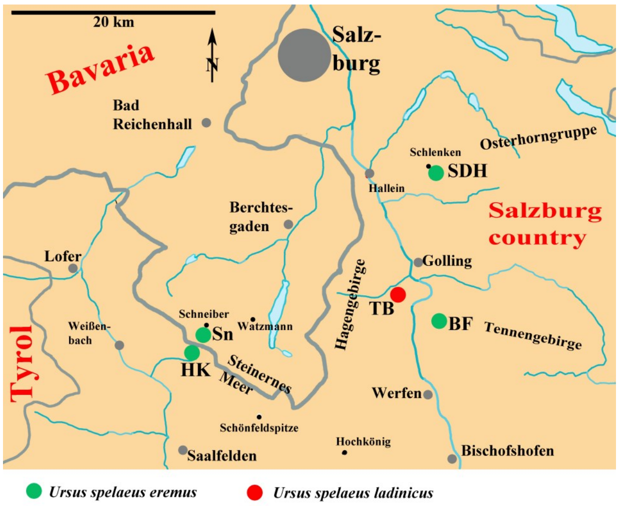

Fig. 1: Geographic location of the Hennenkopf Cave (HK) and the Schneiber Caves (Sn) on the karst plateau »Steinernes Meer« (after Stockhammer, 2020). Abbr.: SDH = Schlenken-Durchgangshöhle, TB = Torrener Cave, BF = Bärenfalle. | **Abb. 1:** Geographische Lage der Hennenkopfhöhle (HK) und der Schneiber Höhlen (Sn) am Karstplateau »Steinernes Meer« (nach Stockhammer, 2020). Abkürzungen: SDH = Schlenken-Durchgangshöhle, TB = Torrener Bärenhöhle, BF = Bärenfalle.

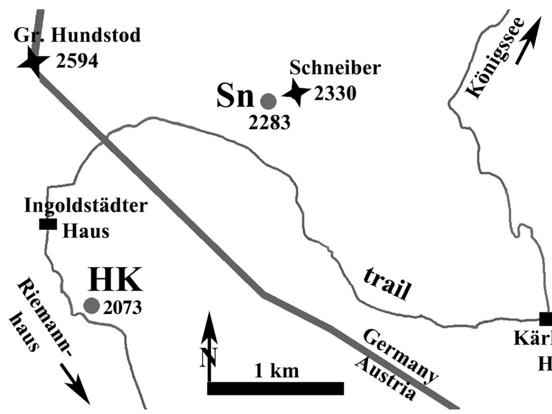

Fig. 2: The Hennenkopf Cave (HK) and Schneiber Caves (Sn) at the Austrian-German border on the karst plateau »Steinernes Meer« (after Stockhammer, 2020). | **Abb. 2**: Hennenkopfhöhle (HK) und Schneiber Höhlen (Sn) an der österreichisch-deutschen Grenze am Karstplateau »Steinernes Meer« (nach Stockhammer, 2020).

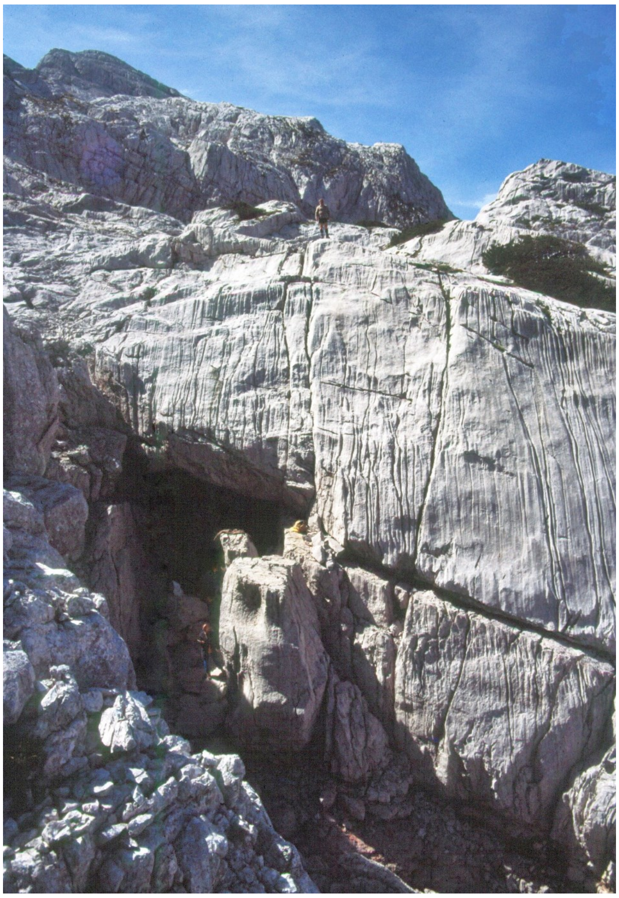

Fig. 3: The main entrance of the Hennenkopf Cave in summer 1989 (photo: R. Pavuza). | **Abb. 3:** Haupteingang der Hennenkopfhöhle im Sommer 1989 (Foto: R. Pavuza).

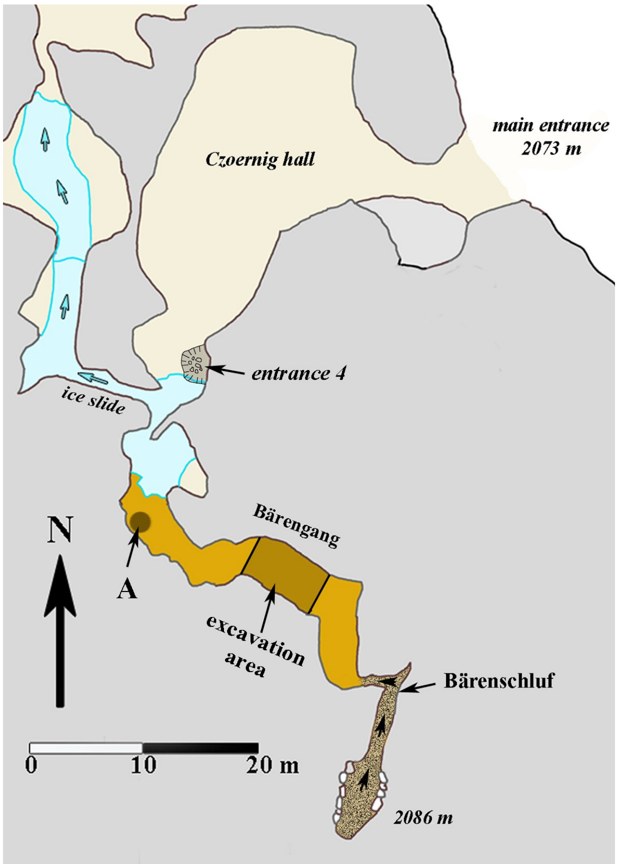

Fig. 4: Schematic sketch of the entrance area of the Hennenkopf Cave with the two excavation areas »A« and quadrant field »E12« to »I18« (see Fig. 7, according to the cave map of the speleologists group HFG Nuremberg 1984), graphic: G. Rabeder. | **Abb. 4:** Skizze des Eingangsbereichs der Hennenkopfhöhle mit den beiden Grabungsbereichen »A« und dem Quadrantenfeld »E12« bis »I18« (siehe Abb. 7, nach dem Höhlenplan der HFG Nürnberg 1984), Grafik: G. Rabeder.

