Morphological responses of cave bears (Ursus spelaeus group) to high-alpine habitats

ABSTRACT

A comparison of metrical and morphological data from more than 30 bear populations belonging to the cave bear group (*U. spelaeus* and its relatives *U. eremus*, *U. ladinicus*, *U. ingressus* as well as their predecessor *U. deningeri*) shows that the different species developed very different adaptations to the altitude of their habitats. Whereas there is a reduction of body size in *Ursus eremus* and *U. ladinicus* correlated with the altitude of the habitat ("alpine nanism") no such correlation can be observed in *U. ingressus*. In *U. ingressus* there is a positive correlation of the tooth indices and the altitude of the habitat, i.e. in the higher sites the teeth are more evolved.

ZUSAMMENFASSUNG

Morphologische Anpassung des Höhlenbären (*Ursus spelaeus*) an hochalpine Habitate

Aus alpinen und außeralpinen Höhlen liegen Höhlenbärenreste in so großen Mengen vor, dass es möglich ist, statistische Methoden zu verwenden und die Bärenfaunen untereinander zu vergleichen. Als „Höhlenbären" verstehen wir, in Abwesenheit von unterschiedlichen Trivialnamen, die Angehörigen der *Ursus spelaeus*-Gruppe d.h. neben *U. spelaeus* auch die nah verwandten Arten *U. eremus*, *U. ladinicus*, *U. ingressus* sowie die mittelpleistozäne Vorläuferform *U. deningeri*. Die hier untersuchten Höhlenbärenfaunen stammen alle aus dem Zeitbereich zwischen etwa 80.000 und 25.000 Jahren vor heute. Zum Vergleich der Körpergröße werden vor allem die Längen- und Breitenwerte der Backenzähne und der Mittelhand- und Mittelfußknochen (Metapodien) herangezogen, weil Zähne und Metapodien einerseits die bei weitem häufigsten Elemente in den Fundinventaren sind und weil andererseits die Körpergröße eng mit der Zahn- und Metapodiengröße gekoppelt ist. Als „morphologische Daten" werden ebenfalls statistisch erhobene „Indices" verstanden, die uns das Evolutionsniveau einer bestimmten Zahnkategorie angeben. Zum Beispiel gibt der so genannte „m2-Enthypoconid-Index" die durchschnittliche Anzahl von zusätzlichen Höckern an einer bestimmten Stelle (= Enthypoconid) des zweiten Unterkieferbackenzahnes an. Dieses ein-, zwei oder mehrhöckerige Enthypoconid wird gebildet, um dem Kaudruck des zweiten Oberkieferbackenzahnes wirkungsvolle Antagonisten entgegen zu setzen. Der P4-Index besagt, wie oft zusätzliche Kauleisten und Höcker entwickelt sind. Es hat sich in den letzten 20 Jahren herausgestellt, dass diese „Indices" einen hohen Aussagewert

Gernot Rabeder
University of Vienna, Institute of Palaeontology and Naturkundliche Station Lunz am See
gernot.rabeder@univie.ac.at

Irena Debeljak
Institute of Paleontology,
Scientific Research Centre SAZU,Novi trg 2, SI-1000, Ljubljana, Slovenia
IrenaDe@zrc-sazu.si

Michael Hofreiter
Max Planck Institute for Evolutionary Anthropology.
hofreite@eva.mpg.de

Gerhard Withalm
University of Vienna, Institute of Palaeontology.
gerhard.withalm@univie.ac.at

Eingelangt: 22.2.2008
Angenommen: 29.6.2008

für die Evolution der Höhlenbären haben. Aus den sehr unterschiedlichen Indices der Backenzähne und dem geologischen Alter wurde geschlossen, dass in den Alpen vor 50.000 bis 30.000 Jahren drei verschiedene Höhlenbärenarten mit den zoologischen Namen *Ursus ladinicus*, *U. eremus* und *U. ingressus* gelebt haben. Diese drei Arten zeichnen sich auch durch unterschiedliche mitochondriale DNA Sequenzen aus, ein Hinweis darauf, dass es sich um getrennte Populationen handelte, zwischen denen wenig oder kein Genfluss stattgefunden hat (Hofreiter, 2005), was für einige Fundstellen auch nachgewiesen wurde (Hofreiter & al., 2004; 2007). Auch wenn die genetischen Daten alleine keine Artunterscheidung erlauben unterstützen sie doch die Trennung der verschiedenen Populationen in unterschiedliche Arten.

