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Correlation between the degree of dental abrasion, ontogenetic age and nutrition of Alpine cave bears (DARA method)

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1. Preface

When Prof. Dr. Gernot Rabeder and Mag. Christine Frischauf created the concept of wear stages of cave bear teeth for the museum “Ursus ladinicus” in St. Kassian (Italy, South Tyrol) in 2010-2011, they noticed that the tooth material of the Ladinic bear had an unexpected degree of abrasion. They had a look at 80 complete and measurable teeth from which only very few showed a low extent of abrasion, whereas teeth with a very high stage of abrasion have not been seen at all. Rabeder and Frischauf first suggested that the cave bears from Conturines cave probably died at young age. Therefore they planned to find out the ontogenetic age of every tooth and this consideration led to the here present study.

2. Introduction

The cave bear species presented in this study have the same ancestor: Ursavus lived about 20 million years ago. In the phylogenetic tree of bears, evolution takes place very slowly. First branches occured in Late Miocene. The genus *Ursus* did not evolve until Pliocene.
Cave bears developed from *Ursus etruscus* Cuvier, 1823 who appeared in Late Pliocene, three million years BP (RABEDER & al., 2000, 2010). The last cave bears lived 29 ka years BP (calibrated) in the Alps (FRISCHAUF & RABEDER, in press).
The cave bear species investigated in this study lived in Middle Pleistocene and Late Pleistocene (Middle Wurmian).

Studies analysing annually produced cementum layers have already been done mostly by wildlife biologists (e.g. STONEBERG & JONKEL, 1966) but also by archaeozoologists, too (e.g. SPIESS, 1976).
DEBELJAK (1996) modified the method of analysing these cementum increments to a simpler procedure and therefore used cave bear material.
The best tooth to analyse the stage of abrasion has been determined to be the first molar inferior (m_1). This is because m_1 is the first tooth that comes out – mostly at the age of at least one year. That means a great probability that even first lower molars from the youngest cave bear individuals show wear patterns. STINER (1998) also confirmed anterior molars to be the most appropriate teeth for age determinations by analysing wear stages of teeth.
The motivation for this study was to find out how much the level of abrasion and the ontogenetic age are interdependent and to work out an explanation for the enigmatic wear stage of Conturines cave bear teeth (first reported, see HOLLAND & RABEDER, 2012).

2.1 Material

The analysed material consisted of 92 first lower molars from five different cave sites (for site description see chapter 2.2 Sites) with following distribution:

- 39 m1 inf. of *Ursus spelaeus eremu*s (RABEDER & al., 2004)

  (23 of Ramesch cave and 16 of Ochsenhalt cave)

- 18 m1 inf. of *Ursus ingressus* (RABEDER & al., 2004) (Gamssulzen cave)

- 18 m1 inf. of *Ursus deningeroides* (MOTTL, 1964) (Herkova jama cave)

- 17 m1 inf. of *Ursus ladinicus* (RABEDER & al., 2004) (Conturines cave)

One species is somewhat overpresented because two of the caves that were chosen for this study were dens for the same species: *Ursus spelaeus eremus.*

The material belongs to the collection of the Paleontological Institute, University of Vienna. No fragments were used, only complete teeth with both roots were applied for this study. The condition of the molars was quite variable. The conservation status reached, from very good with no traces of fragmentation due to the depositional conditions, to relatively bad with mostly one root damaged by corrosion or erosion. However at least one root was always in an acceptable condition, that it was possible to specify if the root tips were closed. Root closure is an important factor for the investigator to be sure that the examined tooth was completely developed.

Following laboratory equipment and materials were used.

Devices	Description
Sliding calliper	Company: diaMax; Measuring system: analogue
Cup stage	Company: Jena Optik
Binocular stereomicroscope	Company: Wild Heerbrugg; magnification up to 50x
Eyepieces	Company: Wild Heerbrugg; 20x magnification
Mounting cups	Company: Struers
Stirrer	Company: Struers
Diamond rotary saw	Company: Diamantfriedl E. Friedl &Co; Type: FR 500; watercooled
Vacuum generator	Company: KNF Neuberger Laboport
Centrifuge	Company: Heraeus Instruments Labofuge 400 (Function Line)
Grinding machine	Company: Buehler Ecomet 3; Variable speed grinder-polisher (up to 500 r.p.m.)
Ultrasonic Cleaner	Company: qteck GmbH Germany P 12i
Plates of glass	Dimensions: each 50 x 50 cm

Tab. 1: List of devices applied for this study.

Chemicals	Description
HCl	Company: W. Neuber´s Enkel Gross-Drogerie; dilution: 4%
Methylene blue	Company: W. Neuber´s Enkel Gross-Drogerie
Two-component resin	Company: Struers; designation: “Epofix Resin” and “Epofix Hardener”
Silicon carbide grindingpowder	Distributor: A.B. Technics Handels GmbH; 180, 600 and 1000 grain size
Tap water	For suspending grinding powder
Lab-Putty	Company: Coltène/Whaledent
Ethyl alcohol	Company: W. Neuber´s Enkel Gross-Drogerie
Acetone	Company: W. Neuber´s Enkel Gross-Drogerie

Tab. 2: List of chemicals used for this study.

2.2 Sites

Cave bear faunas of five different caves were examined.

The **Ramesch cave** (Fig. 1) next to Spital am Pyhrn, Upper Austria, is a High Alpine cave and lies in the "Totes Gebirge" about 1960 m above sea level (HILLE & RABEDER, 1986). 23 m1 (14 dex and nine sin) were studied from this site. The cave is also called "Ramesch Knochenhöhle" because of its high amount of cave bear bones. Six excavations between 1979 and 1984 were realized. These excavations took place during July till August (HILLE & RABEDER, 1986).
Finds of this cave are aged Middle Wurmian and Riss-Wurmian period (teeth investigated in this study belong to Middle Wurmian period without exception). The Uranium-Thorium age determination showed results between 150 and 31 ka BP (HILLE & RABEDER, 1986) (Tab. 3). The radiocarbon datings gave values between 35 and 54 ka BP (calibrated) (PACHER & STUART, 2008) see Tab. 3.
Cave bear specimens of this cave could be associated with the species *Ursus spelaeus eremus* for which the Ramesch cave is the locus typicus (RABEDER & al., 2004).

Another cave site nearby Spital am Pyhrn, Upper Austria, is the **Gamssulzen cave** (Fig. 1) with an altitude of 1300 m above sea level (RABEDER, 1995). 17 examined m1 (eight dex and nine sin) belong to this site.
Between 1988 and 1991 four excavations took place. The period of these excavations varied from about two weeks to about one month (RABEDER & WEICHENBERGER, 1995).
Results of C14 age determination gave an age of 51 ka to 31 ka BP (calibrated data) (PACHER & STUART, 2008; RABEDER, 1995), see Tab. 3. US-series displayed an age of about 25 ka BP (RABEDER, 1995) (also see Tab. 3). Therefore the cave bear finds from this cave can be categorized as Middle Wurmian. The representative of the cave bear fauna in this cave is *Ursus ingressus*. Gamssulzen cave is the locus typicus of *Ursus ingressus* (RABEDER & al., 2004).

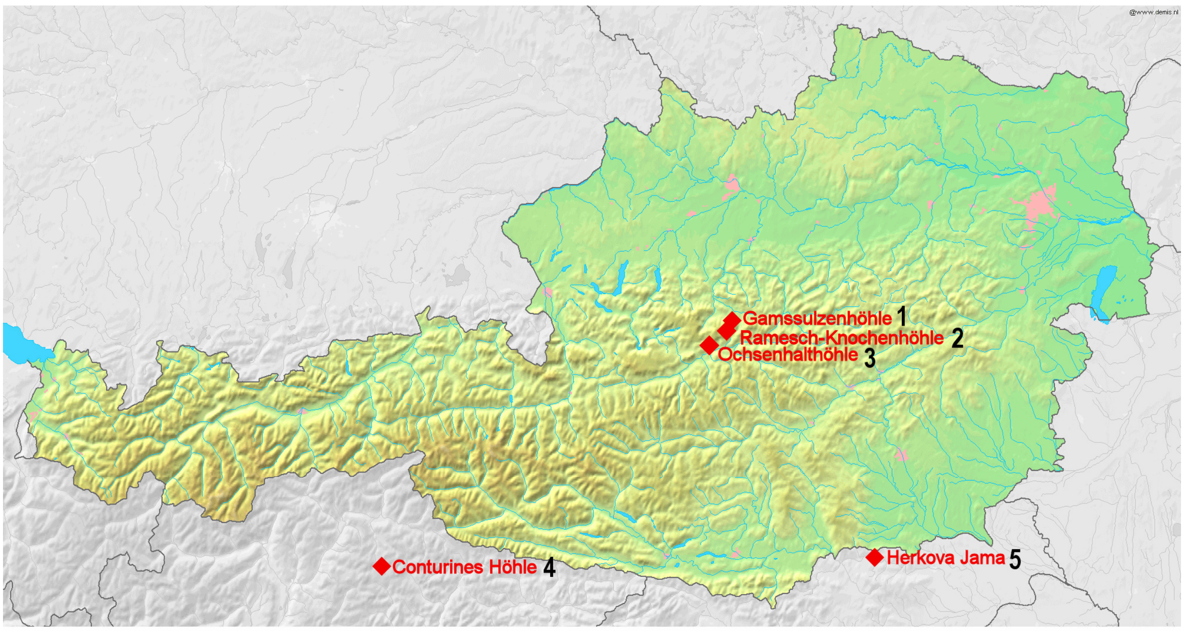
The **Ochsenhalt cave** (Fig. 1) lies as well as the other caves described above- in the mountain range "Totes Gebirge". Its altitude is about 1660 m and it is located near Weißenbach next to Liezen (Styria, Austria) (FRISCHAUF, 2010). 16 m1 (seven dex and nine sin) were studied from this site.
From 2001 till 2006 seven excavations were planned and done (in about min. two days and max. three weeks). The first one in 2001 was a successful test excavation wherefore additional excavations could be arranged (FRISCHAUF, 2010).
For the cave bear remains in the Ochsenhalt cave age determination by U-Th-series has not been applied but an age of about 46 ka to 33 ka BP (calibrated, FRISCHAUF, 2010) could be calculated by the C14 age determination (see Tab. 3). This result is related to the Middle Wurmian till Late Wurmian period. According to the mtDNA analysis and the morphological data the bears of Ochsenhalt cave belong to the taxon *Ursus spelaeus eremus* (RABEDER & al., 2004).

The **Conturines cave** (Fig. 1), also belonging to high alpine caves, can be found nearby St.Vigil, Italia. With its altitude of 2775 m above sea level (RABEDER, 1991) it is the highest known cave bear cave site of Europe. From this cave 17 m1 (eight dex and nine sin) were processed.
There had been three excavations between 1988 and 1990, lasting from one to two months and other excavations after 1990 till 2001 lasting two to three weeks (RABEDER & al., 2006).

The Uranium-Thorium age determination showed results between 116 and 42 ka BP (RABEDER & al., 1994). C14 age analyses delivered data of about 48 ka BP (calibrated) (PACHER & STUART, 2008) (see Tab. 3).
The finds from Conturines cave belong to the Late Pleistocene (Middle Wurmian). The cave bear species *Ursus ladinicus* (RABEDER & al., 2004) can be found in this cave for which the Conturines cave is the locus typicus.

As comparison to the four cave bear species described above, additional cave bear material from a different cave was studied:

The **Herkova jama** cave (Jama pod Herkovimi pecmi) (Fig. 1) is the lowest located one of the five investigated caves with an altitude of 520 m above sea level and contains finds of the oldest cave bear species from the examined caves. The cave is situated close to the border between Austria and Slovenia and near Radlje ob Drave (South Styria, Slovenia) (POHAR, 1981; POHAR & al., 2003).
18 m1 (eight dex and ten sin) were studied from this site.
During 1977-1979 the first excavation was carried out (POHAR, 1981; POHAR & al., 2003). Another excavation in 2003 was realized and lasted for three years.
Although there had been no Uranium-Thorium age determinations, in 2003 C14 dating was done and a first age date was available for this cave: POHAR & al. (2003) obtained a result of about 30 ka BP. This result though is only related to an additional cave bear of the *U. spelaeus* group in this cave.
The cave bear remains investigated in this study could be associated to the species *Ursus deningeroides* (MOTTL, 1964).
Age determination for this species could be realized by comparison with cave bear remains of the Repolust cave. Dimensions and evolutionary levels of Herkova and Repolust cave are very similar (pers. comm. C. Frischauf). The Repolust faunal complex contains remains of Middle Pleistocene species: *Canis mosbachensis, Gulo* cf. *schlosseri, Equus* cf. *mosbachensis, Bison* cf. *schoetensacki, Hystrix* cf. *vinogradovi* (DÖPPES & RABEDER, 1997).



1 Upper Austria (Austria) 2 Upper Austria (Austria) 3 Styria (Austria) 4 South Tyrol (Italy) 5 South Styria (Slovenia)

Fig. 1: Localization of the five investigated caves in Austria, Italia and Slovenia. Adapted from http://mapsof.net/uploads/static-maps/austria_topographic_map.png

Cave site	Lab. nr.	Method	Date year BP	Error +	Error -	C14 CalPal/ US datings	Error +/-	Altitude (m)	Reference
Conturines	Beta-143246	AMS	44 260	900	900	**47685**	1708	2800	Pacher & Stuart 2008
Gamssulzen	Beta-157660	AMS	32 010	320	320	**36187**	533	1300	Pacher & Stuart 2008
Gamssulzen	Beta-157659	AMS	32 190	330	330	**36603**	742	1300	Pacher & Stuart 2008
Gamssulzen	Beta-157664	AMS	41 060	920	920	**44573**	1019	1300	Pacher & Stuart 2008
Gamssulzen	KIA-25287	AMS	44 160	1400	1190	**47676**	1948	1300	Pacher & Stuart 2008
Gamssulzen	Beta-157662	AMS	44 400	1380	1380	**48875**	2161	1300	Pacher & Stuart 2008
Gamssulzen	Beta-157663	AMS	45 410	1560	1560	**48944**	2302	1300	Pacher & Stuart 2008
Gamssulzen	Beta-157665	AMS	47 300	1970	1970	**51256**	3078	1300	Pacher & Stuart 2008
Gamssulzen	Beta-157665	AMS	47 300	1970	1970	**51256**	3078	1300	Pacher & Stuart 2008
Gamssulzen	VRI-GSII	US	25400	1500	1500	**25400**	x	1300	Rabeder 1995
Gamssulzen	Hv 16893	AMS	25965	780	780	**30754**	740	1300	Rabeder 1995
Gamssulzen	Hv 16892	AMS	27520	645	645	**32249**	562	1300	Rabeder 1995
Gamssulzen	VRI-1226	conv.	31500	1300	1100	**36239**	1576	1300	Rabeder 1995
Gamssulzen	VRI-1228	conv.	34300	2400	1900	**38227**	2452	1300	Rabeder 1995
Gamssulzen	VRI-1326	AMS	38000	2000	1900	**42283**	1671	1300	Rabeder 1995
Gamssulzen	VRI-1227	conv.	38000	3300	2300	**41793**	3102	1300	Rabeder 1995
Ochsenhalt	VERA-2191	AMS	28370	140	140	**32761**	1660	1650	Frischauf 2010
Ochsenhalt	KIA-25283	AMS	42 290	970	870	**45874**	1251	1650	Frischauf 2010
Ochsenhalt	VERA-1601	AMS	36240	670	620	**41324**	1660	1650	Pacher & Stuart 2008
Ochsenhalt	VERA-2190	AMS	39260	500	470	**43379**	1660	1650	Pacher & Stuart 2008
Ramesch	RK81-D8-1	US	31300	1900	1800	**31300**	1900	1960	Hille &Rabeder 1986
Ramesch	RK83-L11-1	US	34600	2900	2800	**34600**	2900	1960	Hille &Rabeder 1986
Ramesch	VRI-776	conv.	34900	1800	1500	**39227**	2006	1960	Hille &Rabeder 1986
Ramesch	RK-D7-2	US	36100	3000	2800	**36100**	3000	1960	Hille &Rabeder 1986
Ramesch	VRI-792	conv.	37200	1900	1600	**41398**	1892	1960	Hille &Rabeder 1986
Ramesch	RK80-D7-3	US	38900	2300	2200	**38900**	2300	1960	Hille &Rabeder 1986
Ramesch	RK80-D7-1	US	42400	5300	4900	**42400**	5300	1960	Hille &Rabeder 1986
Ramesch	RK82-U17-1	US	44500	2900	2800	**44500**	2900	1960	Hille &Rabeder 1986
Ramesch	RK81-D8-3	US	51300	2800	2700	**51300**	2800	1960	Hille &Rabeder 1986
Ramesch	RK83-L11-3	US	52000	4700	4500	**52000**	4700	1960	Hille &Rabeder 1986
Ramesch	RK83-L11-2	US	62100	4100	3900	**62100**	4100	1960	Hille &Rabeder 1986
Ramesch	RK62-U16-1	US	64000	5400	5100	**64000**	5400	1960	Hille &Rabeder 1986
Ramesch	RK82-U16-2	US	117400	11300	10000	**117400**	11300	1960	Hille &Rabeder 1986
Ramesch	RK82-U16-2	US	117500	20100	16000	**117500**	20100	1960	Hille &Rabeder 1986
Ramesch	RK83-L12-1	US	128400	12800	11000	**128400**	12800	1960	Hille &Rabeder 1986
Ramesch	RK81-D8-4	US	150400	20100	16000	**150400**	x	1960	Hille &Rabeder 1986
Ramesch	Beta-157670	AMS	31 140	310	310	**35160**	397	1960	Pacher & Stuart 2008
Ramesch	Beta-143242	AMS	43 610	800	800	**47169**	1678	1960	Pacher & Stuart 2008
Ramesch	Beta-157667	AMS	43 700	1270	1270	**47288**	1877	1960	Pacher & Stuart 2008
Ramesch	Beta-157669	AMS	47 600	2060	2060	**51706**	3209	1960	Pacher & Stuart 2008
Ramesch	Beta-143241	AMS	49 520	1600	1600	**54462**	3262	1960	Pacher & Stuart 2008

Tab. 3: Radiometrical datings of cave bear remains from Gamssulzen, Ramesch and Ochsenhalt cave (after FRISCHAUF & RABEDER in press)

2.3 Methods

Four methods have been applied for this research.