Fig. 5: Quadrants F/G 12/13 in the Hennenkopf Cave during the excavation in 1989 (photo: K. Mais). | **Abb. 5:** Quadranten F/G 12/13 in der Hennenkopfhöhle während der Grabung 1989 (Foto: K. Mais).

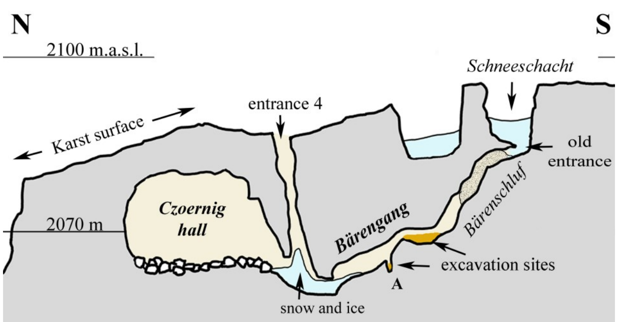

Fig. 6: Schematic longitudinal section of the entrance area of the Hennenkopf Cave, adapted from a sketch by K. Mais from 1990, graphic: G. Rabeder. | **Abb. 6:** Schematischer Längsschnitt des Eingangsbereichs der Hennenkopfhöhle nach einer Skizze von K. Mais von 1990, Grafik: G. Rabeder.

year	1986	1987	1988	1989	1990	1991
date	11.-22.09.	12.-17.09	30.08.-05.09.	04.-09.09	21.-26.08.	02.-08.09.
participants	K. Mais, R. Pavuza, P. Cech, R. Illmann, G. Oßwald, W. Pröstler, J. and H. Götz, C. Gropp	K. Mais, R. Pavuza, P. Cech, R. Illmann	K. Mais, R. Pavuza, P. Cech	K. Mais, R. Pavuza, F. Hujer	K. Mais, R. Pavuza, P. Cech	K. Mais, R. Pavuza, P. Cech
excavated squares	A1-A3, F12, G12, G13, H12, H13	F12 cont., F13-F14, G13-G15	F14 cont., G15 cont., F15, F17, G16-G18, H17	F13 cont., G18	outdoor research program	E13-E15, F14 cont., F15 cont., F17 cont., F16, F18

Tab. 1: Dates of excavation campaigns, participants and excavated sections in the »Bärengang« of the Hennenkopf Cave, 1986-1991. | **Tab. 1:** Daten der Grabungskampagnen, Teilnehmer und ausgegrabenen Abschnitte im »Bärengang« der Hennenkopfhöhle, 1986-1991.

He was assisted by R. Pavuza and P. Cech and by cavers from the caving club HFG Nuremberg. Excavation dates, excavated sections and participants are summarised in **Tab. 1**.

Subsequent excavations were carried out annually in campaigns of approximately one week each during August/September. In 1990, following an extraordinary cold and snowy winter, the cave entrance was difficult to reach and the snow cone of the shaft entrance 4 entirely blocked the access to the excavation site. Work was restricted to outdoor investigations, like measurements of actual denudation rates of Karren and rock surfaces (Pavuza & Oberender, 2013) which are of significance for the interpretation of the development of this part of the cave.

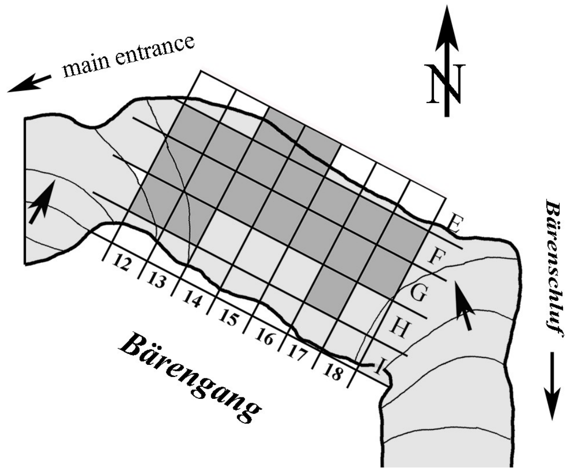

Fig. 7: Excavation map of the site »Bärengang« (Bear Gallery) in the Hennenkopf Cave based on a drawing by K. Mais 1986. | **Abb. 7:** Grabungsplan der Fundstelle »Bärengang« in der Hennenkopfhöhle nach einer Zeichnung von K. Mais 1986.

Excavation sites and work

In September 1986, the Bear Gallery was sectioned into a grid of quadrants (A to H) starting with site »A« above a small shaft at cave survey point 14 ahead of the northern end of the Bear Gallery and continuing in the Bear Gallery with quadrants H12 to E18, adjacent to cave survey point 16 (**Fig. 4, 7**). Site A was separated from the quadrants E-H by a short steep passage, which gives access to the upper part of the Bear Gallery. The remains of cave bears – both bones and teeth – occurred mainly on the surface and in the uppermost layer of the sedimentary sequence. This sometimes detritus-rich cave loam appeared loosened due to frost weathering and overlies plates of a fragmented sinter layer. The loamy sequence between and below the broken sinter was free of fossil remains in most sections.

At its south-western end the Bear Gallery ascends southwards, turns to east and back to south and proceeds into a collapsed vertical shaft ascending to the surface. The shaft was blocked by frozen sediment, ice and snow, therefore impassable during the excavation campaigns.

Working conditions during the excavations were exhausting as the height of Bear Gallery barely exceeds 1.5 m, thus standing upright was impossible (**Fig. 5**). The temperature ranged from 0° to 1°C. Space to move and to place material was scarce. After excavating the small shaft of site A (A1-A3; **Fig. 6**) in 1986 the shaft was filled with the excavated sediment of the sections E1-H18. Prior to the actual excavation of each section, surface findings were collected separately.

Not all quadrants bore fossils, or could be excavated, as they were covered by rock or ice (E11-12, E16-18, H14-16, H18). Each quadrant was further divided into subsectors 1-4.