Durch den Vergleich der Daten von Höhlenbärenresten aus über 30 verschiedenen alpinen und sechs außeralpinen Höhlen ergibt sich, dass die einzelnen Arten sehr unterschiedliche Anpassungen an die Höhenlage ihrer Äsungsgebiete zeigen. Während die Faunen der *Ursus eremus*- und der *ladinicus*-Linie eine höhenabhängige Reduktion ihrer Körpergröße („Gebirgsnanismus") zeigen, ist eine derartige Korrelation bei der *U. ingressus*-Gruppe nicht zu verzeichnen. Die fossilen Reste der *U. ladinicus*-Gruppe (ladinischer Bär) und der *U. eremus*-Gruppe (Rameschbär) sind durchschnittlich in den hoch gelegenen Höhlen deutlich kleiner als in den Höhlen der tieferen Lagen oder anders ausgedrückt: die Größenwerte sind mit der Seehöhe der Höhleneingänge negativ korreliert. Bei der dritten Art, dem erst um 50.000 Jahren vor heute eingewanderten Gamssulzenbären (*Ursus ingressus*), ist keine Korrelation mit der Meereshöhe zu erkennen. Die Mittelwerte aus der höchst gelegenen Fundstelle (Potočka zijalka, 1650 m) sind kaum kleiner als aus der am tiefsten situierten Ilinka-Höhle (33 m). Die Breite der Zahnkronen ist bei den Unterkiefermahlzähnen mit der Seehöhe negativ korreliert, während dies bei den Oberkiefermolaren nicht der Fall ist (*U. ingressus*) oder nur angedeutet (*U. ladinicus* und *U. eremus*).

Bei den morphologischen Daten ist ein ganz anderer Trend zu erkennen. Nach den verschiedenen Indices gibt es bei *U. ingressus* eine starke Abhängigkeit von der Höhenlage der Fundstellen: je höher die Höhle liegt, desto höher waren die Evolutionsniveaus der dort hausenden Bären. Bei den beiden anderen Arten ist diese Korrelation z.T. auch vorhanden, z.T. aber viel schwächer. Das Evolutionsniveau einer Höhlenbärenfauna ist also nicht nur von der zeitlichen Stellung sondern auch von der Seehöhe der Fundstelle abhängig. Auch die unterschiedlichen Geschlechterverhältnisse wurden in die Studie aufgenommen. Weder für die Mittelwerte der Zahnmaße noch für die morphologischen Indices besteht ein Zusammenhang mit dem Sex-Index (prozentualer Anteil an Weibchen). Deutungsversuche für die erkennbaren Trends werden im Kapitel „Diskussion" gebracht, von dem sich eine Übersetzung am Ende des Artikels findet.

PREAMBLE

For several years it was assumed that there was more than one bear species living in the Alps in the time between 40 and 50 ka b.p., the so called Middle-Wurmian (Rabeder, 1995). This hypothesis has recently been supported by DNA-analyses (Hofreiter et al., 2004; Rabeder et al., 2004 and Rabeder & Hofreiter, 2004), resulting in the description of three new species (Rabeder et al., 2004). There were all in all three different species living in the Alps: *Ursus eremus*, *U. ladinicus* and *U. ingressus*, whereas the typical cave bear, *U. spelaeus*, living in high-alpine habitat, is now only known from the Préalpes in France. Moreover, this species was widely distributed outside the Alps in the mountainous regions of Germany, France, and Spain.