2.3.1 DARA method

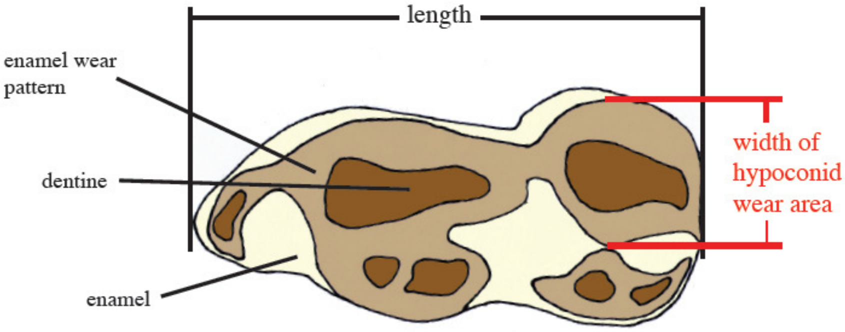
This technique was mainly developed for this study.
DARA (Dental Abrasion Rate Analysis) determines the degree of abrasion related to the ontogenetic age of each m_1.

This method was applied in two steps:

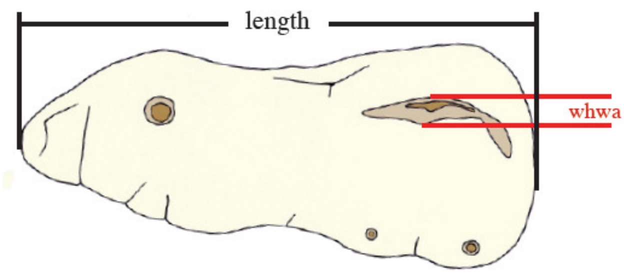
At first the greatest length (from mesial to distal) and greatest width of the hypoconid wear pattern (vertically to the length axis) were measured with a sliding calliper (see Fig. 2). Then the values were calculated as following:

$$\frac{\text{Width of hypoconid wear pattern}}{\text{length}} \times 100 = \text{hwi}$$

So the result of this formula is defined as the hypoconid wear index (hwi).



m1 inf. dex of *Ursus ingressus* from Gamssulzen cave, individual age estimation is about 15 years



m1 inf. dex of *Ursus ladinicus* from Conturines cave, individual age estimation is about 16 years
whwa = width of hypoconid wear area

Fig. 2: Comparison of the measurements with the DARA technique between two differently worn first lower molars.

The reasons why the wear patterns of the hypoconid area were chosen are following:
First, the hypoconid is mostly one of the first cusp that gets worn. Second, the hypoconid is as well, the most worn area of all wear areas on m_1. And third, the hypoconid gets worn much more often than the other cusps. These are the reasons why the hypoconid is the best cusp to examine wear patterns on m_1.

For this reason the hypoconid wear index can be considered as an extent of the degree of abrasion of cave bear teeth.

The next step was to find out the ontogenetic age of each individual. Therefore a technique for analysing cementum increments (annuli) by ground section after DEBELJAK (1996) was applied.

2.3.2 Cementum increments analysing technique of m_1 roots with ground section by Debeljak

Preparation

Selection criteria for each fauna were a sample size of teeth with different sizes of hypoconid wear patters. Every first molar also had to have at least one root closed - without exception.

Each of these first molars was transferred into moulds (made of hard plastic) that fitted to the height of the teeth. The tips of the roots were fixed with glue to the bottom of the moulds. Afterwards synthetic resin was filled in the moulds but we took great care that the top of the crowns of the molars rested resin-free.
The resin-free crowns were important for further examinations (e.g. to classify occlusal wear surfaces into adequate age cohorts (STINER, 1998)).
The synthetic resin (Epofix) consisted of two components: The main component and the hardener. These components were mixed up carefully at a ratio of 25:3. For getting rid off disturbing bubbles the mixture was centrifuged and put into a container with a vacuum atmosphere for a few minutes.
The hardening process took about 24 hours so the next day the teeth in the moulds were ready to get out of them. Before filling in the resin some petroleum jelly was put on the inside of the moulds. This procedure should ensure that peeling away the moulds would be easier. After removing the moulds the molars surrounded by now hard resin were ready for the sawing machine. From each resin block a cross section was cut with a water-cooled, diamond rotary saw so that each tooth was sawed in two halves (DEBELJAK, 1996: 107). The cut was positioned about 4-7 mm below the border between enamel (crown) and cementum (root). After the sawing process the upper halves were ready for the subsequent grinding procedure.

Final steps

The final steps took place on 50 x 50 cm glass plates. But at first it had to be checked if the sawing marks were only superficial or deeper. When they were deep marks the upper resin half with the crown was processed on a grinding machine with 180 grit silicon carbide powder suspended with water on the plate of the machine. Afterwards when the marks were grinded away, the resin block was put in a ultrasound machine for some minutes to make sure that it will be completely cleaned of the 180 grit silicon carbide powder. This is important for the next step. On the first glass plate 600 grit silicon carbide powder was given, suspended with water. For this reason the ground surface has to be 180 grit silicon carbide powder free.

With the more fine grained 600 grit silicon carbide powder it was possible to grind away the more coarse grained scratches from the 180 grit silicon carbide powder. After removing the traces of the 180 grit silicon carbide powder and carefully checking that there were no scratches left or no new scratches, the resin block was put on the next glass plate. Before switching to the next plate the ground surface had to be carefully cleaned. It was necessary to rinse off thoroughly the 600 grit silicon carbide powder with water so that no new scratches could occur on the following plate with the next more fine grained grit powder. The next glass plate was specially only for using with the 1000 grit silicon carbide powder. This powder is used for the last step in the grinding process. It has a polishing character. Grinding the resin block with the suspended 1000 grit silicon carbide powder on the glass plate took only a few minutes. The ground surfaces were moved over the plates in circle or infinity sign formations. This should ensure that the pressure of the fingers is equal at every site of the resin halve so that the grinding was planar. A planar ground surface is indispensable for the subsequent etching step. Without a planar surface the etching would be irregular and this could have negative consequences in making visible and detecting the cementum annuli.
The whole grinding process for one tooth took about 45 to 60 minutes depending on the deepness of the sawing marks.
When the ground surface was planar, polished and showed no scratches the resin block was ready for the next step: etching.
Although DEBELJAK (1996: 107) mentioned H_3PO_4 as acid for etching, HCl was applied for this study (which in fact even worked better because HCl is a stronger acid than H_3PO_4 so that etching was able to be done in a shorter time).
4% diluted HCl was filled ground-covering in an acid resistant petri dish. The ground surface of every resin block was immersed in the acid for about one or (mostly) two minutes (depending on the visibility of the cementum annuli). Shortly after removing from the dish the acid was thoroughly rinsed off the ground surface with water to stop the etching process. Tests with a colorant (methylene blue had been used) showed no significant difference according to the visibility of cementum annuli in comparison with non-dyed sections. There was no improvement of the visibility because the contrast in the annuli area did not change. But DEBELJAK (1996: 107) already underlined that this technique is able to be modified if necessary.

Examination of the cementum increments

After the etching process, to analyse and count the cementum annuli under a microscope, the tooth was fixed in dough on a cup stage upside-down so that the etched surface faced up. With this mechanical stage precise movements are possible which is very helpful because it is quite tricky to find out the best position of the incidence of light at every section. As DEBELJAK (1996:107) mentioned, the best position was […*when strong light was falling oblique from one side, perpendicular to the course of increments*] mostly.
Depending on the angle of view sometimes every pair of one dark and one bright line (like DEBELJAK (1996: 106) proceeded in her work) was counted as one annulus and sometimes the prominences of the lines were counted (see Fig. 3). In any case the total number of countings was the same no matter which counting technique was applied.

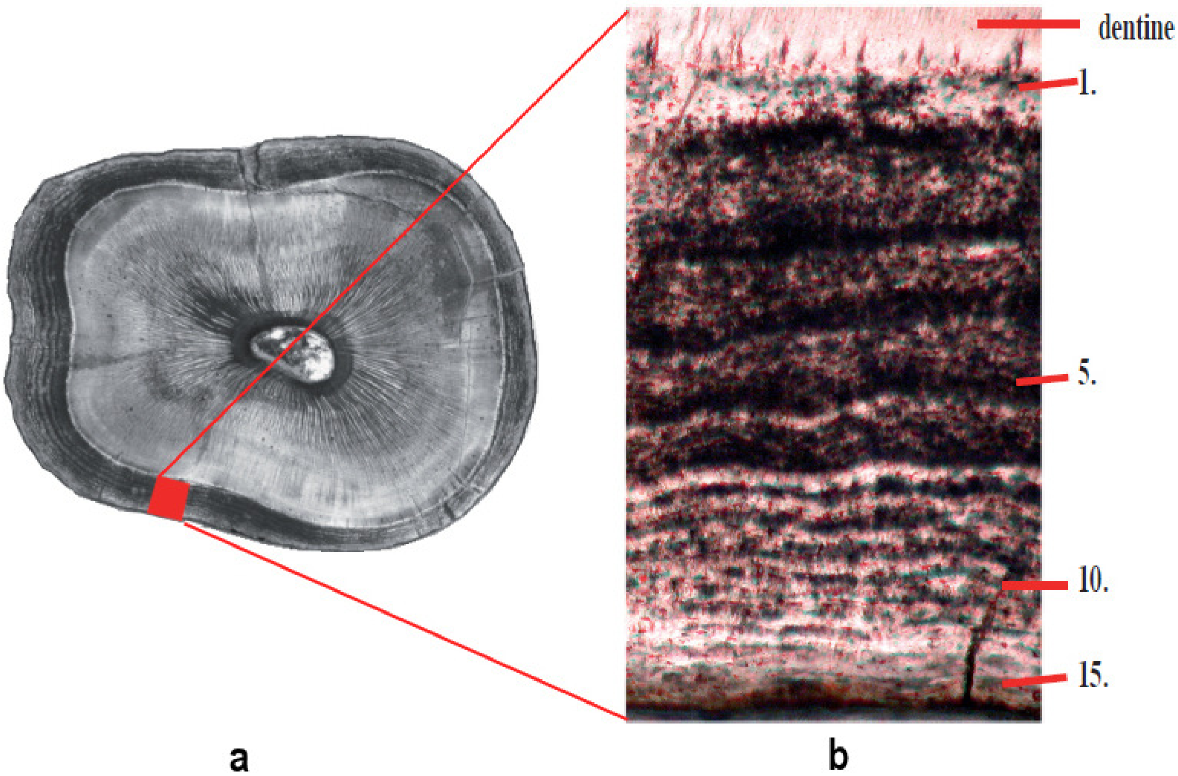


Fig. 3: a) Cross section of a first lower molar from Conturines cave. magnification ca. 3x
b) Section detail of the cementum layer of the tooth shown in a). The first, fifth, 10th and 15th annulus is marked with numbers. Note the difference of width of the annuli: Annuli one to five are broader (they emerged earlier) and annuli six to 15 are narrower (they emerged later). magnification 40x

<u>Problems with the method</u>

Quite often it was hard to detect all the cementum annuli. There were some problems like e.g. unsuccessful etching (because of irregular growth of cementum it was not possible to etch steadily so the results were whether a "faded" look or some cracks). Another problem was the colour of the cementum: In some cases it had nearly the same colour like the dentin, whereby it was difficult to differentiate between the two layers and to identify the first ring in the cementum (the first annulus). Of course there were also a couple of teeth whose conservation status was in quite bad condition. It was obvious - even macroscopically sighted - that the cementum was removed by corrosion or erosion caused by depositional conditions. Therefore it was only possible to examine the cementum increments on the positions where the cementum layer was still present.

2.3.3 Age cohort classification after STINER (1998)

Another method investigating wear stages of cave bear teeth was applied. STINER (1998) suggested a new scheme where she divided different degrees of abrasion in suitable, concordant cohorts.
Her classification scheme ranged from cohort I to cohort IX with following division (see Fig. 4):

Age cohort I to III: juvenile
Age cohort IV to VII: prime adult
Age cohort VIII and IX: old adult

The first lower molars chosen for this study were grouped in appropriate cohorts. Age cohort I, however, was not used for classification as this cohort represents age stage of teeth that has not developed enough to show any wear patterns (like e.g. germs).

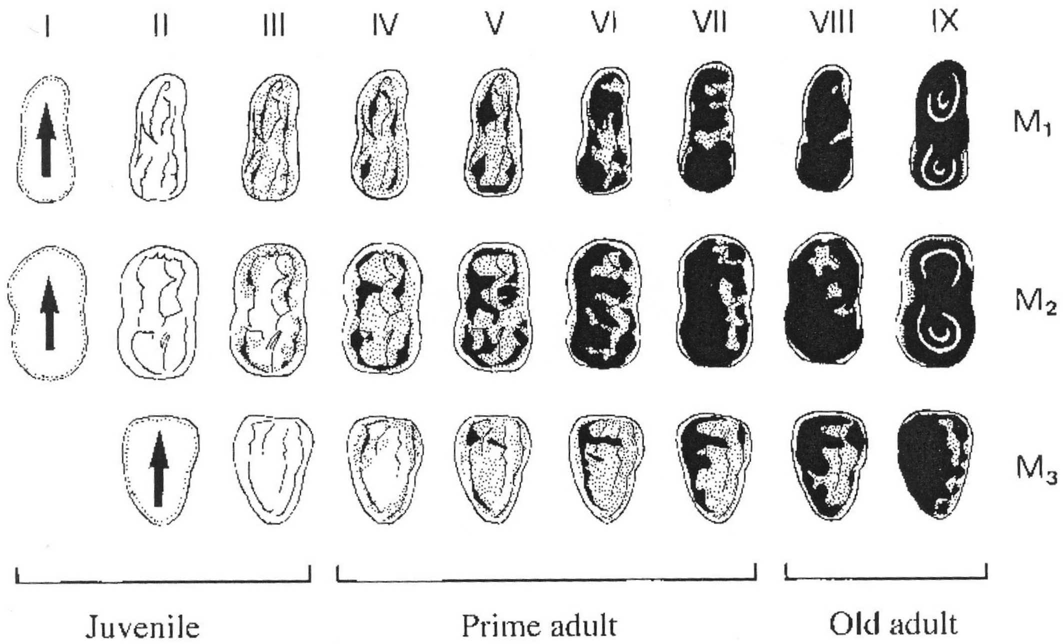


Fig. 4: Age cohort scheme adapted from STINER (1998). Only the top row of this sketch was used for classification. The arrow in age cohort I signifies that the tooth is still emerging. The dotted texture symbolizes worn enamel; black structures represent dentin exposure and white lines on black background in age cohort IX means that teeth of this category are that heavily worn that even the pulp cavity is exposed.