Vertical collecting units were mostly 10 cm each. On site A (A1-A3) the reference line was 50 cm above surface, on site E-H the surface was not quite horizontal with a range from -50 cm (G12, F12, F13) to -70 cm (E14) or more (-72 cm G17) below the reference line. The thickness of the fossil-bearing sediment varied considerably due to speleothem- and rock embeddings in the sediment. Several quadrants such as F14 were partly covered by sinter plates, with fossil findings solely on the surface, whereas sediment and bones in neighbouring quadrants (such as G14) extended to -90 cm and even -110 cm below the reference line between broken parts of a basal sinter layer. Overall, the fossil bearing sediment covered an area of approximately 6 m length, 3 m width and 60 cm thickness at a maximum. Fossil finds concentrated in quadrants F-H/13-15 from the surface down to 80 cm below the reference line.

Considering the location within the cave system and the chaotic stratification of the cave bear remnants and the sedimentology of the sequence, it was evident from the beginning that the fossil site represents a secondary deposit.

Preparation and first investigations (until 1997)

Due to the low temperatures and the frequent out-freezing of the sediment, the fossils were in a bad state of preservation. Most of the bones were fragmented. After the excavation campaigns all material underwent conservation using wood glue (polyvinyl-acetate) according to the state of the art at that time (**Fig. 4, 6, 7**). However, the bone sample from G13/3 (from a depth of -65 cm) designated for ^{14}C dating remained untreated.

For a first presentation of results (Cech & Pavuza, 1994), all identifiable material was classified, counted and measured at the Karst and Cave Department of the Natural History Museum

Vienna. The cave bear bones proved to be mainly non-adult material. Most abundant were teeth, metapodials and phalanges. For a more detailed summary of results see Cech et al. (1997).

The collagen from a bone from quadrant G13/3 was ^{14}C dated (Centrum vor Isotopen Onderzoek, Univ. Groningen, Lab. Nr. GrN-22361) and yielded an ^{14}C age of 50,200 ± 7,200/2,700 years, or > 43,900 years respectively, using another criterion (provided by the Lab). Calibration (using OxCal) finally yielded an age older than 49 ka. An attempt of dating one of the basal sinter layer blocks with U/Th (by CERAK, Faculté Polytechnique de Mons, Belgium) failed due to the abundance of alien ^{230}Th. This points most probably to a subsequent temporal flooding of this cave passage. Thus, we can assume that at least the basal sinter layers had been flooded at least once within the last 50 ka. It might be significant in this context that the secondary deposit of the Hennenkopf Cave lacks – contrary to the nearby Paradies Cave – younger bear remnants up to 24 ka. The destruction of the now vanished primary bear cave may have been a major single geomorphologic event. The current limestone removal rate in the area above the cave – measured by corrosion/erosion -rates in Karren as well as estimated with the help of hydrogeochemical modelling – does not allow the removal of more than about 10 cm rock per 10 ka (Pavuza & Oberender, 2013) in the comparatively flat surface area above the Bear Gallery.

Grain size distribution of sedimentary samples from quadrant G16/2 was also investigated (**Tab. 2**). Underneath a comparatively coarse top layer, where the fraction < 0.063 mm was removed most probably by out-freezing, a section dominated by fine grained sediments – with many bones in clearly secondary deposition – finally lead to a basal sequence with significantly enhanced coarse grained sediments lacking bones. This sequence overlies broken sinter layers, also infiltrating the cracks of this layer.

Material and methods

The fossil material mainly consists of fragments of juvenile cave bears. Determinable elements of adult bears are primarily isolated teeth and metapodials (**Tab. 3**). The best-preserved finding is a left mandible with all molars and the canine (**Tab. 4-5, Fig. 8**). In addition to the bear remains, undeterminable bat remains and a vole residue were found (Cech et al., 1997). The teeth and metapodials, some of which are available in statistically significant quantities, are used for the taxonomic assignment of the bear remains. For this purpose, the metric and morphological values were collected. For comparison with other cave bear fauna, the metric values and morphodynamic indices have been standardized. The mean values of *Ursus ingressus* from the Gamssulzen Cave serve as standards (Rabeder, 1995, 1999; Rabeder et al., 2019). Diagrams are used to check whether the fossil association of the Hennenkopf Cave originates from one or more taxa of the genus *Ursus*.

Fig. 8: Lateral view of the left cave bear mandible from the Hennenkopf Cave (inventory number NHM 2013/0309/0001, photo: J. Stockhammer). | **Abb. 8**: Seitliche Ansicht des linken Unterkiefers eines Höhlenbären aus der Hennenkopfhöhle (Inventarnummer 2013/0309/0001, Foto: J. Stockhammer).

grain size in mm / depth	> 6.3	6.3-2.0	2.0-0.63	0.63-0.2	0.2-0.063	< 0.063
surface	9	19	21	14	11	26
2-10 cm	3	3	2	2	5	85
10-20 cm	4	3	2	1	5	85
20-30 cm	3	1	1	2	4	89
30-40 cm	16	3	2	1	5	73

Tab. 2: Grain size distribution of the sedimentary sequence from quadrant G16/2 in the Hennenkopf Cave. | **Tab. 2:** Korngrößenverteilung der Sedimentabfolge aus dem Quadranten G16/2 in der Hennenkopfhöhle.

Description of ursid remains

Metric of mandible

The only well-preserved mandible (**Fig. 8**) from the Hennenkopf Cave is relatively small and is from a female (**see Tab. 4-5**). In the scatter diagram, the dimensions of the m1 inf. of this mandible lies in the cluster of the females (**Fig. 9**). Belonging to *U. arctos* can be excluded because alveoli of the anterior premolars are missing and the p4 inf. belongs to the morphotype C1 (with metaconid and paraconid).

teeth	I1,2 sup.	I3 sup.	i1 inf.	i2 inf.	i3 inf.	canini	P4 sup.	p4 inf.	M1 sup.	M2 sup.	m1 inf.	m2 inf.	m3 inf.	sum.
number	109	44	38	55	50	13	23	44	11	11	32	30	22	482

metapods	Mc1	Mc2	Mc3	Mc4	Mc5	mt1	mt2	mt3	mt4	mt5	sum
number	9	7	5	10	6	7	11	13	6	9	83

Tab: 3: Numbers of adult teeth and metapods from *Ursus* sp. from the Hennenkopf Cave. | **Tab. 3:** Anzahl der adulten Zähne und Metapodien von *Ursus* sp. aus der Hennenkopfhöhle.

element	inv. nr.	side	condylar length	coronoid height	tooth row C – m3 inf.	tooth row p4 – m3 inf.	tooth row m1 – m3 inf.
mandible	NHM 2013/0309/0001	sin.	253.6	115.5	151.7	84.5	70.5

Tab. 4: Measurements of mandible of *Ursus* sp. from the Hennenkopf Cave (after Stockhammer, 2020). | **Tab. 4:** Maße des Unterkiefers von *Ursus* sp. aus der Hennenkopfhöhle (nach Stockhammer, 2020).