Because there are many caves in the Alps which are or were filled with bone-bearing sediments it is possible to use statistical methods to reveal the differences between these fossil populations (= "faunas"). The large differences in means and distributions of the metrical and morphological parameters cannot be explained only by taxonomical differences, i.e. speciation. For the parameter body size it was presumed that there is a negative correlation with the altitude of the habitat, see Ehrenberg (1929) who introduced the term "hochalpine Kleinform", literally translated "high-alpine smallform". He concluded that this kind of dwarfism is a special adaptation to the high-alpine habitat, because of short summers and long winters, which result in a shortened vegetation period. A test of this hypothesis, in combination with knowledge of the new taxonomy, resulted only in a partial proof of Ehrenberg's theory. Contrary to his hypothesis, a first comparison of morphodynamic indices showed a different picture, with different trends being visible in different taxa.

In this study, we are concerned with the following questions:

1. What – if any – is the correlation of the different metrical and morphological parameters with the taxonomic attribution of the fossil bear populations on the one hand and with the altitude of the habitat (the cave) on the other hand?

   A large number of new radiometric- and DNA analyses have shown that approximately 50 ka ago a massive bear migrated into the Alps. This bear was therefore named *Ursus ingressus*. *U. ingressus* migrated into those regions that were formerly inhabi-

ted by *U. eremus* and probably by *U. ladinicus* since 80 ka b.p. (Hofreiter et al., 2004; Rabeder & Hofreiter, 2004; Rabeder et al., 2004). This interesting fact led to the second question.

2. Are there any observable shifts in body size, plumpness of extremities and morphology of the teeth of *U. eremus* during its replacement by *U. ingressus* and are there consequently changes in the data of the latter species?
3. What are the differences of the aforementioned three species in relation to the altitude of the habitat?
4. What – if such shifts and/or differences exist – are the probable causes of these potential adaptations and why was *U. ingressus* more successful than its predecessors were?

The question whether or not the taxa *U. eremus*, *U. ladinicus* and *U. ingressus* should be regarded as species is not the main target of this study. However, as the taxonomic distinction is of importance to the topic discussed, we would like to give a few explanations on this subject: *Ursus ingressus* is defined by remarkable metrical, morphological, and genetic differences to *U. eremus*. Even more significant is the fact that both species lived side by side (sympatrically) for approximately 15 ka (from 47 ka till 31 ka b.p.) without any detectable gene flow between the two populations. This means that there was a behavioural mechanism to avoid interbreeding between these two species of bears (Hofreiter et al., 2004; Rabeder et al., 2004). Consequently this is one of the few possibilities in vertebrate palaeontology to apply the concept of biological species and not only the morpho-species concept.

There is a similar situation in *U. eremus* and *U. ladinicus*, but the evidence is not so clear. At approximately the same time (>50 ka b.p.) both bears lived in the "Totes Gebirge" (Austria). Whereas haplotypes attributable to *U. ladinicus* were found in Brieglersberghöhle, those of *U. eremus* were found in Ramesch- and Salzofenhöhle; for more details see Rabeder et al., 2005. The problem in the case of these two forms is, that until now, there is only a small number of reliable radiometric dates available. The reason for this is the temporal limitation of the ^{14}C-AMS-method. However, it should be noted that occurrences of haplotypes of two of the proposed four species in a single location have almost never been found, and where this was the case, it could be shown that the different species were temporally separated (Hofreiter et al. 2007). This is a critical point for the analyses presented, as the four taxa therefore represented different gene pools between which little or most likely no gene flow took place. Therefore, even if interbreeding had been possible, it did not occur to an extent that would prevent different adaptive responses to environmental changes, a situation similar to modern brown and polar bears, which also represent distinct gene pools, despite occasional interbreeding between the two species.