2.3.4 Microwear

This method was applied under supervision of Katharina Bastl at the end of the study to find out an answer for the difference in abrasion between the unworn teeth of the Conturines cave and the worn teeth of the other caves. As comparative material m_1 of the Gamssulzen cave were chosen.

At first suitable m_1 were selected which had wear patterns but whose patterns were not too heavy worn. The best cusp for detecting microwear features turned out to be the metacone in this study.

For analysing microwear features it was necessary to prepare casts of suitable m_1 because it has been found out that examining microwear patterns on tooth casts worked better than identifying and counting pits and scratches on the tooth of interest directly (SOLOUNIAS & SEMPREBON, 2002).
Therefore the teeth were at first treated with a cotton swab soaked in alcohol first and acetone afterwards for carefully cleaning the wear facets.
Afterwards, for building the cast, at first molding substance was applied on the appropriate teeth. For the application a molding gun was used in whose tip the components for the molding substance were mixed together.
After the hardening of the molding substance (which took some minutes) it was possible to form a wall of lab putty around the mold. As substance for the cast, transparent resin was chosen. This resin was filled in the resulting mold between the molding substance and the lab putty. The lab putty prevented liquid resin from spilling out. After ca. 24 hours the hardening process of the resin was completed and it was possible to take out the resin cast, so it could be then used for further investigations:

For the examination of microwear features under a stereo microscope at low magnification (35x) (SOLOUNIAS & SEMPREBON, 2002), an additional external illumination was used to make them visible. Therefore a fiberoptic light source was directed along the surface of the casts at a low angle to visualize all features (see Fig. 5). For counting pits and scratches a standard square area of 0.4 mm x 0.4 mm was chosen.
Six first lower molars could be used for the microwear method (five from Conturines Cave and one from Gamssulzen cave).

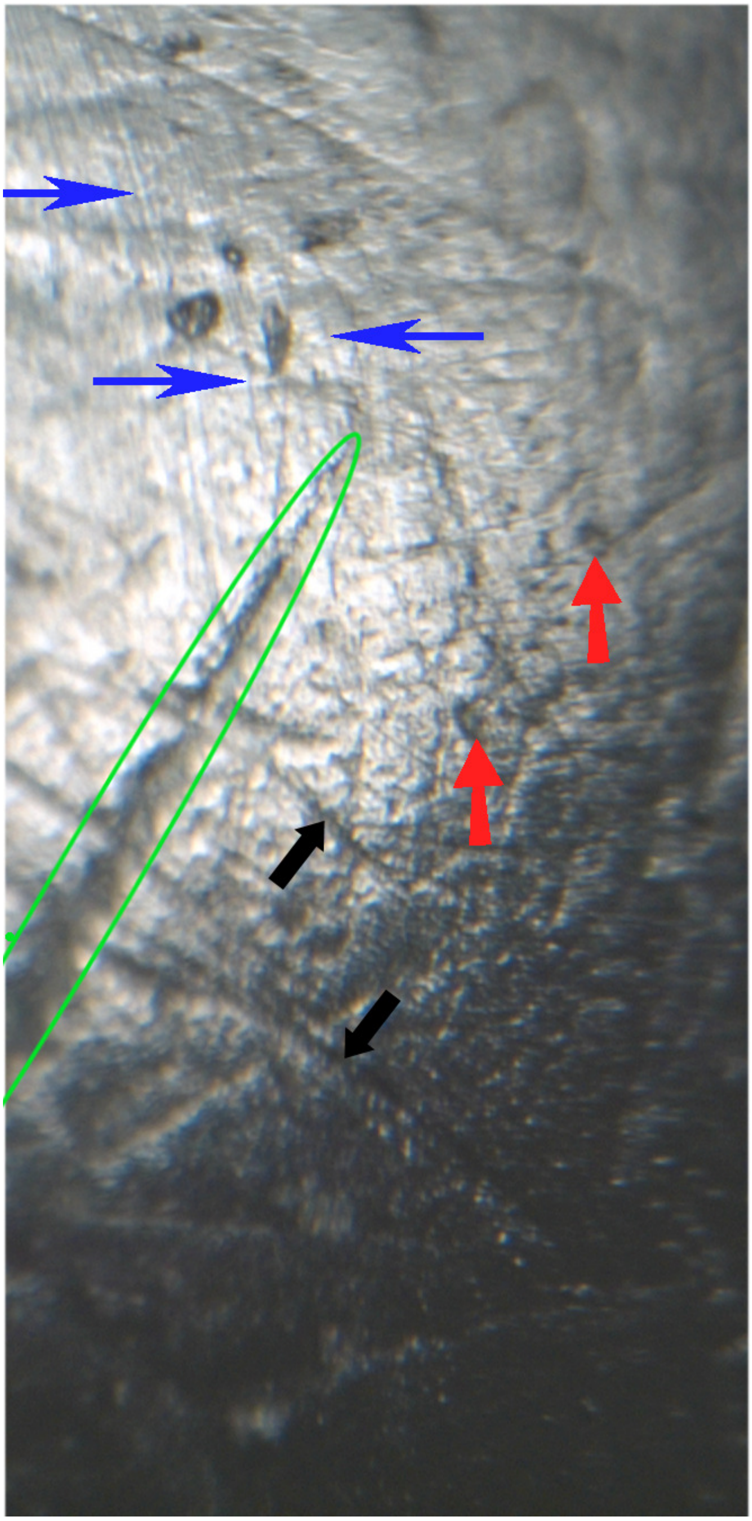


Fig. 5: Occlusal wear surface of a tooth from Conturines cave (metaconid).
Microwear features:
blue arrows = fine scratches, red arrows = puncture pits, black arrows = coarse scratches, green ellipse = hypercoarse scratch;
magnification 35x

3. Results

In this study four cave bear species from five different caves were examined.
The comparison between the species was expected to give an answer to the question of first, if there is a significant correlation between abrasion and ontogenetic age and second dietary habits.

3.1 Age cohorts

For investigating the dependence of age cohorts towards ontogentic age, graphs for all cave specimen have been done (Fig. 6 - 10). Therefore the ontogenetic age represented by the number of cementum annuli is plotted together with the age cohorts determined for every sample.

STINER (1998) recommended the following division for age levels:

Age cohort I to III: juvenile
Age cohort IV to VII: prime adult
Age cohort VIII and IX: old adult

Ramesch cave (*U. spelaeus eremus*)

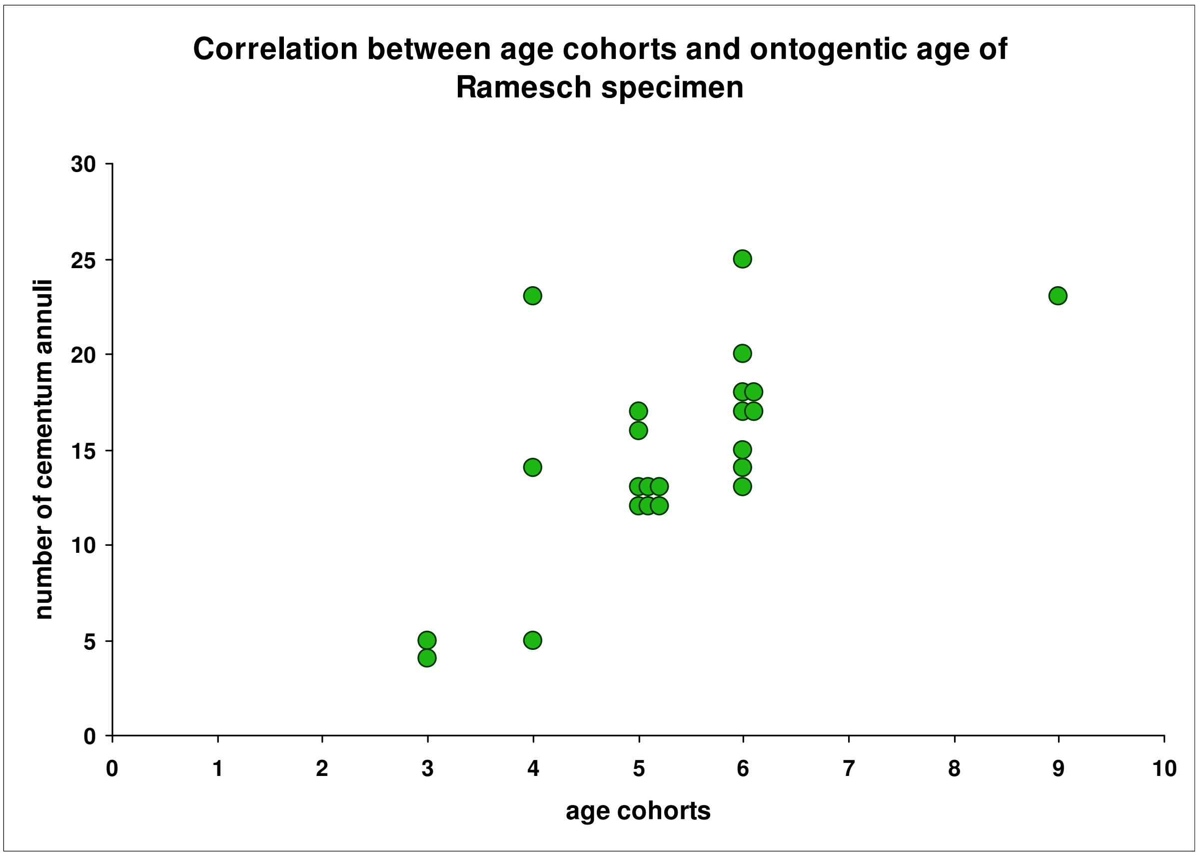


Fig. 6: Specimen classified into age cohorts and plotted together with corresponding number of cementum annuli (ontogenetic age). Samples are from Ramesch cave, species: *U. spelaeus eremus.*

Specimen from Ramesch cave could be classified into age cohorts III to VI however one single sample was grouped in age cohort IX (see Fig. 6).

Although some values confirm correct age cohort scoring (see samples with exact same number of cementum annuli – substitutional for years of life - in age cohort V and VI in Fig. 6) there is a wide range of ontogenetic ages. Specimen of age cohort IV for example is associated to prime adult, adult and old adult individuals and specimen of age cohort VI also vary between prime adult and old adult individuals.

The aspect of overlapping is also distinctly displayed by the outlier of age cohort IX. This sample is overlapping with samples of in particular age cohort IV and also age cohort VI which represent about the same age.

<u>Ochsenhalt cave</u> (*U. spelaeus eremus*)

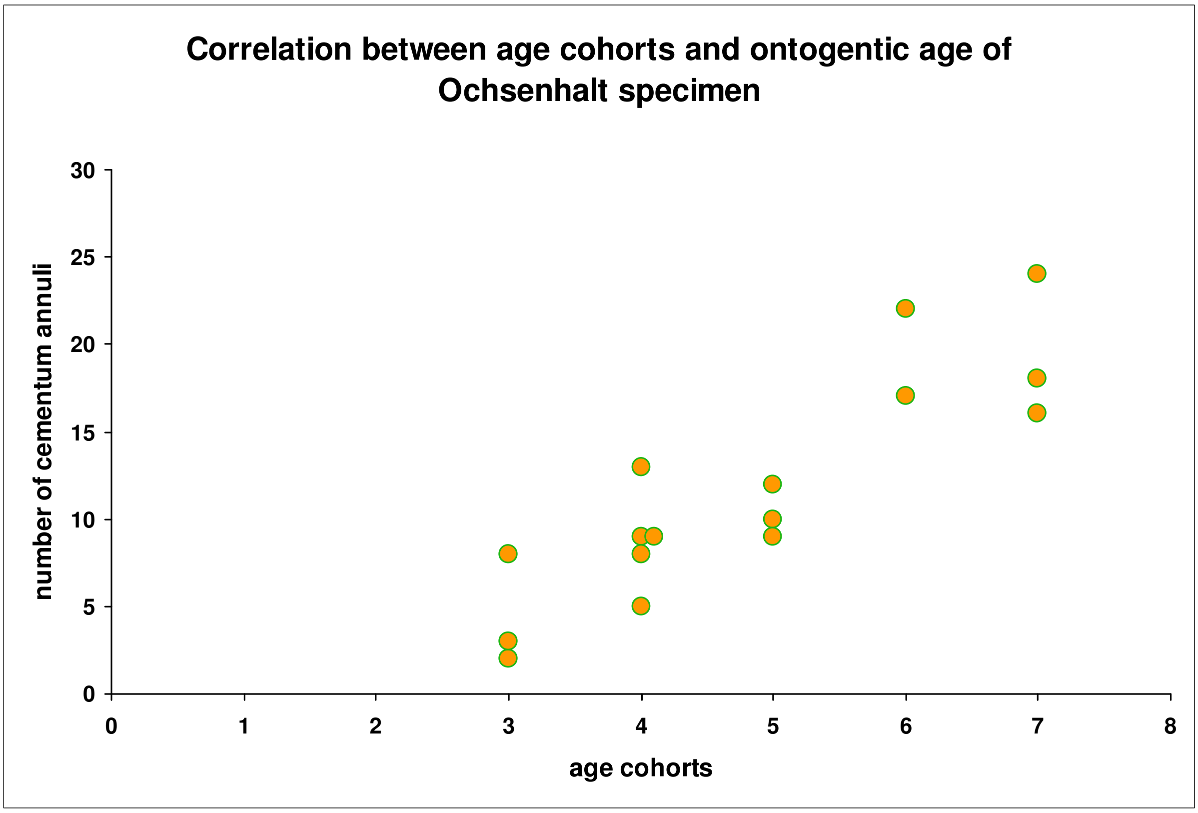


Fig. 7: Specimen classified into age cohorts and plotted together with corresponding number of cementum annuli (ontogenetic age). Samples are from Ochsenhalt cave, species: *U. spelaeus eremus.*

Specimen from Ochsenhalt cave could be classified into age cohorts III to VII which is displayed in Fig. 7.

There is a tendency increase, which means that specimen with young age level are grouped in age cohorts with lower numbers and specimen with old age levels are grouped in age cohorts with higher numbers.

Nevertheless also in Fig. 7, nearly every age cohort shows overlapping with the other ones. Correct age cohort scoring is ineffective because the sample range in each age cohort differs of about at least five years.