Metric and morphology of incisors

The preservation of the fossil incisors varies, the quantity of the i1 inf. (28) is much smaller than that of the i2 inf. (42), which suggests that one or more relocations of the cave sediment have occurred. Overall, the incisors of the Hennenkopf Cave are about 7% smaller than the incisors of the standard fauna from the Gamssulzen Cave (**Tab. 6**). The dimensions of the I3 sup. are relatively small. The low length and width values with around 87% and 86% of the Gamssulzen level are not due to the small number of pieces (**see Fig. 10**). The scatter diagram shows a balanced distribution with a balanced sex index (see chapter »metric of canines, sex index«).

Metric of canines, sex index

The number of measurable canines is only 13, with eight female and only five male canines (**Tab. 7**). This small number does not allow conclusions about the sex index (= number of females / number total * 100) or the sex dimorphism index (SDI = mean value the lengths of male pieces divided by the mean value of the female pieces times 100) see Stockhammer (2020). Other teeth show a predominance of male (I3 sup., **Fig. 10**) or female specimens (m1 inf., **Fig. 9**)

Metric and morphology of cheek teeth

The standardized means of length and width also vary in the molars, which can be attributed to the small quantities of some teeth (**Tab. 8**). The morphodynamic indices of the premolars (P4 sup. index, p4 inf. index and P4/4 index) and the m2 inf. (enthypoconid index) are affirmed by sufficient quantities of specimens (**Tab. 8**). This is not the case for the metaloph index of the M2 sup. with a number of only ten teeth.

Metric of metapodials

The length and the distal width of the epiphyses of the low number of measurable matapodials were determined and the plumpness index was calculated (Withalm, 2001). The bear metapodials of the Hennenkopf Cave are on average 4% shorter but about 3% slimmer than the standard fauna of *U. ingressus* from the Gamssulzen Cave (**Tab. 9**). The thickening of the metapodials of the first ray is noticeable: the metacarpal 1 is on average almost 6% plumper, the metatarsal 1 is only around 1% slimmer than that of the Gamssulzen fauna! Unfortunately, the significance of this data is low due to the small number of measurable metapodials and does not allow any further conclusions.

Grinding marks on the incisors

Abrasion marks appear on almost all teeth and are signs of detrition from chewing on plants. The size of the grinding marks increases during ontogenetic age. Nevertheless, there is also a

inv. nr.	element	length	width	morphotype
mandible NHM 2013/0309/0001	p4 inf.	12.8	8.4	C1
	m1 inf.	26.7	12.2	worn
	m2 inf.	26.4	15.9	worn
	m3 inf.	22.9	16	worn

Tab. 5: Measurements of teeth of ursid mandible from the Hennenkopf Cave. | **Tab. 5:** Maße der Zähne des Unterkiefers von *Ursus* sp. aus der Hennenkopfhöhle.

Element		length	width	md index
i1 inf.	mean	6.02	7.9	133.33
	stand.	91.74	82.5	165.32
	n	28	28	12
I1,2 sup.	mean	9.3	10.23	104.12
	stand.	93.18	97.04	51.92
	n	108	109	97
i2 inf.	mean	9.24	9.5	100
	stand.	96.41	87.52	100
	n	42	42	23
i3 inf.	mean	12.68	10.79	246.43
	stand.	96.03	86.65	96.04
	n	34	34	28
I3 sup.	mean	16.33	12.65	26.32
	stand.	87.21	85.7	26.32
	n	25	24	19
all incisivi	mean	93.36	91	
	n	237	237	

Tab. 6: Weighted mean values of the dimensions and morphodynamic indices of the incisors of *Ursus* sp. from the Hennenkopf Cave (measurements according to Stockhammer, 2020). Abbr.: md index = morphodynamic index, n = number, stand. = standardized. | **Tab. 6:** Mittelwerte der Dimensionen und morphodynamische Indices der Schneidezähne von *Ursus* sp. aus der Hennenkopfhöhle (Maße nach Stockhammer, 2020). Abkürzungen: md index = morphodynamischer Index, n = Anzahl, stand. = standardisiert.

Hennenkopf	Canini	I3 sup.	m1 inf.	sum/mean
male	5	12	14	31
female	8	11	17	36
total	13	23	31	67
sex index	61.54	47.83	54.84	53.73

Tab. 7: Number of female and male specimens in three different tooth categories of *Ursus* sp. from Hennenkopf Cave. | **Tab. 7:** Anzahl der weiblichen und männlichen *Ursus* sp. bei drei verschiedenen Zahnkategorien aus der Hennenkopfhöhle.

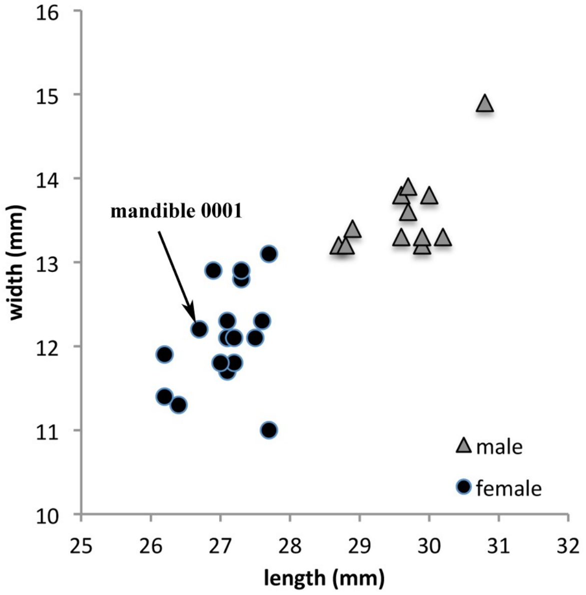

Fig. 9: Scatter diagram of length and width of m1 inf. of *Ursus* sp. from the Hennenkopf Cave. Note the position of the m1 inf. of the only preserved mandible (0001). | **Abb. 9:** Streudiagramm der Länge und Breite des m1 inf. von *Ursus* sp. aus der Hennenkopfhöhle. Man beachte die Position des m1 inf. des einzigen erhaltenen Unterkiefers (0001).