Finally, it should be noted that it is very likely that there are older synonyms for *U. ingressus*, which migrated from East towards West as, for instance, "*Ursus spelaeus (odessanus)*" Nordmann (1858). "Odessanus" is not a valid taxonomic name because its author, Alexander Nordmann used this term only for a geographic description of this bear and did not erect a distinct species or subspecies. In fact he explicitely wrote: "2. Der Odessaer fossile Bär ist identisch mit dem Höhlenbären des übrigen Europas." (The fossil bear from Odessa is identical to the cave bear in other parts of Europe.).

MATERIAL AND METHODS

This survey is based on a large amount of statistical data obtained from fossil bear populations, which were found in caves within and outside of the Alps. Most of the material was excavated with novel methodology. Most of these excavations were carried out under the supervision of G. Rabeder (University of Vienna and Austrian Academy of Sciences), in cooperation with universities, academies, museums, and collectors from Austria and abroad, including, Croatia, France, Italy, Slovenia, Switzerland and Ukraine. If possible additions to the data set were made from old excavations.

Only those faunas that produced enough teeth and metapodial bones for statistical analysis were used in this study and where the taxonomic attribution to one of the aforementioned species is proven by means of DNA-analyses (exceptions: Repolust Höhle, Herkova jama and Mokriška jama) and/or trustworthy morphological parameters (p4-index, P4-index, p4/4-index, m2-enthypoconid-index, M2-metaloph-index, m3/m2-length-index, index of plumpness; see Rabeder (1999) and Withalm (2001). The realibility of these indices has been tested in different ways. Thus, the taxa belonging to diverse cave bear faunas (e.g. Ajdovska, Divje babe, Merkensteinhöhle, Ochsenhalthöhle, Potočka zijalka, Sulzfluhhöhlen) had been recognized correctly by morphodynamic indices prior to DNA-analysis.

Fig.1: Examples of tooth evolution: one primitive and one advanced form of P4 sup. (upper row) and of M2 sup. (lower row)

Beispiele der Zahnevolution: Eine urtümliche und eine hoch entwickelte Form des P4 sup. (obere Reihe) und des M2 sup. (untere Reihe).