<u>Gamssulzen cave</u> (*U. Ingressus*)

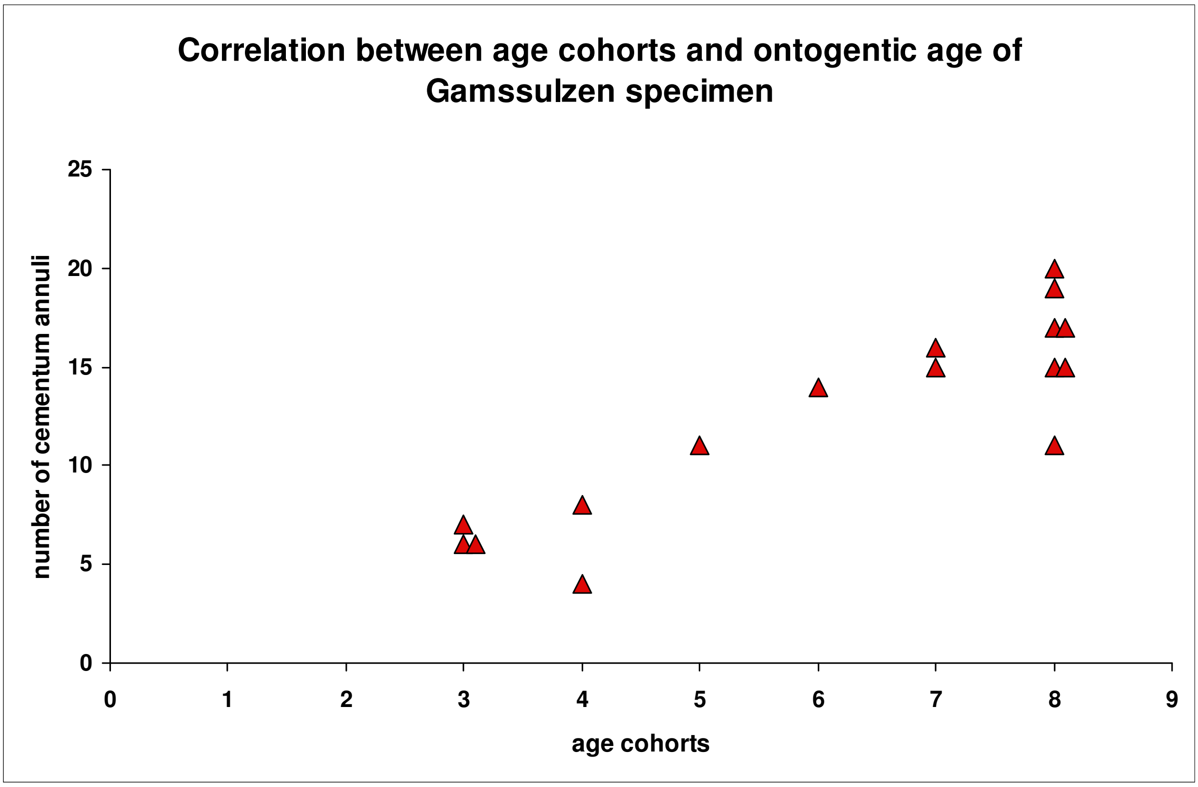


Fig. 8: Specimen classified into age cohorts and plotted together with corresponding number of cementum annuli (ontogenetic age). Samples are from Gamssulzen cave, species: *U. ingressus.*

Ursus ingressus specimen were classified into age cohorts III to VIII.

Like in Fig. 7, the distribution of the specimen from Gamssulzen cave also shows a tendency increase, which can be seen in Fig. 8.

Most specimen were attributed to the age cohort VIII, but those values also differ too much: between 10 and 20 years of life.

<u>Herkova jama cave</u> (*U. deningeroides*)

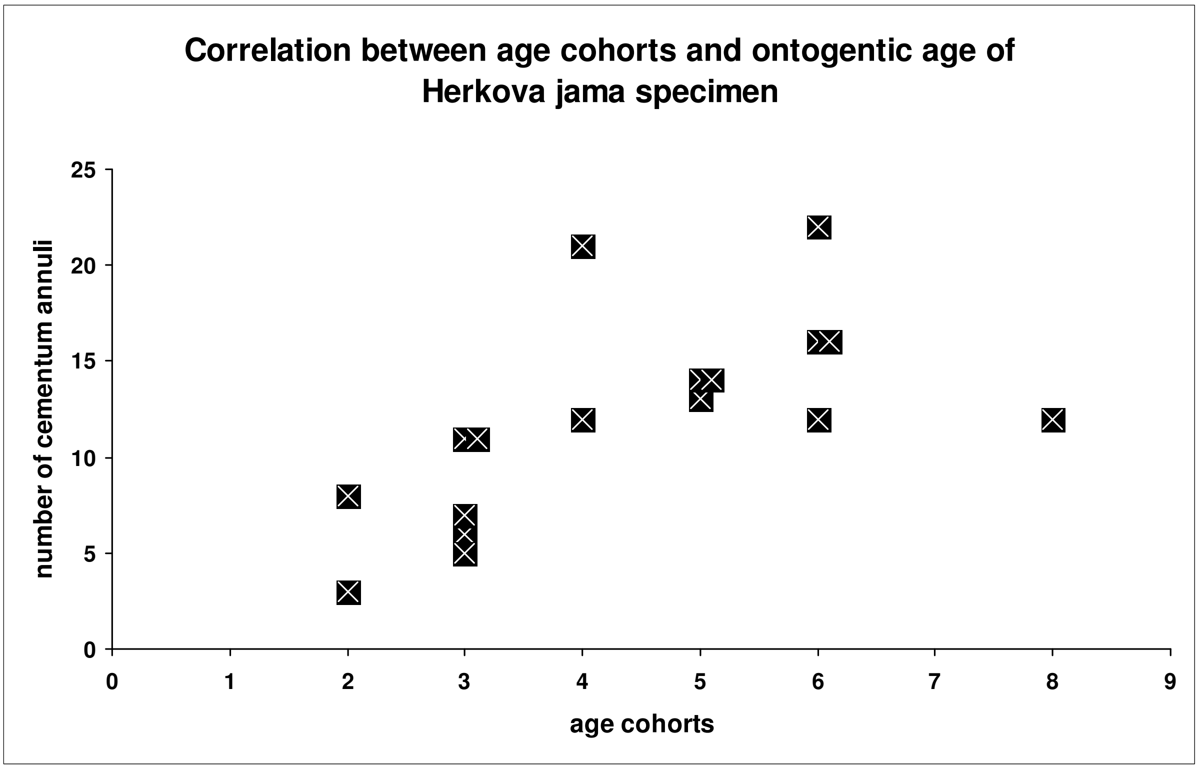


Fig. 9: Specimen classified into age cohorts and plotted together with corresponding number of cementum annuli (ontogenetic age). Samples are from Herkova jama cave, species: *U. deningeroides.*

U. deningeroides specimen from Herkova jama cave could be assigned to age cohorts II to VIII, however it was not able to relate to a sample of age cohort VII .

Fig. 9 shows no increase of the Herkova jama sample size. On the contrary, the distribution is irregular and the values of the different age cohorts are mostly overlapping (individuals of an ontogenetic age of about 11/12 years plotted in age cohort III, IV, V, VI and VIII).

Samples of *Ursus denigeroides* were interestingly even classified into age cohort II which is not the case at the sample sizes of Ramesch, Ochsenhalt and Gamssulzen cave.

<u>Conturines Cave</u> (*U. ladinicus*)

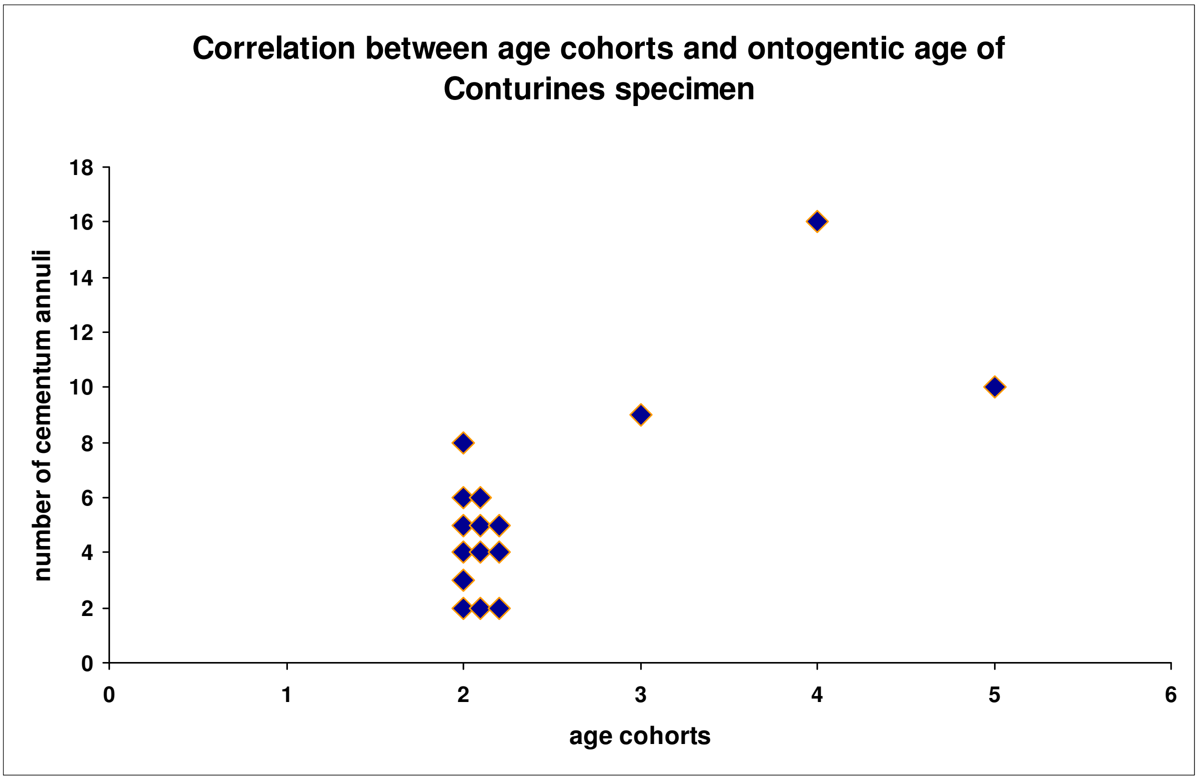


Fig. 10: Specimen classified into age cohorts and plotted together with corresponding number of cementum annuli (ontogenetic age). Samples are from Conturines cave, species: *U. ladinicus.*

Specimen of Conturines cave show a sharp clustering in age cohort II (see Fig. 10).

The ontogenetic ages of individuals in this age cohort range from two to eight years of life.

Again age cohort classification is not reliable because the single sample of age cohort V shows an ontogenetic age of 10 years, which means a difference of just two years more than the “oldest” individual of age cohort II which value is about eight years of life.

Total distribution of all caves

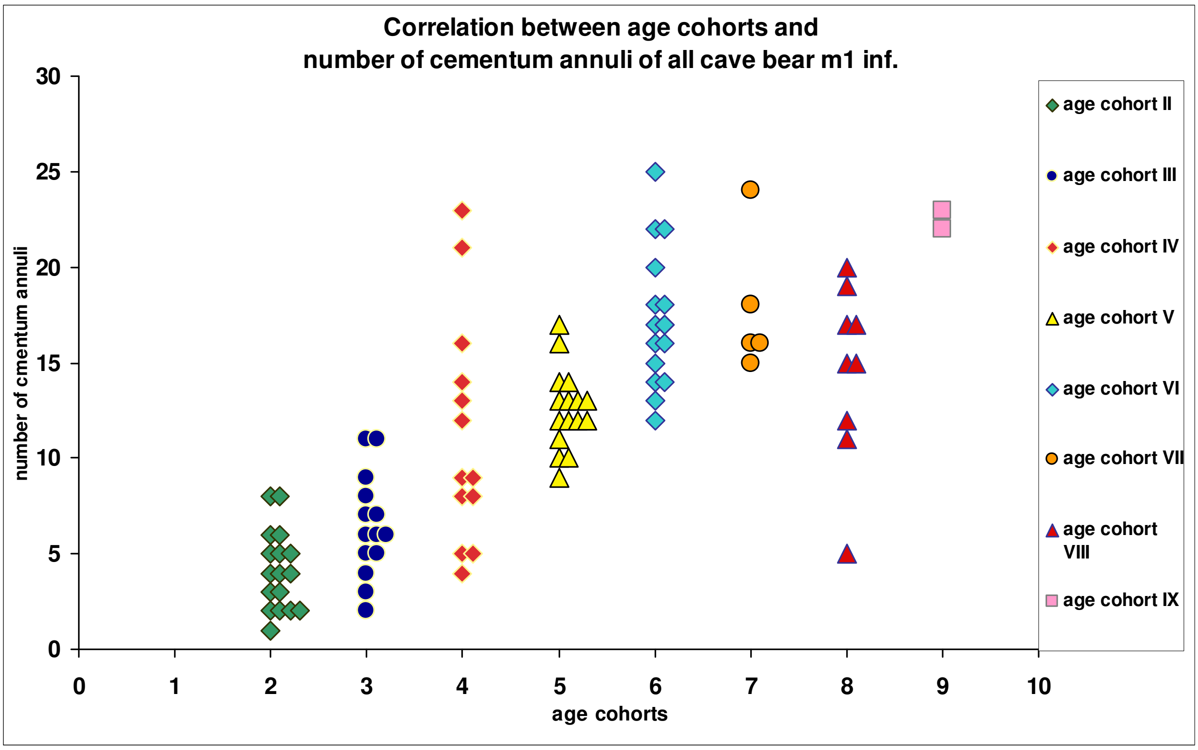


Fig. 11: Specimen from all examined caves classified into age cohorts and plotted together with corresponding number of cementum annuli (ontogenetic age).

In Fig. 11 ontogenetic age (represented by the number of cementum annuli) was tried to correlate with matching age cohorts for all investigated specimen.

From age cohort II to VII there is a light increase recognisable but it´s not regular. The age cohort VIII is an outlier in this distribution and does not follow up the trend of increase. There is no explanation why especially this cohort is outranging.

Considering the wide range of age cohort IV it is distinctly noticeable that samples of this stage are not only overlapping with the outranging samples of age cohort VIII, but also with samples of nearly all other age cohorts. Likewise there is a partially overlapping among the other stages, too.

It is obvious that there is a tendency dependence between these two parameters, but for accurate assessment of the ontogenetic ages after grouping in age cohorts the overlapping in general is too great.

3.2 Coefficient of dental abrasion rate (C_{DAR})

3.2.1 C_{DAR} correlated to faunas

The hypoconid wear index and the number of annuli were plotted together to make a statement if the extent of the abrasion (which is defined by the index named above) could be depending on the ontogenetic age for each fauna (Fig. 12 - 16).

The resulting C_{DAR} (increase value of the regression line) is a measure for the average annual abrasion rate of each fauna.

Ramesch cave (*U. spelaeus eremus*)

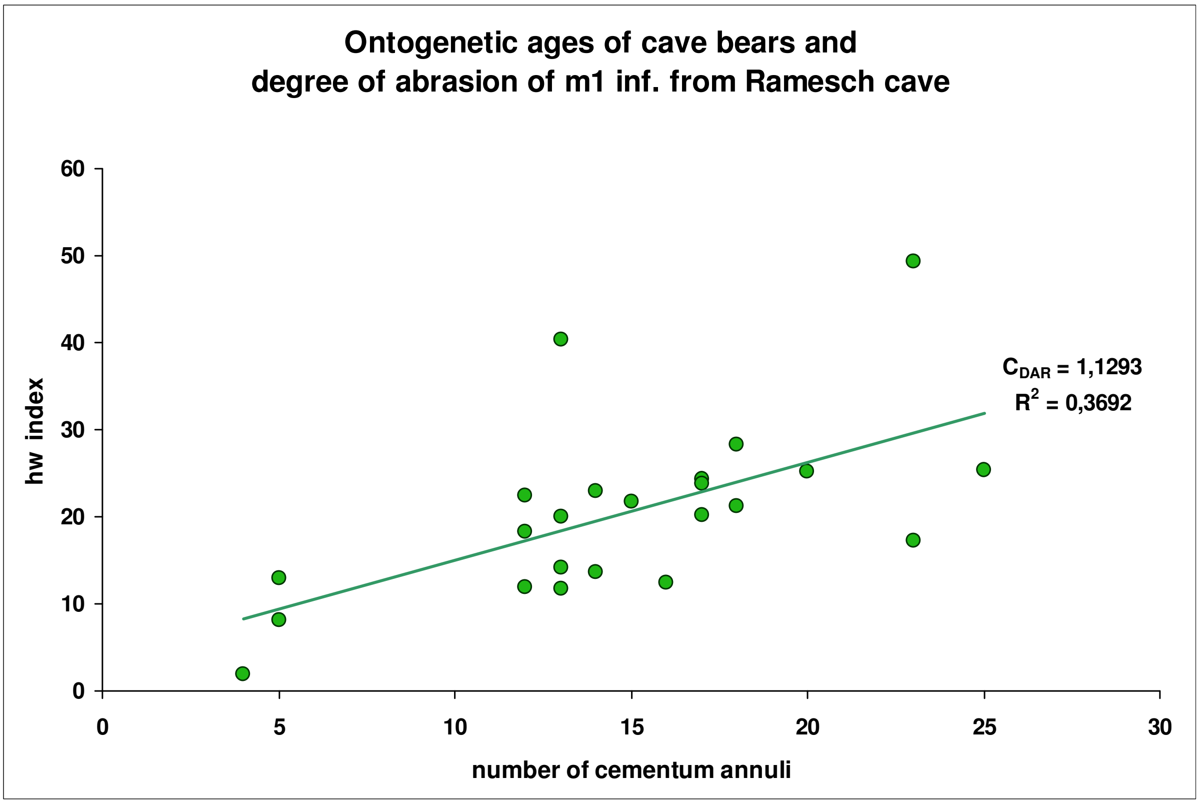


Fig. 12: Correlation between the degree of abrasion (hypoconid wear (hw) index) and the ontogenetic age (number of cementum annuli). Samples are from Ramesch cave, species: *U. spelaeus eremus.*

As can be seen in Fig. 12 there is a slightly dependence between the two parameters, however the coefficient of determination is relatively low.