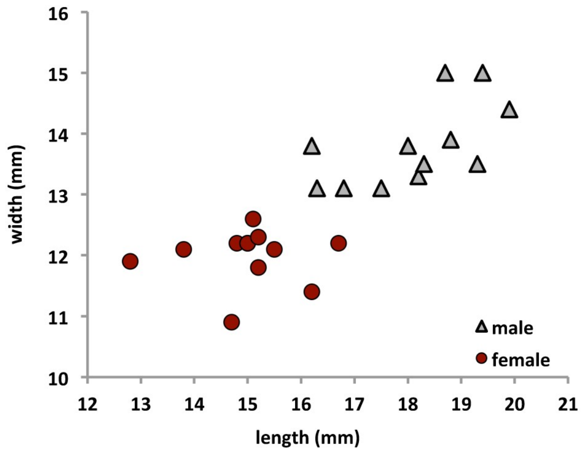

Fig. 10: Scatter diagram of length and width of the 3rd maxillary incisors (I3 sup.) of *Ursus* sp. from the Hennenkopf Cave. | **Abb. 10:** Streudiagramm der Länge und der Breite der 3. Oberkiefer-Schneidezähne (I3 sup.) von *Ursus* sp. der Hennenkopfhöhle.

negative correlation between the number of the grinding marks and the altitude of the sites: the higher the cave, the less the abrasion on the teeth (Holland, 2013). Cut marks on the front teeth can be clearly noticeable. On canines, they are described as »Kiskevély blades« and on the incisors as »wedge-shaped defects« (Frischauf et al., 2016; Stockhammer, 2020). The relative frequency of the cut marks also correlates with the altitude. It is suspected that the proportion of grasses that constitutes the cave bear's diet causes this phenomenon. Grass formed the most common plant food because the desertification (Nagel et al., 2018) in the lower pre-Alpine areas was much higher than in the more precipitation-rich areas of the high mountains.

Results

Systematic Palaeontology

The morphodynamic values of the incisivi (Rabeder, 1999) are very different to each other, which may be due to the partly small quantities (e.g. i1 inf.: only 12 pieces and a standardized value of more than 165 %). The morphodynamic index of I1,2 appears to be statistically verified: the value of 97 copies is only 52 % of the Gamssulzen level (see chapter Discussion). In the material of the Hennenkopf Cave only 3 specimens from 189 adult incisors (one i1 inf., one i3 inf. and one I1,2) show the so-called »wedge-shaped defects«, which is a percentage of only 1.59 %. The location of the data point of the Hennenkopf Cave corresponds to its altitude in the diagram (**Fig. 11**).

The numerical predominance of measurable canines of the female remains can also be confirmed by the much more common m1 inf. (**Fig. 9**), while the scatter diagram of the I3 sup. (**Fig. 10**) suggests male dominance – but only by a small num-

Element		length	width	md index
p4 inf.	mean	13.81	9.52	117.44
	stand.	90.63	92.23	59.25
	n	44	44	43
P4 sup.	mean	18.53	12.55	79.55
	stand	92.08	88.33	35.33
	n	23	23	22
P4/4-Index	value	-	-	96.66
	stand.	-	-	45.75
m1 inf.	mean	28.18	12.72	-
	stand.	93.3	87.7	-
	n	32	31	-
M1 sup.	mean	25.56	17.29	-
	stand.	88.95	87.53	-
	n	11	8	-
m2 inf.	mean	28.68	17.11	151.79
	stand.	93.62	93.75	81.91
	n	30	30	28
M2 sup.	mean	41.66	21.29	190.91
	stand.	93.83	94.86	151.18
	n	10	11	10
m3 inf.	mean	25.7	17.9	-
	stand.	90.96	93.67	-
	n	22	22	-
all cheek teeth	mean	91.96	91.27	-
	n	172	167	-
all molars	mean	92.5	91.53	-
	n	105	102	-

Tab. 8: Weighted Mean values of the dimensions and morphodynamic indices of cheek teeth of *Ursus* sp. from the Hennenkopf Cave (measurements according to Stockhammer, 2020). Abbr.: md index = morphodynamic index, n = number, stand. = standardized. | **Tab. 8:** Mittelwerte der Dimensionen und morphodynamische Indices der Backenzähne von *Ursus* sp. aus der Hennenkopfhöhle (Maße nach Stockhammer, 2020). Abkürzungen: md index = morphodynamischer Index, n = Anzahl, stand. = standardisiert.

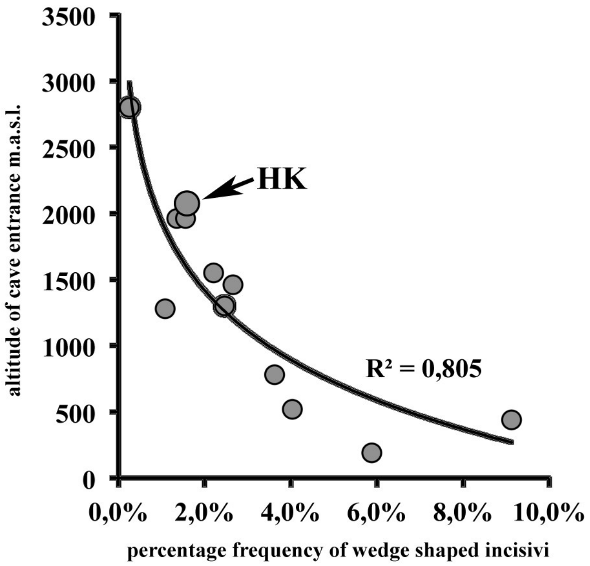

Fig. 11: Correlation between the percentage frequency of incisors with wedge-shaped defects and the altitude of cave entrance (according to FRISCHAUF et al., 2016). Abbr.: HK = Hennenkopf Cave, R2 = determination coefficient. | **Abb. 11:** Korrelation zwischen der prozentualen Häufigkeit von Schneidezähnen mit keilförmigen Defekten und der Höhe des Höhleneingangs (nach FRISCHAUF et al., 2016). Abkürzungen: HK = Hennenkopfhöhle, R2 = Bestimmungskoeffizient.

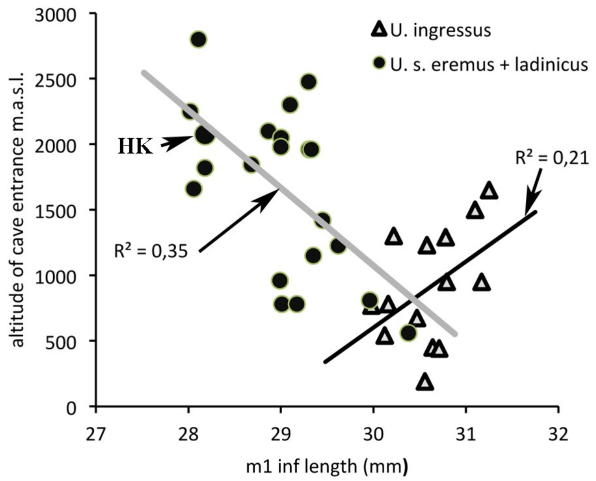

Fig. 12: The mean values of the m1 inf. lengths of Alpine and some non-Alpine cave bear faunas in correlation with the altitude of the sites. The data point of the Hennenkopf Cave (HK) is in the common cluster of faunas with *Ursus s. eremus* and *U. s. ladinicus*. | **Abb. 12:** Die Mittelwerte der m1 inf.-Längen von alpinen und einigen außeralpinen Höhlenbärenfaunen in Korrelation mit der Höhenlage der Fundstellen. Der Datenpunkt der Hennenkopfhöhle (HK) liegt im gemeinsamen Cluster der Faunen mit *Ursus s. eremus* und *U. s. ladinicus*.