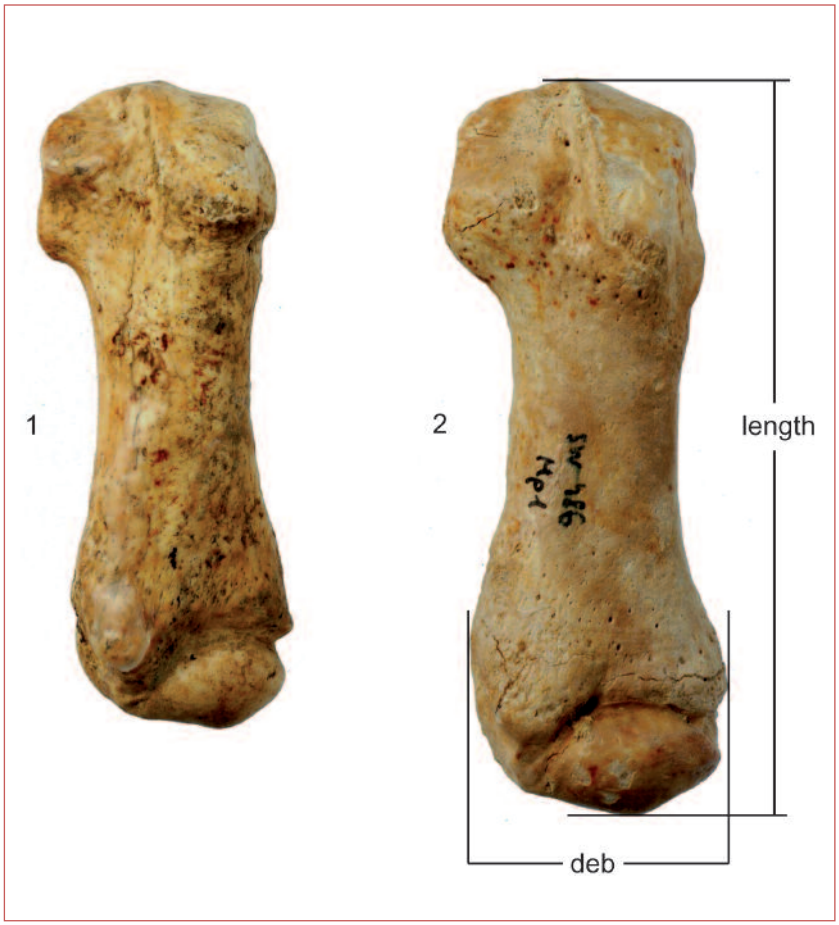


Fig. 2: Metacarpale 5 dex, anterior view from *Ursus deningeri* (1) and *Ursus eremus* (2); length = measured length; deb = distal epiphyseal breath.

Messstrecken am Metacarpale 5 dex (in Vorderansicht) von *Ursus deningeri* (1) und *Ursus eremus* (2); length = Länge, deb = distale Breite an den Epiphysen.

Table 1: List of cave bear sites included in this study.

Name of Site Alpine	Abbreviation	Country No.	Altitude	Species	Literature	Chronology
Divje babe	Db	SLO	450	*ingressus*	(1, 14, 15)	Middle to Late Wurmian
Brettstein-Bärenhöhle	BS	A, 1625/33	1700	*ladinicus* + *eremus*	(2)	Middle Wurmian
Brieglersberghöhle	BB	A 1625/24	1960	*ladinicus*	(2, 3)	Middle Wurmian
Ander dles Conturines	Cu	I	2800	*ladinicus*	(4, 5)	Middle Wurmian
Gamssulzenhöhle	GS	A, 1637/3	1300	*ingressus*	(2, 5, 6)	Middle to Late Wurmian
Hartelsgrabenhöhle	HG	A, 1714/1	1230	*ingressus*	(2, 7)	Middle Wurmian
Herdengelhöhle 200-330	HD 4-6	A, 1823/4	878	*ingressus*	(2, 5)	Middle to Late Wurmian
Herdengelhöhle 330-360	HD 3	A, 1823/4	878	*eremus*	(2, 5)	Middle Wurmian
Herkova jama	Hj	SLO	520	*deningeri*	(18)	Middle Pleistocene
Kugelstein-Tropfsteinhöhle	Kst 2	A, 2784/3	482	*ingressus*	(2)	Late Wurmian
Lieglloch	LL	A, 1622/1	1290	*ingressus*	(2, 5)	Middle to Late Wurmian
Merkensteinhöhle	Mst	A, 1911/32	441	*ingressus*	(2)	Middle Wurmian
Grotte Merveilleuse	Mv	F	1100	*ladinicus*	new	Middle Wurmian
Mixnitz, Drachenhöhle	MixJ	A, 2839/1	949	*ingressus*	(2, 8)	Middle to Late Wurmian
Mokriška jama	Mj	SLO	1500	*ingressus*	(17)	Middle Wurmian
Nixloch	NL	A, 1665/1	770	*ingressus*	(2, 5)	Late Wurmian
Ochsenhalthöhle	OH	A, 1624/40	1660	*eremus*	new	Middle Wurmian
Potočka zijalka	PZ	SLO	1650	*ingressus*	(9)	Middle to Late Wurmian
Grotte Préletang	PLE	F	1225	*ladinicus*	new	Middle Wurmian
Ramesch 1, 0-50	RK 1	A, 1636/8	1960	*eremus*	(2, 5)	Middle Wurmian
Ramesch 2, 50-100	RK 2	A, 1636/8	1960	*eremus*	(2, 5)	Middle Wurmian
Ramesch 3, 100-200	RK 3	A, 1636/8	1960	*eremus*	(2, 5)	Middle Wurmian
Ramesch 4, 200-250	RK 4	A, 1636/8	1960	*eremus*	(2, 5)	Middle Wurmian
Repolusthöhle	Rep	A, 2837/1	525	*deningeri*	(2, 5)	Middle Pleistocene
Salzofenhöhle	SO	A, 1624/31	2005	*eremus*	(2, 5)	Middle Wurmian
Schreiberwandhöhle	Sr	A, 1543/27	2250	*eremus*	(2)	Middle Wurmian
Schwabenreithhöhle	SW	A, 1823/32	959	*eremus*	(2, 5)	Early Wurmian
Sulzfluhhöhlen	SF	CH	2300	*ladinicus*	(2, 10)	Middle Wurmian
Windener Bärenhöhle	Wi	A, 2911/1	190	*ingressus*	(2)	Late Wurmian
Extra-alpine						
Ajdovska jama	Aj	SLO	244	*ladinicus*	new	Early Wurmian?
Ilinka near Odessa	Ilinka	UA	33	*ingressus*	new	Middle Wurmian
Križna jama	Kj	SLO	675	*ingressus*	(11)	Middle Wurmian
Loutraki Aridea Cave	LAC	GR	540	*ingressus*	(12)	Middle Wurmian
Grotta di Pocala	Po	I	139	*eremus*	(13)	Early Wurmian?
Vindija G	Vi G	HR	275	*ingressus*	(14)	Late Wurmian