The two outliers were measured correctly, it is not explainable why they are out of range. Eliminating the outliers lowers the increase. Its value would then be 0,8903 (C_{DAR}). But it would also increase the coefficient of determination to a value of 0,5162, which would correspond with the coefficient of determination of the samples from Ochsenhalt cave (same species).

<u>Ochsenhalt cave</u> (*U. spelaeus eremus*)

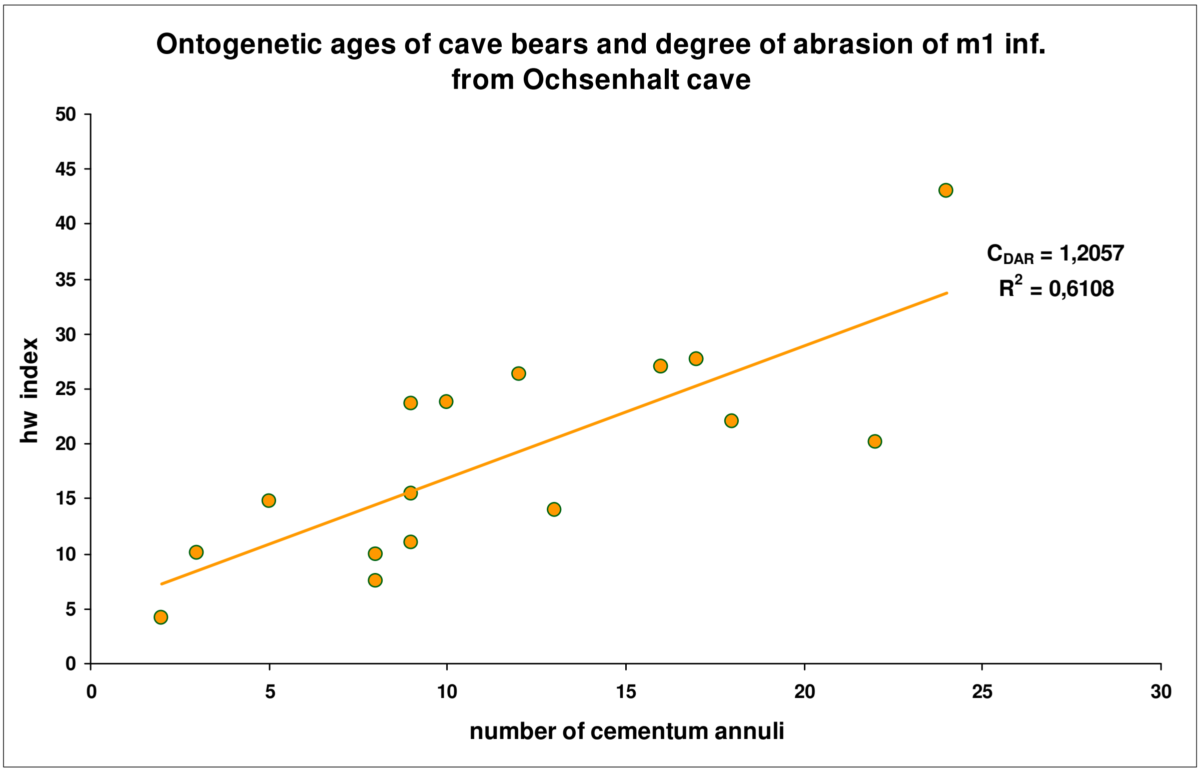


Fig. 13: Correlation between the degree of abrasion (hypoconid wear (hw) index) and the ontogenetic age (number of cementum annuli). Samples are from Ochsenhalt cave, species: *U. spelaeus eremus.*

The values of the two parameters of the Ochsenhalt cave (see Fig. 13) show a higher coefficient of determination than the values of the parameters of the Ramesch cave despite all specimens of the two caves belong to the same species *(U. s. eremus).*
As already written above, the value of the coefficient of determination of Fig. 13 however would be similar to the one in Fig. 12 considering the distribution of Ramesch samples without outliers.

The distribution in Fig. 13 is more regular than the one of Ramesch cave specimen. The increase however is similar to the increase-value (C_{DAR}) of the distribution of the sample size from Ramesch cave (ignoring the outliers of the latter).

Gamssulzen cave (*U. ingressus*)

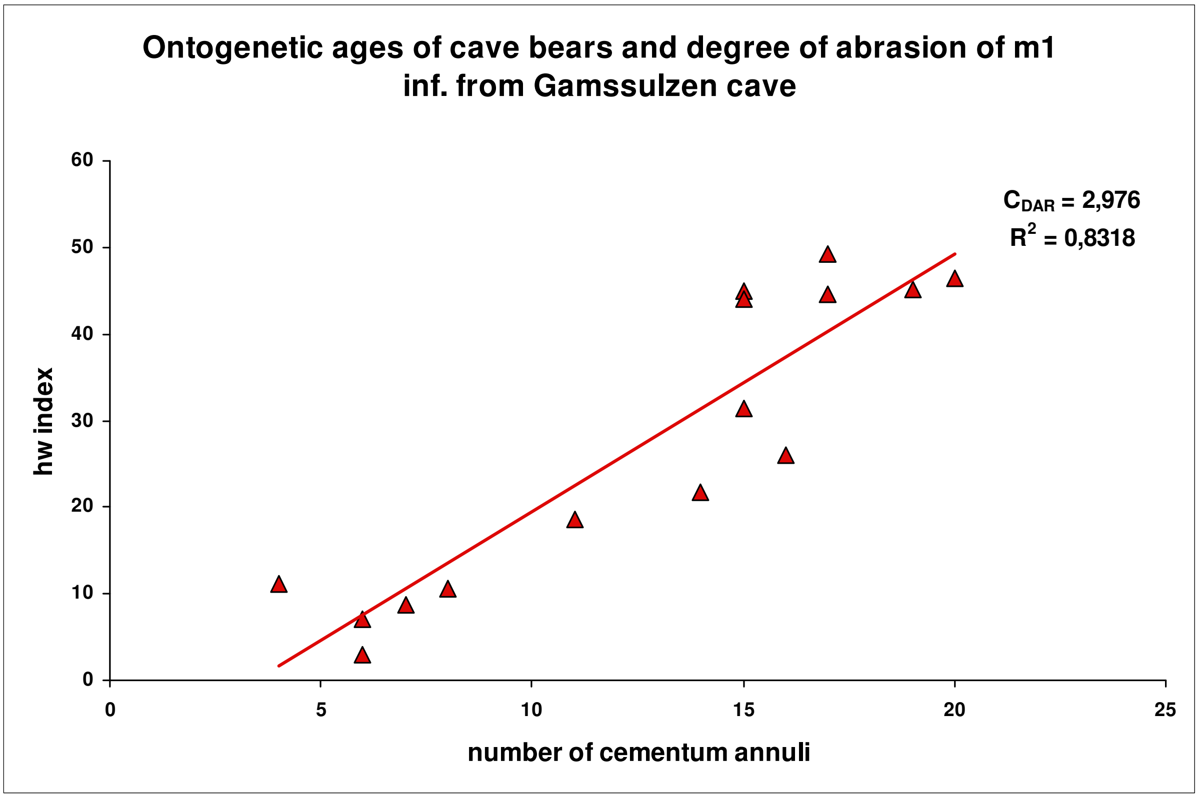


Fig. 14: Correlation between the degree of abrasion (hypoconid wear (hw) index) and the ontogenetic age (number of cementum annuli). Samples are from Gamssulzen cave, species: *U. ingressus.*

The distribution of the Gamssulzen cave plot shows a relatively high coefficient of determination and is quite regular (Fig. 14).

Three values had to be eliminated from this range.

The state of preservation of two m_1 was too bad to allow accurate counting of cementum annuli (most probably a major part of the cementum layer had been already corroded or eroded away).

The third value belongs to a first lower molar which had a too oblique abrasion on the hypoconid (and on the other cusps, too), so the measured value would have been falsified.

The increase of the Gamssulzen cave specimen distribution with a value of 2,976 (C_{DAR}) is the highest among the five examined caves.

Herkova jama cave (*U. deningeroides*)

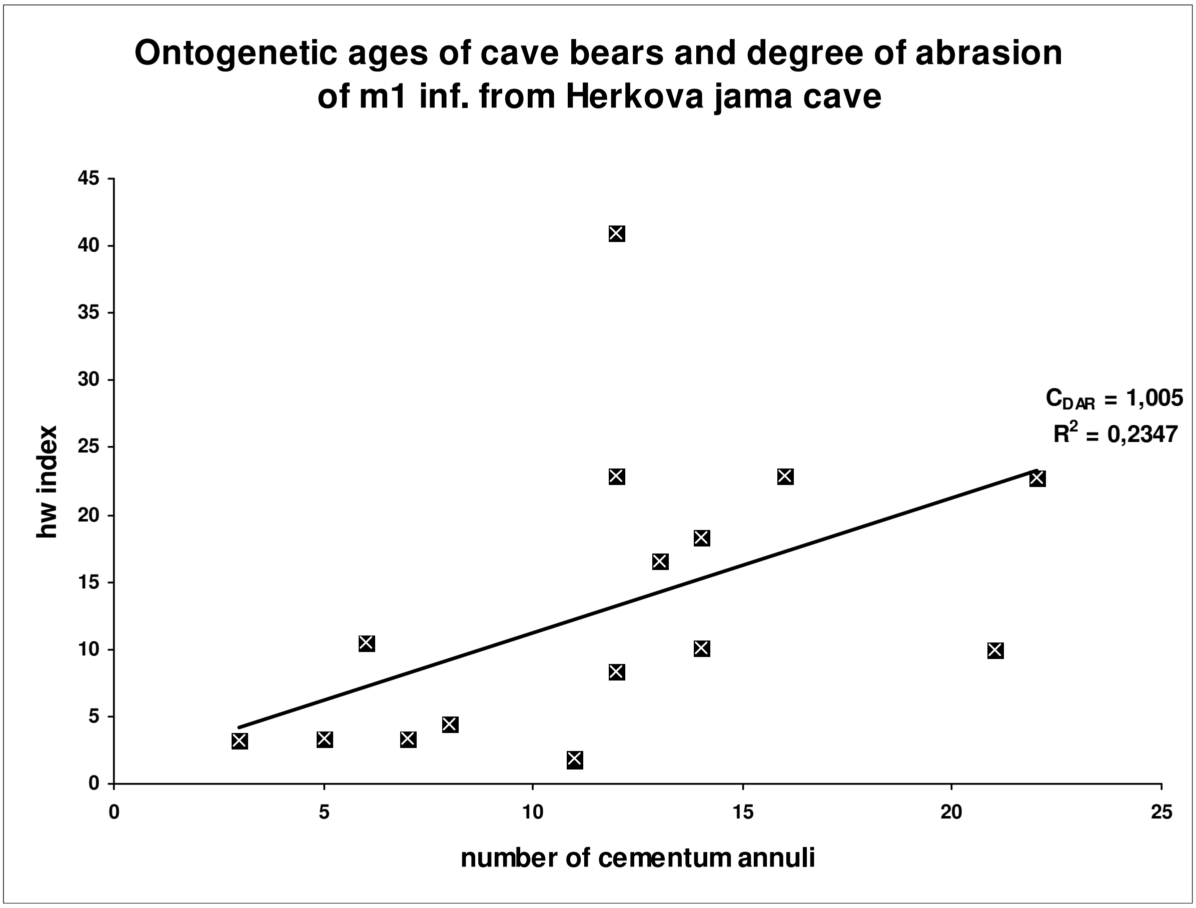


Fig. 15: Correlation between the degree of abrasion (hypoconid wear (hw) index) and the ontogenetic age (number of cementum annuli). Samples are from Herkova jama cave, species: *U. deningeroides.*

The distribution of Herkova jama specimen is the most irregular one among the examined caves. Therefore the sample size shows the lowest coefficient of determination from all caves (see Fig. 15).
The dependence between degree of abrasion and ontogentic age of the cave bear species *U. deningeroides* from the Herkova jama cave however is not the lowest of all caves.

The outlier again is not explainable, however the measuring was done correctly. Eliminating the outlier would give a value of increase of 1,001 (C_{DAR}), so there would be no big difference. The coefficient of determination (without outlier) would be 0,4158.

One value (a first lower molar with an ontogenetic age of approximately five years and an abrasion index of 47) was eliminated from this distribution because the cementum layer was in a very bad state of preservation.

Generally it is possible to explain the irregular distribution and low coefficient of determination because of corrosion or erosion reasons. Nearly all specimen of Herkova jama cave were in a bad state of preservation because of these chemical and physical processes.

Conturines Cave (*U. ladinicus*)

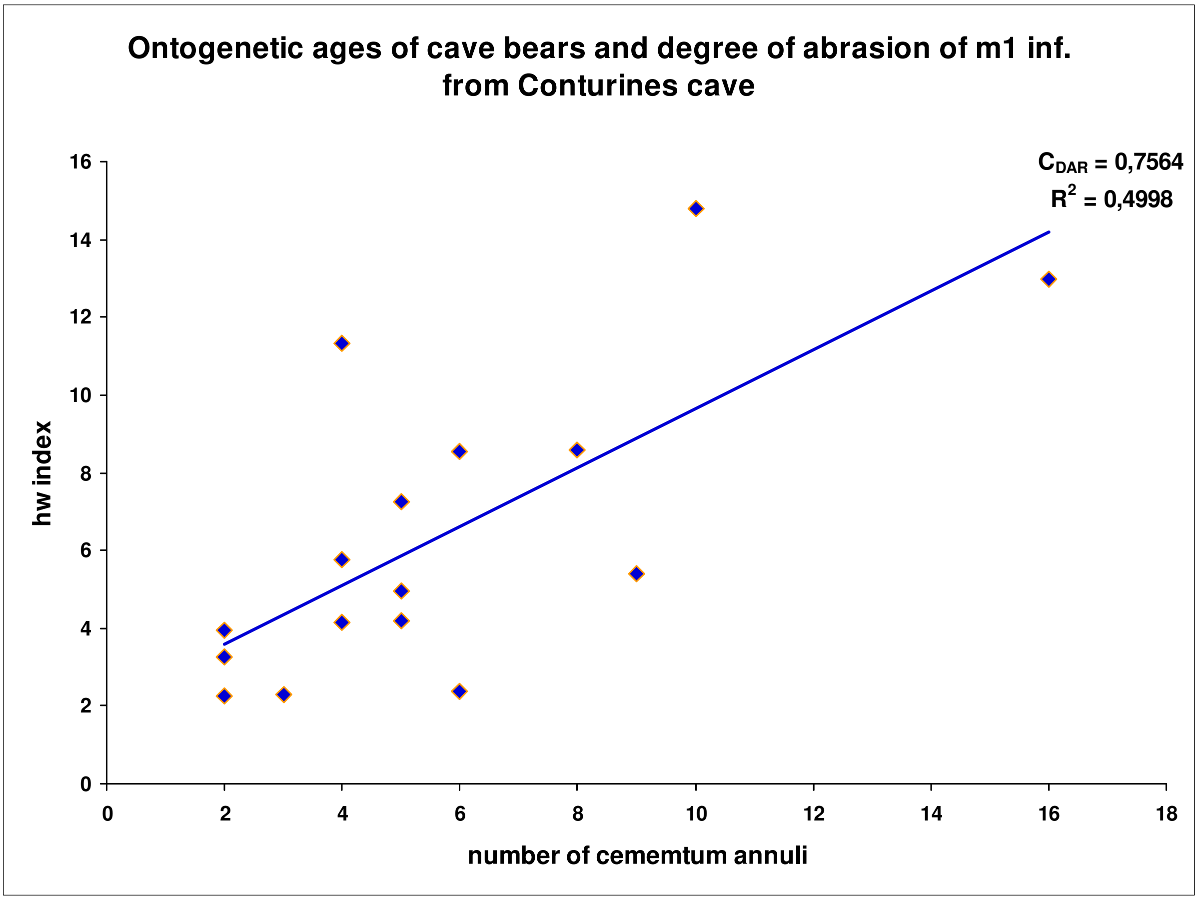


Fig. 16: Correlation between the degree of abrasion (hypoconid wear (hw) index) and the ontogenetic age (number of cementum annuli). Samples are from Conturines cave, species: *U. ladinicus.*

As can be seen in Fig. 16, the dependence between degree of abrasion and ontogentic age of the cave bear species *U. ladinicus* from the Conturines cave is quite low (more precisely it is the lowest dependence among the investigated caves).