Element	n	length	dew	PI	length stand.	dew stand.	PI stand.
Mc1	9	61.84	19.87	32.12	97.39	102.94	105.66
Mc2	7	73.09	23.99	32.85	99.17	94.81	95.76
Mc3	6	75.83	24.23	31.98	95.03	91.45	96.34
Mc4	10	79.38	25.02	31.51	94.95	89.36	94.09
Mc5	6	78.03	26.03	33.37	94.59	89.16	94.28
mt1	7	51.39	17.01	33.09	96.77	96.13	99.27
mt2	11	64.26	19.52	30.36	95.49	91.63	95.92
mt3	13	72.82	21.08	28.97	94.2	90.07	95.7
mt4	6	80.35	21.45	26.7	95.31	87.55	91.87
mt5	9	80.5	22.17	27.55	93.93	91	96.75
total*	84				95.57	92.4	96.69

Tab. 9: Mean values of lengths, widths and plumpness index of metapodials of *Ursus* sp. from the Hennenkopf Cave (according to STOCKHAMMER, 2020). Abbr.: dew = distal epiphyseal width, Mc = metacarpale, mt = metatarsale, PI = plumpness index (= dew / length * 100), stand. = standardized, total* = all metapods, means weighted. | **Tab. 9:** Mittelwerte von Längen, Breiten und Plumpheitsindex der Metapodien von *Ursus* sp. aus der Hennenkopfhöhle (nach STOCKHAMMER, 2020). Abkürzungen: dew = distale Epiphysenbreite, Mc = metacarpale, mt = metatarsale, PI = Plumpheitsindex, stand. = standardisiert, total* = Mittelwert aller Metapodien.

ber. The average of the three distributions gives a value that is just over 50 %, indicating a balanced gender ratio. The mean length of cheek teeth vary between 89 and 94 %. The weighted means of all categories are similar to the values of the incisivi, around 93 % for the lengths and 92 % for the widths of the teeth. The values of the morphodynamic indices of the premolars (P4 sup. index, p4 inf. index and P4/4 index) and the m2 inf. (enthypoconid index) are far below the level of *Ursus ingressus* from the standard fauna of Gamssulzen Cave (RABEDER, 1999). Comparisons with other cave bear fauna are discussed later. The teeth of the cave bears from the Hennenkopf Cave are approx. 7 % smaller than those of the standard fauna and therefore can be assigned to the so-called »high Alpine small form« (EHRENBERG & SICKENBERG, 1929).

(Geo)Chronology

Until recently there was no AMS age of the bear remains of the Hennenkopf Cave, besides a radiocarbon date »older than 49,000« years BP. From the Schneiber Caves, just two kilometres away (Paradise Cave and Schneiber Cave; **see Fig. 2**) several ^{14}C data are available which show ^{14}C ages between around 24,000 and > 49,000 years BP (**Tab. 10**). After calibrating this data using OxCal 4.4. (RAMSEY, 1995) with the IntCal20 dataset (REIMER et al., 2020), the period in which the cave bears inhabited the karst plateau of the »Steinernes Meer« was found to be around 28,000 to more than 49,000 years before today (STOCKHAMMER, 2020). New ^{14}C data from bone samples also show similar information for the Hennenkopf Cave (**Tab. 10**). Further ^{14}C analyses are in progress.

Discussion

It has been known for a long time that the metric but also the morphological values of Alpine cave bear associations are height-dependent (RABEDER et al., 2008). While their metric mean values can be negatively correlated with the altitude of the sites (e.g. in the *Ursus s. eremus* group), the morphological indices are usually positively correlated. In the following diagrams the position of the Hennenkopf fauna in comparison to the other Alpine but also extra-Alpine fauna is discussed (**Fig. 12-17**).

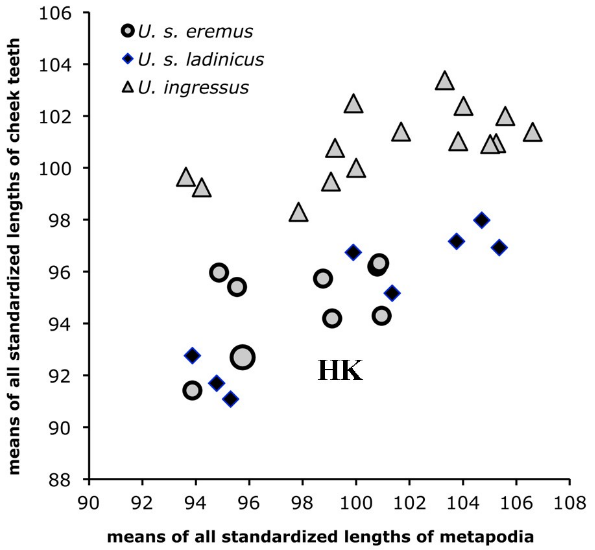

Fig. 13: LDH diagram of Alpine and non-Alpine cave bear fauna. The data point of the Hennenkopf fauna (HK) is in the common cluster of *Ursus spelaeus eremus* and *U. s. ladinicus*. | **Abb. 13:** LDH-Diagramm von alpinen and außeralpinen Höhlenbärenfaunen. Der Datenpunkt der Hennenkopf Fauna (HK) liegt im gemeinsamen Cluster von *Ursus spelaeus eremus* und *U. s. ladinicus*.

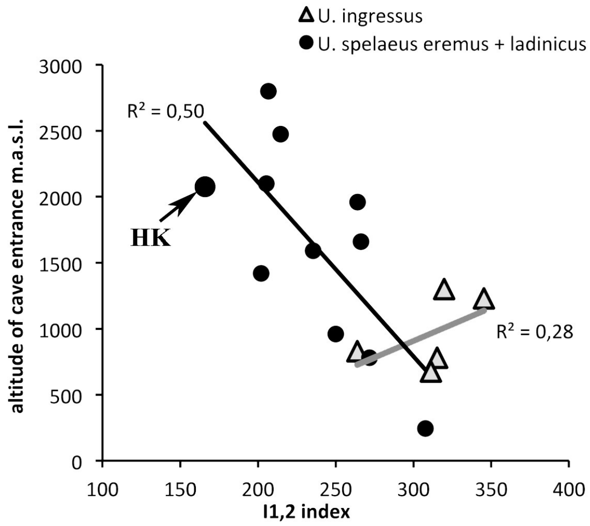

Fig. 14: Correlation of the values of the I1,2 index of Alpine and some non-Alpine cave bear faunas with the altitude of the sites. The data point of the Hennenkopf Cave (HK) is in the cluster of *Ursus spelaeus* faunas. Abbr.: R2 = determination coefficient. | **Abb. 14:** Korrelation der Werte des I1,2 Index von alpinen und einigen außeralpinen Höhlenbärenfaunen mit der Höhenlage der Fundstellen. Der Datenpunkt der Hennenkopfhöhle (HK) liegt im Cluster der *Ursus spelaeus*-Faunen. Abkürzungen: R2 = Bestimmungskoeffizient.

»Gebirgsnanismus« (mountain nanism)

K. Ehrenberg was the first to recognize that the cave bears from high Alpine sites (Schreiberwand Cave) had much smaller dimensions than the ones from lower-lying caves e.g. Drachenhöhle (Dragon Cave) near Mixnitz (Ehrenberg & Sickenberg, 1929). These relatively small cave bears were called »high Alpine small forms«. The reduction in dimensions (also called mountain nanism) by almost 10 % is interpreted as an adaptation to mountain life with shorter summers and shorter feeding phases (Rabeder & Frischauf, 2016; Rabeder et al., 2008, 2019). The reduction in the faunas of *Ursus spelaeus eremus* and *U. s. ladinicus* is negatively correlated with the height of the cave entrances, while in faunas with *Ursus ingressus* a positive correlation can be seen (**Fig. 12**). The dimensions of the bears of the Hennenkopf Cave follow the trend of cave faunas with remains of *U. spelaeus eremus* and *U. s. ladinicus*. The example of the tooth length of the m1 inf. (**Fig. 12**) shows that the data point of the Hennenkopf Cave agrees well with the cluster of *Ursus spelaeus*.

LDH diagram

In the LDH diagram (**Fig. 13**, »Locomotion versus Dietary Habits diagram«) the average length of the metapodials as a measure of locomotion and the average length of molars is related to the chewing performance (Kavcik-Graumann et al., 2016; Rabeder et al., 2019). The standardized mean values are used for better comparability. The values of *Ursus ingressus* from the Gamssulzen Cave served as the standard (Laughlan et al., 2020; Rabeder, 1995; Withalm, 2001). In this diagram, the fauna of the Hennenkopf Cave lies in the cluster of *Ursus spelaeus eremus* and *Ursus spelaeus ladinicus*, while the point cloud of *Ursus ingressus* clearly stands out due to the longer molars.

I1,2 index

The evolution of the cave bear dentition (Rabeder, 1999) also affects the incisivi. The changes in the 1st and 2nd maxillary incisors (I1,2 sup.) are most evident: Starting from the original morphotype »d«, which is typical for *Ursus deningeri*, the lingual cingulum is completely rebuilt and up to four accessory cusps are developed (morphotypes p, r and s). These changes are evaluated numerically in the I1,2 overall index (= »Gesamtindex« see Rabeder, 1999). A comparison of the Alpine fauna and some non-Alpine faunas shows that this index is correlated with the altitude of the caves – a negative correlation for the fauna of the *Ursus spelaeus* group, but positive for the fauna with *Ursus ingressus* (**Fig. 14**). The fauna of the Hennenkopf Cave has thereby the lowest value of all Alpine faunas.

Morphodynamic indices of premolars

The evolutionary trends in the cave bear dentition are most clearly shown in the 4th premolars. The changes from the most primitive morphotype A to the most developed morphotype G (P4 sup.) or F3 (p4 inf.) are noticeable (Rabeder, 1999; Nagel & Rabeder, 1992). The index values of the Hennenkopf bears are relatively low (**Fig. 15**). The bears also fit in the common cluster of *U. s. eremus* and *U. s. ladinicus*, while *U. ingressus* can be excluded. The correlation between index and altitude is positive for all three taxa. The index increases in faunas with *U. ingressus* much faster than in the other two.

Enthypoconid index of m2 inf.

The enthypoconid is a single or multi-cusped structure on the occlusal surfaces of the 1st and 2nd mandibular molars. It forms

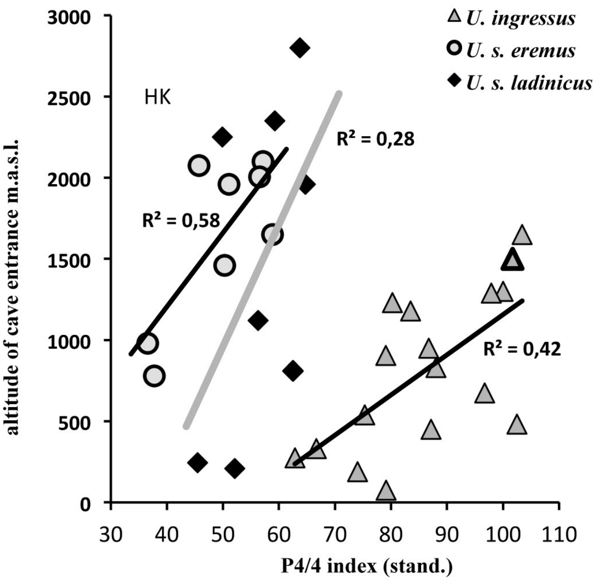

Fig. 15: Correlation of the values of the P4/4 index of Alpine and some non-Alpine cave bear fauna with the altitude of the sites. The data point of the Hennenkopf Cave (HK) is in the cluster of *Ursus spelaeus* faunas. Abbr.: R2 = determination coefficient. | **Abb. 15:** Korrelation der Werte des P4/4 Index von alpinen und einigen außeralpinen Höhlenbärenfaunen mit der Höhenlage der Fundstellen. Der Datenpunkt der Hennenkopfhöhle (HK) liegt im Cluster der *Ursus spelaeus*-Faunen. Abkürzungen: R2 = Bestimmungskoeffizient.

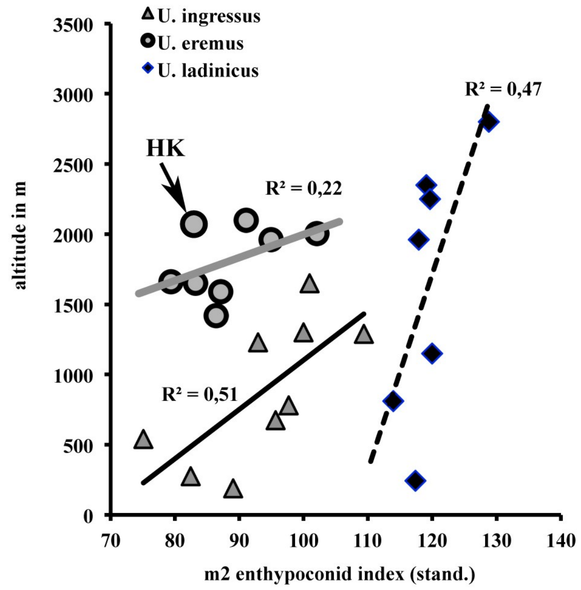

Fig. 16: Correlation of the values of the m2 enthypoconid index of Alpine and some non-Alpine cave bear fauna with the altitude of the sites. The data point of the Hennenkopf Cave (HK) is in the cluster of *Ursus s. eremus* faunas. Abbr.: HK = Hennenkopf Cave, R2 = determination coefficient. | **Abb. 16:** Korrelation der Werte des m2 Enthypoconid-Index von alpinen und einigen außeralpinen Höhlenbärenfaunen mit der Höhenlage der Fundstellen. Der Datenpunkt der Hennenkopfhöhle (HK) liegt im Cluster der *Ursus s. eremus*-Faunen.