There is a relatively wide gap between 10 and 16 years which can be caused by several reasons, for instance no random selection of the teeth was realisable.

The two outliers of this distribution are also not explainable because they were again measured correctly.
Without the outliers the value of increase of the distribution in Fig. 16 would even be somewhat lower: 0,6778 (C_{DAR}), although the coefficient of determination would be 0,6789 which is a higher value than the one of the original coefficient of determination: 0,4998.

Total distribution of all C_{DAR}

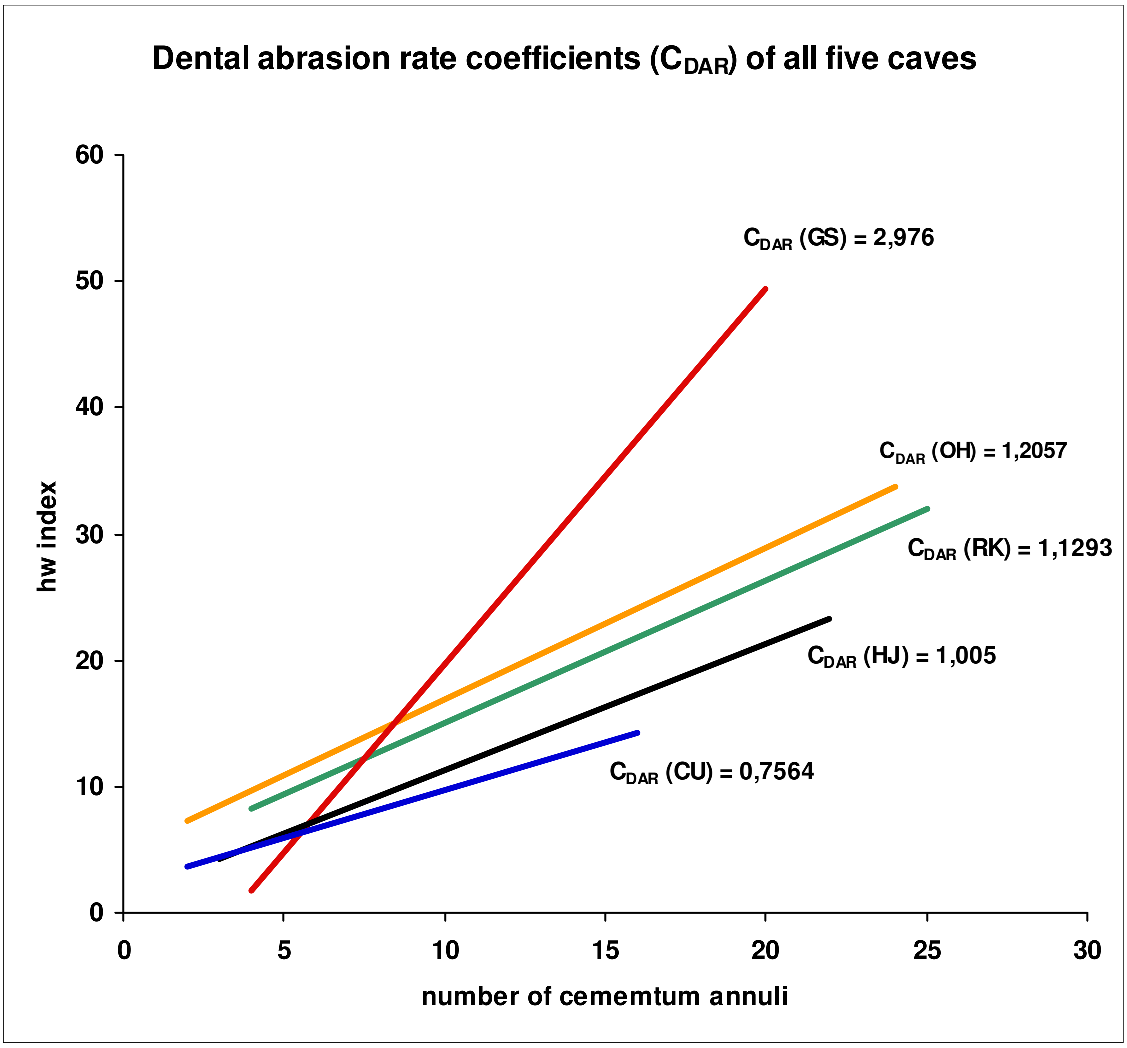


Fig. 17: Comparison of C_{DAR} (dental abrasion rate coefficient) of cave bear specimen from all five examined caves (built upon number of cementum annuli correlated to hypoconid wear index). Key: GS = Gamssulzen cave;
OH = Ochsenhalt cave; RK = Ramesch cave; HJ = Herkova jama cave and CU = Conturines cave.

As can be seen in Fig. 17, the DAR coefficient values of the caves differ from each other. The greatest difference is displayed by specimen of Gamssulzen and Conturines cave: The values from Gamssulzen cave have the highest coefficient and those of Conturines cave are characterized by the lowest coefficient. Thus it can be assumed that the two cave bear faunas of these caves (*U. ingressus* for Gamssulzen cave and *U. ladinicus* for Conturines cave) had distinctly different abrasion rates.
Although the same species appeared in both caves (*U. spelaeus eremus*) the abrasion rates of Ramesch and Ochsenhalt cave bear specimen slightly differ.

3.2.2 C_{DAR} and C13 isotope data

The dental abrasion rate coefficient was additionally correlated to carbon isotope values (data from measurements by HORACEK & al., 2012).

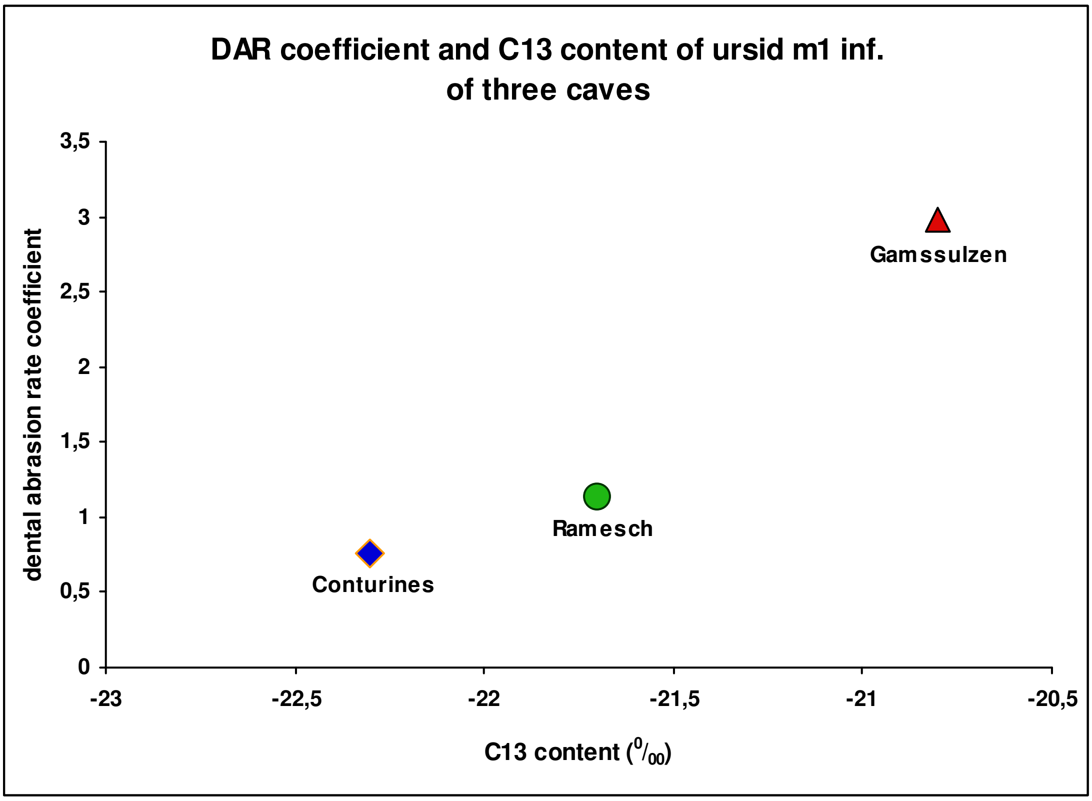


Fig. 18: Correlation between the dental abrasion rate coefficient (DAR coefficient) and the content of C13 from cave bear specimen of Conturines cave, Ramesch cave and Gamssulzen cave.

In Fig. 18 the dental abrasion rate coefficient (DAR coefficient) has been related to the content of c13 measured from specimen of three of the five examined caves of this study (the other two have not yet been measured).

Fig. 18 shows a positive correlation of DAR coefficient and C13 data from specimen of Conturines cave, Ramesch cave and Gamssulzen cave.

The graph displays that the C13 content of the cave bear specimens from Conturines cave as well as the DAR coefficient of this cave have the lowest values compared to Ramesch and Gamssulzen cave.

3.2.3 C_{DAR} correlated to altitude of entrance of cave sites

Furthermore the dental abrasion rate coefficient was also plotted together with the altitude of the caves.

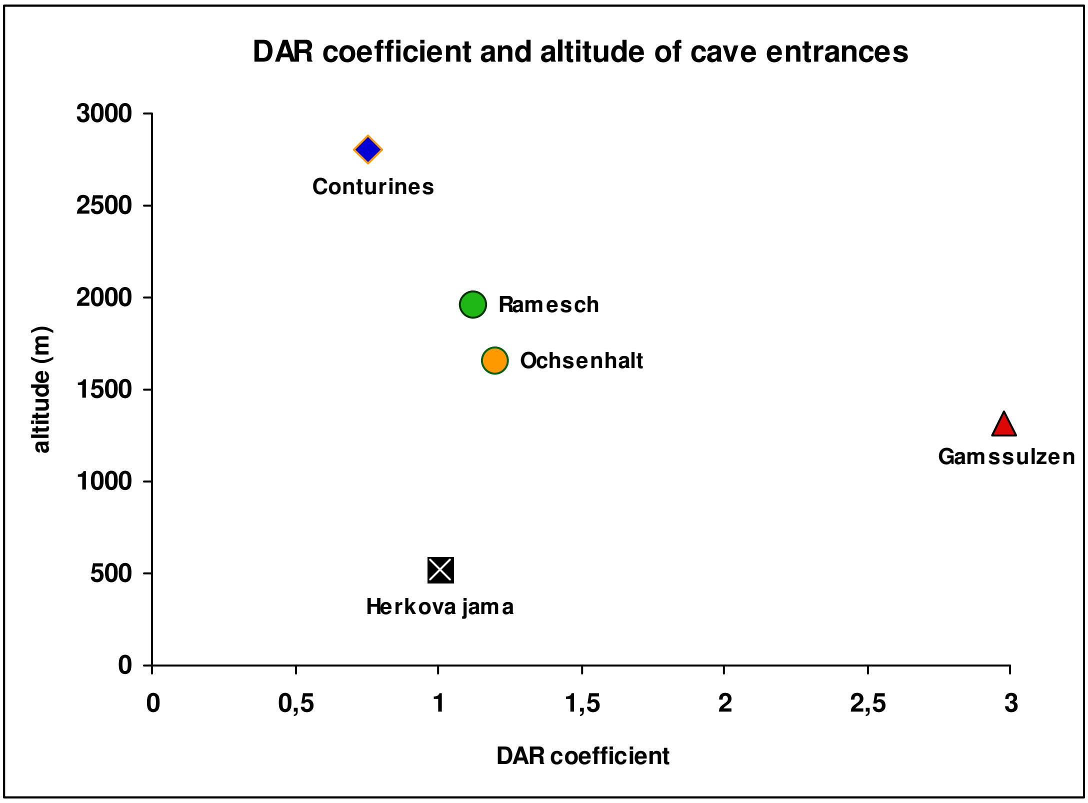


Fig. 19: Correlation between the dental abrasion rate coefficient (DAR coefficient) of cave bear specimen of all five examined caves and the level of cave entrances' altitude.

As can be seen in Fig. 19, the parameters altitude and C_{DAR} are interdepending. More specifically in this constellation it is a negative correlation.

Fig. 19 also confirms the fact (seen in Fig. 18 before) that *U. ladinicus* specimen from Conturines cave as the cave with the highest altitude among the three given caves in this graph evince the lowest DAR coefficient.

Both Ramesch and Ochsenhalt cave - representing the same species (*U. s. eremus*)- show a very similar dental abrasion rate coefficient (C_{DAR}). However they differ according their level of altitude.

U. deningeroides specimen of Herkova jama cave are outranging because it is the lowest situated cave among the investigated caves. The abrasion rate of this fauna approximately corresponds to *U. s. eremus* specimen (relates rather with the Ramesch fauna than to Ochsenhalt fauna).

3.2.4 Evolutionary level (C_{DAR} correlated to p4/4 index)

On the basis of premolar cusp development it is possible to make a statement of the evolutionary levels of the faunas. For visualizing a possible relationship between abrasion rate and evolutionary level their indices were plotted together.

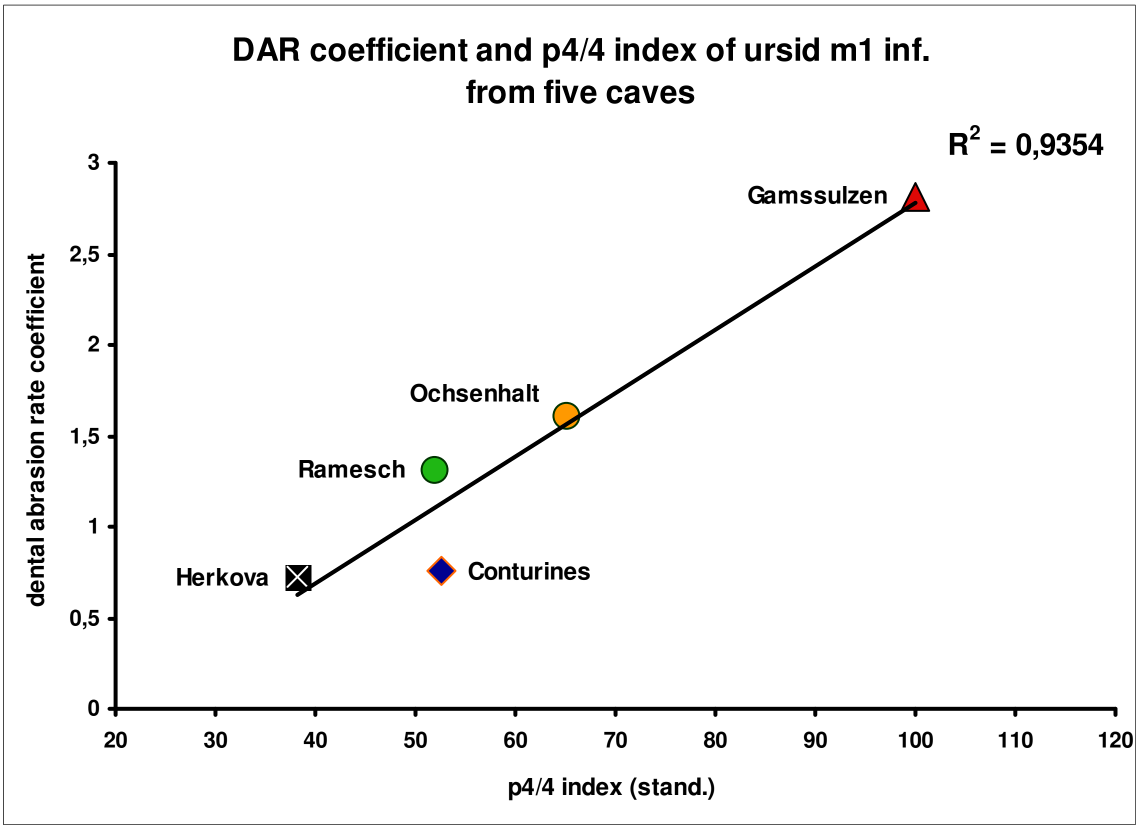


Fig. 20: DAR coefficients and evolution levels (p4/4 indices) of cave bear specimen from all five investigated caves plotted together. P4/4 index data of Gamssulzen, Ochsenhalt, Ramesch and Conturines adapted from RABEDER (1999). Herkova jama p4/4 index data pers. comm. C. Frischauf.

As can be noticed in Fig. 20, there is a very high significant positive correlation between evolution levels and the dental abrasion rate coefficient of cave bear tooth specimen from the different caves (note that coefficient of determination is about 0,94).

One cave (Conturines) however is outranging.
Dismissing Conturines cave data from this plot would even give a linear dependence of 0,99!

3.3 Correlation between alpine vegetation and cave bears according to their carbon isotope contents

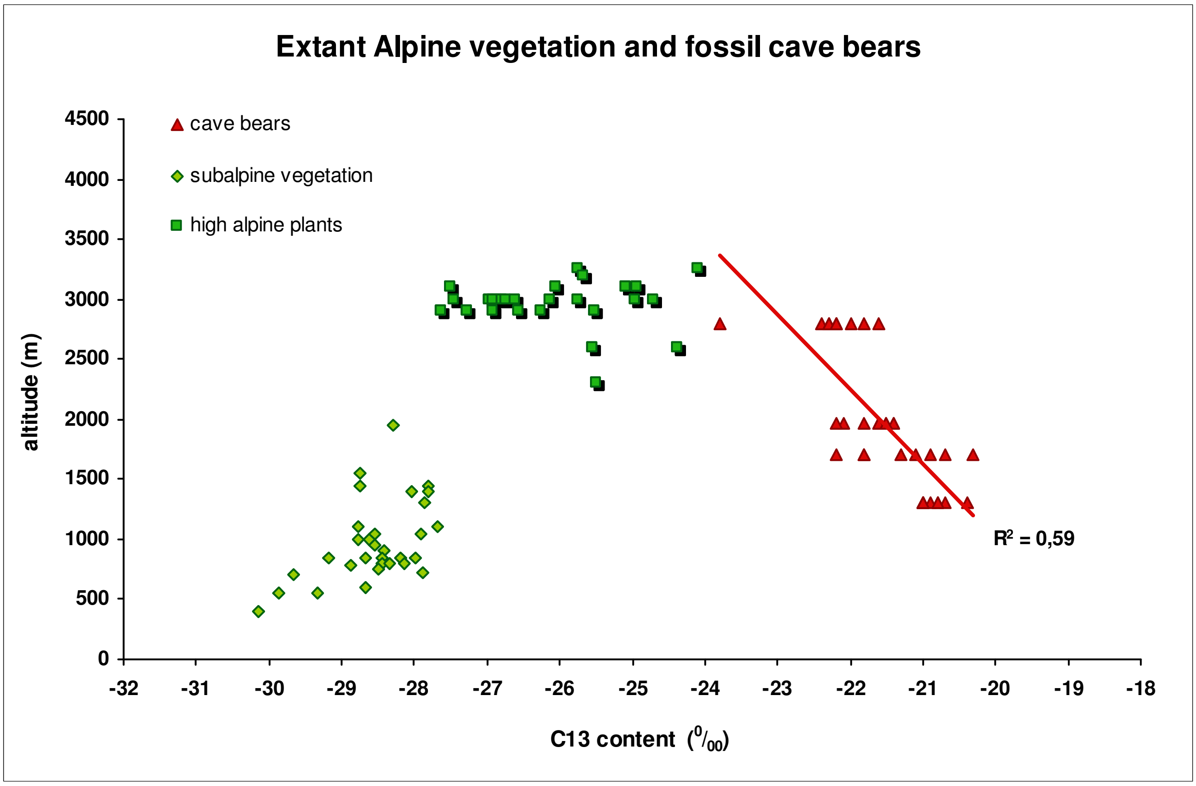


Fig. 21: Comparison between the contents of C13 and the level of altitudes from extant subalpine and high alpine plants (MÄNNEL & al., 2007) and Late Pleistocene cave bear remains (altitude values from cave entrances) (HORACEK & al., 2012).

Fig. 21 shows altitude levels of different vegetation forms and of cave entrances from cave bear faunas.
This parameter is plotted against the C13 content of these vegetation forms and of cave bear remains from the faunas. This compilation shall give a hint which kind of plants cave bears feed at which altitude.

It can be seen in Fig. 21 that there is a negative correlation between cave bear carbon isotope data and level of altitude (see red trend line).
Subalpine vegetation groups at the lower range of the scale with an higher amount of C13 whereas high alpine vegetation clusters at the middle range of the scale and reveals a lower content of carbon isotopes than subalpine vegetation.
All cave bear samples show the lowest C13 content values compared to extant high alpine and subalpine vegetation.

3.4 Microwear

The microwear analysis after SOLOUNIAS and SEMPREBON (2002) was applied for the first time on cave bears and for this study, under supervision of Katharina Bastl. The sample size consisted of first lower molars only and can be attributed to *Ursus ladinicus* from Conturines cave and *Ursus ingressus* from Gamssulzen cave.
Counting of microwear features was also performed together with K. Bastl. Nearly all known features were observed and counted: fine scratches, coarse scratches, small pits, large pits and puncture pits (see Tab. 4). It has to be noted, that indicators of a coarse diet - gouges and hypercoarse scratches (besides of one outranging value of the latter) - were absent. Small pits were present in moderate to high numbers compared to the first large, carnivorous dataset of BASTL & al. (2012). A special feature, the puncture pit, was observed in cave bears (see Tab. 4). These puncture pits however could be detected only on four of six m_1.
The sample size was too small to be able to make a significant statistical statement. According to the specifity of abrasion features, there was no difference between the Gamssulzen bear and the Ladinic bear, on the contrary *U. ingressus* (Gamssulzen cave) plotted right into the distribution of *U. ladinicus* (Conturines cave).

fauna	small pits average	large pits average	puncture pits	total pits	fine scratches average	coarse scratches average	hypercoarse scratches average
Conturines bear	88,5	15	0	103,5	16	2	0
Conturines bear	86	14	0	100	5,5	6	2
Conturines bear	102	31,5	3,5	137	13,5	2	0
Conturines bear	97	26,5	1	124,5	8,5	5,5	0
Conturines bear	99,5	24,5	2,5	126,5	9,5	3,5	0
Gamssulzen bear	95,5	24,5	2,5	122,5	13,5	3,5	0

Tab. 4: Total counting of common microwear features of all applicable tooth specimen. Investigated species: *Ursus ladinicus* from Conturines cave (Ladinic bear) and *Ursus ingressus* from Gamssulzen cave (Gamssulzen bear).

Bastl, pers. comm. in comparison to the carnivorous dataset of BASTL & al. (2012) showed that microwear features values of the cave bear samples evince more scratches, more large pits but less total pits than the carnivores examined by BASTL & al. (2012). Furthermore the cave bear specimen build their own cluster and show hardly overlapping with the carnivore samples.
This result was expectable as the dataset of BASTL & al. (2012) contained no carnivores with comparable diets.

4. Discussion

Investigations of this study provided results that surprisingly showed great differences according to aspects of ontogenetic age, abrasion rates and diets between the examined cave bear faunas.
The abovementioned aspects are further discussed in comparison with each other and related to other studied parameters like e.g. C13 contents, microwear patterns and age cohort classification.

Ontogenetic age and abrasion rates

The results showed a close correlation between number of cementum annuli (which represents the ontogenetic age) and hypoconid wear index. (Fig. 12 - 16)

However there are considerable differences between the faunas according to the abrasion rate (see Fig. 17). The abrasion rates of the faunas differ from each other and there is no overlapping. Even the abrasion rates of Ramesch and Ochsenhalt faunas slightly differ from another, although it is the same species.
Hence it can be assumed that cave bear populations of every cave site are characterized by their own typical abrasion rate and that the question of individual abrasion rates is not a matter of species but of the cave sites own cave bear populations.

In summary it may be concluded that the different abrasion rates give a clue for different dietary preferences which is further discussed (see further section "microwear analysis and nutrition").

Ontogenetic age and age cohorts

Determing ontogenetic ages for individuals of the cave bear faunas with help of age cohort classification was mostly ineffective. Reliable scoring of samples in age cohorts was depending on the fauna. Two faunas showed a tendency correlation between ontogenetic age and age cohort, displayed by an increase of “older individuals” classified in age cohorts with higher numbers: *U. spelaeus eremus* from Ochsenhalt cave (see Fig. 7) and *Ursus ingressus* from Gamssulzen cave (see Fig. 8).

Interestingly *U. spelaeus eremus* specimen of Ramesch cave revealed no dependence between ontogenetic age and age cohort scoring at all. This fact raises the question whether cave bears of Ramesch cave were adapted to a different nutrition than cave bears of the same species from Ochsenhalt cave. STINER (1998) already supposed that cave bear populations in distinct habitats have different abrasion rates depending on dietary patterns.

Nevertheless there is too much overlapping of samples in every fauna (Fig. 11) which indicates that it is not possible to estimate a correct age for every individual by age cohort classification after Stiner.

In her study developing this method of age-scoring, STINER (1998) declared the technique neither to be a trial for estimating age in real years, nor that its stages represent equivalent spans of time.

This study evidences, that it is indeed not possible, to figure out exact ages in life years of individuals with this age-scoring method.

Abrasion rates and C13 contents

Up to now C13 contents of specimen from only three cave sites (Gamssulzen, Ramesch and Conturines) were measured and published (BOCHERENS & al., 2011; HORACEK & al., 2012) As can be seen in Fig. 18, there is a close correlation between the dental abrasion rate coefficient and C13 data which means the smaller the DAR coefficient the lower the C13 content value. Potentially this correlation is associated with the part of harder plants like e.g. grass and herbs.

The aspect of C13 measurements related to altitude levels is further discussed in the next section.

C13 data and altitude levels

We originally supposed that the content of C13 isotopes in cave bear finds from Conturines cave must be the highest because this cave is situated at the highest altitude of all known cave sites which yielded cave bear material. This supposition was supported by insights of MÄNNEL & al. (2007). They showed that an increase of C13 contents (sampled from hair of ruminants) is connected with increasing level of altitude. KÖRNER & al. (1991) also observed the phenomenon of higher amounts of carbon isotopes in high mountain vegetation than in plants settled at low altitudes. Therefore they concluded that C13 discrimination decreases with altitude.

In this study our original supposition was falsified as we found out (see Fig. 21) that *U. ladinicus* remains (and remains of the other faunas, too) revealed distinctly lower C13 content data than those from extant vegetation at an equivalent level of altitude. This leaded to the assumption that the climate in the Middle Wurmian had to be warmer than nowadays with the possibility of settlement of subalpine plants at a higher altitude, which is further discussed in the next section.

On the basis of our current knowledge the negative correlation between C13 content data of cave bear remains and level of altitude (see Fig. 21) is not yet explainable.

Nutrition and alpine climate

The nutrition of cave bears was very often a controversial issue in former times. It could be pointed out in different studies (also evidenced and discussed in recent literature: DÖPPES & al. (2011)) that cave bears were at least an herbivorous species.

An important aspect that should be considered and which could give a clue about the type of cave bear diets, is the climate. As DÖPPES & al. (2011) have found out and confirmed, the landscape around Conturines cave in the Middle Wurmian was very different to nowadays. Today this cave is situated in a rocky and snowy zone almost without any vegetation (upper alpine level).

The Middle Wurmian period had to be warmer than the climate today; this was concluded in all present analyses. It could be confirmed that the Alps were free of ice and the timber line was some hundred meters higher than today (DÖPPES & al., 2011).

Another proof for the warmer climate in the Middle Wurmian are results of palynological analyses (HILLE and RABEDER, 1986). They showed that high alpine cave bears faunas like *U. ladinicus*, too, most likely consumed mainly subalpine plants. This diet was only possible if the Middle Wurmian indeed used to be warmer than today so that the timber line was situated much higher than in the Alps nowadays.
Recent C13 isotope studies (BOCHERENS & al., 2011; HORACEK & al., 2012) verify this diet pattern.

Microwear analysis and nutrition

To explore the specific dietary habits of cave bear faunas the microwear method after SOLOUNIAS and SEMPREBON (2002) was applied for the first time and turned out to be a good approach to fastly identify the likely content of their nutrition.

Although the sample size was far too small and it was possible to use only six first lower molars which were applicable for examining microwear features, it was possible to get a first hint of probably dietary habits of two of the cave bear faunas (*U. ingressus* from Gamssulzen cave and *U. ladinicus* from Conturines cave) involved in this study.

As small pits are a characteristic wear feature for mostly all predators (BASTL & al., 2012), they also had been found on all six cave bear samples applied in microwear method.

The most important feature that had been discovered on the specimen was puncture pits. They occurred in a high frequency and are valuable in quality because they are a direct evidence for frugivory. This indicates that the cave bears partially were frugivores. More frugivorous species can be distinguished from more tree-foliage species by a higher frequency of more coarse scratches and generally more pits (GODFREY & al., 2004). Most scratches that could be counted on the cave bear molars were fine scratches which contradicts that the two cave bear faunas could have been mainly frugivores.

Additionally it must be remarked that two of the six molars had no puncture pits at all, which can be interpreted as special diet habit of these individuals – maybe they had a different nutrition preference or did not consume any fruits at least recently.

Considering the ratio of puncture pits to fine scratches it can be assumed that Gamssulzen and Ladinic bear have been mixed "fruit and foliage" consumers.

Since the dietary features occurred equally both in the two examined species it was not possible to give an explanation to the question why the teeth of *U. ladinicus* of Conturines cave only had very little abrasion.

For more detailed information it would be necessary to examine also specimen of *U. ladinicus* of other caves and especially analysing microwear features with a much larger sample size.

Nutrition and evolution levels of teeth (p4/4 index)

Gamssulzen samples are plotting not only at the highest date of p4/4 index - which means they dispose the highest evolution level - but also at the highest date of the DAR coefficient.

This relationship could indicate that perhaps the Gamssulzen cave bears were best adapted to coarse diets and therefore were able to wear down their teeth distinctly more than other cave bear faunas.

The Deninger bear (*U. deningeroides*) as the oldest and most primitive bear among the four cave bear species reveals the lowest evolution level which was expectable as the Deninger bear lived far earlier, in the Middle Pleistocene (whereas the other cave bear faunas lived in the Late Pleistocene).

Surprisingly *U. ladinicus* is outranging the trend line of development of the evolution levels of teeth (see Fig. 20). Although the Ladinic bear shows a likewise p4/4 index and thus a comparable evolution level as the Ramesch bear, he reveals a similar abrasion rate as the Deninger bear. The latter fact is astonishing as the Deninger bear lived in a different (earlier) time period than the Ladinic bear.