lingually (within) the hypoconid as an opponent to the paracon of the M2 sup. The enthypoconid of m2 inf. is the most important characteristic for distinguishing *Ursus s. ladinicus* and *U. s. eremus*. Several DNA analyses (Conturines Cave, Brieglersberg Cave, Ajdovska Cave, Merveilleuse Cave) suggest that the m2 enthypoconid index is a taxonomically usable criterion (Frischauf et al., 2010; Rabeder et al., 2004, 2005, 2011; Rabeder & Hofreiter, 2004). The data point of the Hennenkopf fauna lies in the cluster of *Ursus s. eremus* (**Fig. 16**).

Cave bear paleodiet

Originally, it was thought that cave bears were carnivorous due to their imposing canines. As early as 1912 O. Abel concluded from the large chewing surfaces of the molars that cave bears were herbivorous and that they used their large canines not for the acquisition of food, but as a threat and rutting weapon (Döppes et al., 2018; Frischauf et al., 2016). More recently, the herbivore character of the cave bears could be much better specified by the following methods:

— The values of the ^{13}C and ^{15}N content of the cave bear bones (Bocherens et al., 2011; Horacek et al., 2013) as proxy for diet.
— The molar chewing rates (Holland, 2013)
— Microwear features (Münzel et al., 2014)
— From the frequency of the grinding figures on the incisors and canines (Frischauf et al., 2016; Fig. 17).
— From the »3D geometry« of the mandible compared to other Ursids (van Heteren et al., 2016).

All methods conclude that cave bears were highly adapted herbivores, mainly feeding on leaves of deciduous trees and herbs (Bocherens, 2019).

Conclusions

After preliminary studies of the cave bear remnants (Cech & Pavuza, 1994; Cech et al., 1997), the entire cave bear material found in the Hennenkopf Cave during the 1986 to 1991 excavations could be analysed completely. The site turned out to be an important addition to the larger history of the cave bear population in the Alpine region.

Cave bears inhabited the karst plateau of the »Steinernes Meer« in the time from over 50,000 to at least 28,000 years before today. According to the morphology of their teeth, they belong to the taxon *Ursus spelaeus eremus* Rabeder, Hofreiter, Nagel & Withalm, 2004. Because most of this plateau lies above 2,000 m a.s.l. and is today almost free of vegetation, the cave bear remains are important climatic witnesses to the warm period of the so-called Middle Wurmian. The location of the cave can be assigned to the »Alpine« respectively the »nivale« level. Such an extreme environment that is today poor in vegetation gives rise to the question how the cave bears fed on karst plateaus above 2,000 m above sea level. Cave bears were, as discussed above, pure herbivores, mainly feeding from herbs and leaves (»foliage«) of deciduous trees.

Since those species grow in much lower locations (montane to subalpine vegetation level) today, it can be concluded that the deciduous forest boundary (beech fir border) was at least 1,000 m higher in the Alpine cave bear era than today. The average summer temperature was probably up to 6-8 °C higher than today, marking a stark shift in climate conditions (see Kavcik-Graumann et al., 2023).

name	sample name	labor nr.	method	element	^{14}C age	error +	error -	Ref.	2σ calBP	C:N	C (%)	collagene (%)
Hennenkopf	HK-G13/3	GrN-22361	conv.	bone	50,200	7,200	2,700	(1)	> 49,000	–	–	–
	HK-607	MAMS-43821	AMS	phb	48,430	1,280	1,280	(4)	> 49,000	3.3	30.8	4.2
	HK-622	MAMS-43822	AMS	phb1	> 49,000	–	–	(4)	> 49,000	3.2	30.4	6.4
	HK-606	MAMS- 43823	AMS	ulna dist.	> 49,000	–	–	(4)	> 49, 000	3.2	28	3.1
	HK-612	MAMS- 43824	AMS	rad. dist.	44,460	800	800	(4)	49,565-46,098	3.2	24.7	2.1
Schneiber	Sn-1	MAMS-17798	AMS	costa f.	no collagen			(4)	–	–	–	–
	Sn-3	VERA-4418	AMS	Mc5	42,400	1,400	1,200	(2)	49,203-43,622	–	–	–
Paradies	Sn-2	VERA-4417	AMS	mt2	47,100	2,600	1,900	(2)	49,658	–	–	–
	Sn-4	Ua-16529	AMS	hum	26,850	500	500	(5)	31,842-29,810	–	–	–
	Sn-4	VERA-4629	AMS	hum	24,120	150	150	(3)	28,536-27,817	–	–	–
	Sn-4 UF1	VERA-4629	AMS-UF1	hum	29,631	300	290	(3)	34,257-33,182	–	–	–
	Sn-4 UF2	VERA-4629	AMS-UF1	hum	32,720	400	380	(3)	38,141-35,877	–	–	–

Tab. 10: Radiocarbon data of cave bear remains from the Hennenkopf Cave and from the neighbouring Schneiber Cave system (Schneiber Cave and Paradise Cave). Abbr.: dist. = distal, HK = Hennenkopf Cave, hum = humerus, PH = Paradise Cave, phb = phalanx basalis, rad = radius, ref. = references, Sn = Schneiber Cave. References: (1) Cech et al., 1997, (2) Döppes et al., 2011, (3) Stockhammer, 2020, (4) new, (5) Pacher et al., 2007. | **Tab. 10:** Radiokarbondaten von Höhlenbärenresten aus der Hennenkopfhöhle und aus dem benachbarten Schneiber-Höhlensystem (Schneiberhöhle und Paradieshöhle). Abkürzungen: dist. = distal, HK = Hennenkopfhöhle, hum = Humerus, PH = Paradieshöhle, phb = Phalanx basalis, rad = Radius, ref. = Literatur, Sn = Schneiberhöhle. Literatur: (1) Cech et al., 1997, (2) Döppes et al., 2011, (3) Stockhammer, 2020, (4) new, (5) Pacher et al., 2007.

The restricted age range of the cave bears of the Hennenkopf Cave compared with the closely located Schneiber Caves as well as the sedimentological situation indicates that the remnants of the cave bears were transported from an overlying, now vanished part of the cave.

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