The phenomenon that cave bears of the species *U. ladinicus* do not follow the general evolution trend is maybe a question of adaption to this extraordinary high altitude differing from all other known cave bear caves.
Therefore, also for this investigation, it is necessary to analyse other faunas of *U. ladinicus* to check if the outranging phenomenon is a matter of all faunas of this species or not.

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7. Abstract

A new method called DARA (dental abrasion rate analysis) was developed for this study. This method combines the technique of counting cementum rings (annuli) for determination of the ontogenetic age after DEBELJAK (1996) with a new method for the quantification of dentine and enamel wear of first lower molars (m_1) from five Alpine caves.

Additionally different wear stages of m_1 (after STINER, 1998) were correlated to the ontogenetic age, which was determined by application of the annuli counting technique. Furthermore the microwear method after SOLOUNIAS and SEMPREBON (2002) has been done for providing extra explanatory approaches for different levels of abrasion and possible dietary patterns of cave bears.
Therefore cave bear teeth from five Alpine caves were chosen for this study with all four Alpine cave bear taxa involved.
Specimen of the following cave bear faunas have been investigated: *Ursus ladinicus* (RABEDER & al. ,2004) (Conturines cave), *U. ingressus* (RABEDER & al., 2004) (Gamssulzen cave), *U. deningeroides* (MOTTL, 1964) (Herkova jama cave) and *U. spelaeus eremus* (RABEDER & al., 2004) (Ramesch cave and Ochsenhalt cave).

The reason for applying the abovementioned methods was the enigmatic low extent of abrasion of cave bear teeth from Conturines cave. Nearly no abrasion could be detected on these teeth, which is remarkable considering the different degrees of abrasion of teeth in other cave bear taxa.
The correlation between ontogenetic ages determined with the cementum ring method and the wear index (hypoconid wear index hwi) is distinctly higher than with classification of the different stages of abrasion in age cohorts.
Thus for assessment of correct ontogenetic ages it is more effective applying DARA than age cohort classification of STINER (1998).
The annual abrasion rates however (displayed by the DAR coefficient) differ according to the taxon, level of altitude of the cave entrances and C13 content determined for the cave bear material.
Microwear results point out that cave bears exclusively fed herbivore and it could be evidenced that they at least partially also had a frugivor nutrition.

Zusammenfassung

Für diese Studie wurde eine neue Methode namens Dental Abrasion Rate Analysis = DARA (zu deutsch: Zahn-Abrasionsraten-Analyse) entwickelt. Diese Methode kombiniert die Auszählung von Zementringen (Annuli) für die Bestimmung des ontogenetischen Alters nach DEBELJAK (1996) mit einer neuen Methode zur Quantifizierung der Abkauung von Schmelz und Dentin an den ersten Unterkiefermolaren (m_1) von Höhlenbären aus fünf alpinen Höhlen. Weiterhin wurden verschiedene Abkauungsstadien der m_1 (s. STINER, 1998) mit dem ontogenetischen Alter in Zusammenhang gebracht, indem auch hier die Zementring-Methode angewendet wurde.

Abschließend wurde die Microwear Methode nach SOLOUNIAS und SEMPREBON (2002) durchgeführt, um zusätzliche Lösungsvorschläge für die verschiedenen Abkauungsgrade sowie Erkenntnisse über mögliche Ernährungsmuster der Höhlenbären zu liefern.

Für die Durchführung dieser Studie wurde Höhlenbär-Zahnmaterial von fünf verschiedenen alpinen Höhlen mit allen vier Höhlenbärentaxa inkludiert ausgewählt.

Es wurden Exemplare der folgenden Faunen untersucht: *Ursus ladinicus* (RABEDER & al., 2004) (Conturineshöhle), *U. ingressus* (RABEDER & al., 2004) (Gamssulzenhöhle), *U. deningeroides* (MOTTL, 1964) (Herkova jama Höhle) und *U. spelaeus eremus* (RABEDER & al., 2004) (Ramesch Knochenhöhle und Ochsenhalthöhle).

Der Grund für die Anwendung der obengenannten Methoden war der, dass die Höhlenbärzähne der Conturines Höhle ausnahmslos einen ungewöhnlich geringen Abrasionsgrad aufwiesen. Es konnte fast keine Abnutzung der Zähne festgestellt werden, was sehr auffällig ist, da die anderen Höhlenbärtaxa zwar durchaus unterschiedliche Abkauungsgrade zeigten, aber die Abkauung immer sichtbar war.

Die Korrelation der mit der Zementring-Methode erhobenen ontogenetischen Alter mit dem Abrasionindex (Hypoconid-Abkauungs-Index hwi) ist wesentlich höher als mit der Klassifizierung der verschiedenen Abrasionsgrade in jeweilige Kohorten.
Daher ist es effektiver, das korrekte ontogentische Alter mit der DARA-Methode als mit der Alters-Kohorten Klassifikation nach Stiner (1998) zu bestimmen.
Die jährlichen Abrasionsraten (die durch den Abrasionsraten-Koeffizient C_{DAR} dargestellt werden) unterscheiden sich jedoch je nach Taxon, Altitude der Höhleneingänge und dem C13 Gehalt des Höhlenbär-Materials.
Die Ergebnisse der Microwear Untersuchung zeigen, dass sich die Höhlenbären ausschließlich herbivor ernährt haben und es konnte weiterhin nachgewiesen werden, dass sie sich zu einem gewissen Teil auch frugivor ernährt haben.

Keywords: DARA, age cohorts, cementum annuli, ontogenetic age, dental abrasion rate, cave bear, microwear, C13 content, altitude of cave entrances, palaeodiet, palaeoclimate

8. Appendix

8.1 Table of measurements

inv.no.	sub.no.	side	length	hyd width	hw index	annuli	species
RK 192	-	dex	28,50	3,6	12,46	16	*Ursus spelaeus eremus*
RK 257	1	dex	26,80	3,2	11,94	12	*Ursus spelaeus eremus*
RK 310	-	sin	29,60	2,4	8,11	5	*Ursus spelaeus eremus*
RK 312	-	dex	29,00	6,3	21,72	15	*Ursus spelaeus eremus*
RK 319	-	dex	27,15	13,4	49,36	23	*Ursus spelaeus eremus*
RK 346	-	dex	26,65	5,4	20,08	13	*Ursus spelaeus eremus*
RK 370	-	sin	29,05	5,3	18,24	12	*Ursus spelaeus eremus*
RK 389	-	dex	28,10	4,9	17,26	23	*Ursus spelaeus eremus*
RK 392	-	dex	30,00	12,1	40,33	13	*Ursus spelaeus eremus*
RK 394	-	dex	31,45	3,7	11,76	13	*Ursus spelaeus eremus*
RK 399	-	sin	30,50	6,9	22,46	12	*Ursus spelaeus eremus*
RK 413	-	dex	27,90	7,0	25,09	20	*Ursus spelaeus eremus*
RK 417	-	dex	31,50	8,9	28,25	18	*Ursus spelaeus eremus*
RK 427	-	dex	29,65	6,0	20,24	17	*Ursus spelaeus eremus*
RK 457	-	sin	30,00	6,4	21,17	18	*Ursus spelaeus eremus*
RK 488	-	sin	30,80	0,6	1,95	4	*Ursus spelaeus eremus*
RK 494	1	dex	29,35	4,2	14,14	13	*Ursus spelaeus eremus*
RK 494	2	dex	27,05	6,9	25,32	25	*Ursus spelaeus eremus*
RK 500	-	sin	27,85	6,4	22,98	14	*Ursus spelaeus eremus*
RK 502	-	sin	27,10	3,5	12,92	5	*Ursus spelaeus eremus*
RK 540	-	dex	28,55	6,8	23,82	17	*Ursus spelaeus eremus*
RK 544	-	sin	28,70	7,0	24,39	17	*Ursus spelaeus eremus*
RK 659	-	dex	29,60	4,1	13,69	14	*Ursus spelaeus eremus*
OH 25	1	sin	30,70	4,6	14,82	5	*Ursus spelaeus eremus*
OH 34	2	dex	30,00	8,1	27,00	16	*Ursus spelaeus eremus*
OH 41	2	sin	26,80	2,7	10,07	3	*Ursus spelaeus eremus*
OH 45	2	sin	30,80	6,8	22,08	18	*Ursus spelaeus eremus*
OH 51	1	sin	29,80	7,9	26,34	12	*Ursus spelaeus eremus*
OH 81	2	sin	28,70	6,8	23,69	9	*Ursus spelaeus eremus*
OH 81	3	sin	31,50	3,2	10,00	8	*Ursus spelaeus eremus*
OH 96	1	sin	28,20	4,0	14,00	13	*Ursus spelaeus eremus*
OH 102	1	dex	27,50	6,6	23,82	10	*Ursus spelaeus eremus*
OH 103	4	sin	29,50	4,6	15,42	9	*Ursus spelaeus eremus*
OH 114	1	sin	30,80	2,3	7,47	8	*Ursus spelaeus eremus*
OH 114	2	dex	26,35	2,9	11,01	9	*Ursus spelaeus eremus*
OH 133	2	dex	27,95	1,2	4,11	2	*Ursus spelaeus eremus*
OH 143	4	dex	28,30	5,7	20,14	22	*Ursus spelaeus eremus*
OH 163	1	dex	31,20	13,4	42,95	24	*Ursus spelaeus eremus*
OH 168	1	dex	27,10	7,5	27,68	17	*Ursus spelaeus eremus*
GS 2	3	sin	28,80	5,4	18,58	11	*Ursus ingressus*
GS 105	1	dex	29,50	13,3	45,08	19	*Ursus ingressus*
GS 109	1	dex	29,10	13,1	45,02	15	*Ursus ingressus*
GS 118	1	dex	31,40	13,8	43,95	15	*Ursus ingressus*
GS 136	1	dex	31,00	11,1	35,81	13	*Ursus ingressus*
GS 167	1	dex	30,00	2,6	8,67	7	*Ursus ingressus*
GS 167	2	dex	31,40	9,9	31,37	15	*Ursus ingressus*
GS 168	1	dex	33,75	3,6	10,52	8	*Ursus ingressus*
GS 196	1	dex	28,10	13,1	46,44	11	*Ursus ingressus*

inv.no.	sub.no.	side	length	hyd width	hw index	annuli	species
GS 208	2	sin	30,50	1,3	4,10	2	*Ursus ingressus*
GS 300	2	sin	28,30	13,2	46,47	20	*Ursus ingressus*
GS 546	1	sin	27,75	13,7	49,19	17	*Ursus ingressus*
GS 547	1	sin	29,70	7,7	25,93	16	*Ursus ingressus*
GS 625	1	sin	30,60	6,7	21,73	14	*Ursus ingressus*
GS 636	1	dex	30,45	3,4	11,17	4	*Ursus ingressus*
GS 639	1	dex	31,00	2,2	7,10	6	*Ursus ingressus*
GS 682	2	dex	32,70	1,0	3,06	6	*Ursus ingressus*
GS 708	1	sin	31,00	13,8	44,52	17	*Ursus ingressus*
HJ 15	1	dex	27,90	0,5	1,79	11	*Ursus deningeroides*
HJ 39	1	sin	26,40	10,8	40,91	12	*Ursus deningeroides*
HJ 57	-	dex	27,90	1,0	3,41	5	*Ursus deningeroides*
HJ 87	1	dex	25,10	0,8	3,19	3	*Ursus deningeroides*
HJ 105	-	dex	25,10	2,5	9,96	21	*Ursus deningeroides*
HJ 110	1	dex	26,15	2,2	8,41	12	*Ursus deningeroides*
HJ 131	1	dex	24,70	2,5	10,12	14	*Ursus deningeroides*
HJ 131	2	dex	24,90	5,7	22,89	16	*Ursus deningeroides*
HJ 132	-	sin	24,60	1,1	4,47	8	*Ursus deningeroides*
HJ 147	2	sin	26,80	2,8	10,45	6	*Ursus deningeroides*
HJ 160	-	sin	26,00	4,3	16,54	13	*Ursus deningeroides*
HJ 173	2	dex	22,40	10,6	47,32	5	*Ursus deningeroides*
HJ 176	1	sin	28,00	6,4	22,86	12	*Ursus deningeroides*
HJ 184	5	sin	26,35	6,0	22,77	22	*Ursus deningeroides*
HJ 190	1	sin	26,90	0,5	1,86	11	*Ursus deningeroides*
HJ 191	3	sin	26,40	0,9	3,41	7	*Ursus deningeroides*
HJ 208	1	sin	26,70	6,1	22,85	16	*Ursus deningeroides*
HJ 210	2	sin	27,25	5,0	18,35	14	*Ursus deningeroides*
CU 1	1	sin	28,00	1,1	3,93	2	*Ursus ladinicus*
CU 1	3	sin	26,40	0,7	2,65	1	*Ursus ladinicus*
CU 1	5	sin	30,30	2,2	7,26	5	*Ursus ladinicus*
CU 14	-	dex	28,50	3,7	12,98	16	*Ursus ladinicus*
CU 17	1	dex	28,20	1,4	4,96	5	*Ursus ladinicus*
CU 19	1	sin	30,05	3,4	11,31	4	*Ursus ladinicus*
CU 30	-	sin	27,80	1,6	5,76	4	*Ursus ladinicus*
CU 33	1	sin	26,80	0,6	2,24	2	*Ursus ladinicus*
CU 53	3	sin	26,30	1,1	4,18	5	*Ursus ladinicus*
CU 500	1	dex	29,10	2,5	8,59	8	*Ursus ladinicus*
CU 500	2	dex	29,20	2,5	8,56	6	*Ursus ladinicus*
CU 505	-	dex	29,70	1,6	5,39	9	*Ursus ladinicus*
CU 576	1	sin	27,60	0,7	2,36	6	*Ursus ladinicus*
CU 577	-	dex	27,60	0,9	3,26	2	*Ursus ladinicus*
CU 679	-	sin	27,80	1,2	4,14	4	*Ursus ladinicus*
CU 680	-	dex	26,20	0,6	2,29	3	*Ursus ladinicus*
CU 709	-	dex	26,00	3,9	14,81	10	*Ursus ladinicus*

Tab. 5: Measurements of m_1 of cave bears out of five Alpine caves

8.2 List of Abbreviations

AMS = Accelarator mass spectrometry
BP = before present
C14 = radiocarbon isotope
CalPal = Cologne Radiocarbon Calibration & Paleoclimate Research Package.
conv. = conventional radiocarbon age dating
CU = Conturines cave
DAR coefficient = dental abrasion rate coefficient
DARA = dental abrasion rate analysis
dex = dexter
GS = Gamssulzen cave
HJ = Herkova jama cave
hwi / hw index = hypoconid wear index
hyd width = hypoconid width
inv.no. = inventory number
ka = kilo anni
Lab.nr. = laboratory number
m_1 / m1 inf. = first lower molar
OH = Ochsenhalt cave
p4/4 index = morphodynamic index of fourth upper and lower premolar (RABEDER 1999)
RK = Ramesch cave
sin = sinister
sub.no. = sub number
US datings = uranium-thorium series datings
U-Th = Uranium/Thorium
whwa = width of hypoconid wear area

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07-08/2006	Molecular diagnostic-microarray technics at University of Leipzig, Max-Bürger-Forschungszentrum, working group Dr. Ahnert

Conference attendance

03/2013	Arbeitskreis Wirbeltierpaläontologie in der Paläontologischen Gesellschaft at Laimering, Germany
09/2012	International Cave Bear Symposium at Băile Herculane, Romania
03/2012	Arbeitskreis Wirbeltierpaläontologie in der Paläontologischen Gesellschaft at Neustadt, Germany
11/2011	Wissenschaftliche Herbsttagung der ÖGKM at Vienna, Austria

Publications

Holland, L. & Rabeder, G., 2012. Correlation between wear stages of teeth and plant nutrition of cave bears (Ursidae, Mammalia) from Alpine caves – 18th International Cave Bear Symposium (ICBS) Baîle Herculane, Romania 20-22 September 2012, poster abstr.: 53

Languages

English
French