Relevant references: (1) Debeljak, 2002a; (2) Döppes & Rabeder, 1997; (3) Rabeder et al., 2005; (4) Rabeder, 1991; (5) Rabeder, 1999; (6) Rabeder, 1995; (7) Rabeder, 2005; (8) Abel & Kyrle, 1931; (9) Pacher et al., 2004; (10) Rabeder, 2004; (11) Pohar et al., 2002; (12) Tsoukala & Rabeder, 2006; (13) Calligaris et al., 2006; (14) Wild et al., 2001; (15) Debeljak, 2002b; (16) Turk, 2007; (17) Rakovec, 1976; (18) Pohar, 1981.

RESULTS

General Remarks: In the following, the results will be presented as diagrams. All data points are significant means in statistical sense. These data points represent mean lengths and widths of molars and metapodial bones as well as morphodynamic indices; see Rabeder (1999) and Withalm (2001). For better comparability these parameters are standardized against the means of *U. ingressus* from Gamssulzenhöhle (Austria), see

Rabeder (1999). The used altitudes in the diagrams always represent the altitude of the main entrance of the cave in meters above sea level. The applied regression lines show partly low R^2-values and should be regarded as trend lines only. For almost all caves, DNA data exist with regard to the question of taxa identification. Consequently, exclusion of the few sites for which no DNA data are available (partially due to insufficient preservation) does not change the overall picture or the conclusions.

Length of molars

There is a negative correlation of the molar length with the altitude of the cave entrance in *Ursus eremus* and *U. ladinicus*, see fig. 3 and 4. With respect to this parameter, the term "hochalpine Kleinform" sensu Ehrenberg (1929) is true only for these two species. There is no correlation between molar length and altitudes of the entrance of the caves at all in *Ursus ingressus*, see also fig. 3 and 4.

Width of molars

There is also a negative correlation between the relative width of molars and the altitude of the site. The correlation of the aforementioned character is only weak for the upper molars with two exceptions: the bears from Conturines- and Schreiberwand cave. See fig. 5 for the example of the upper M1. In general, the correlation between the width and the altitude is much stronger with the lower molars but is dependent on the species: the strongest correlation is visible in *U. ladinicus*; in contrast, the weakest correlation can be observed in *U. ingressus*, see fig. 6.

Greatest length of metapodial bones

The greatest length of metapodial bones displays a negative correlation with the altitude of the cave entrance, and unlike to the situation of the molars, all three cave-bear lineages, including *U. ingressus*, follow this trend. This is shown in fig. 7, which is a scatter-plot of means of greatest length against altitude of site.

Plumpness of metapodial bones

There is a weak correlation between the index of plumpness (ip = (distal epiphyseal width / length) x 100) of the fifth metacarpal bone and the altitude of the site in *U. ingressus* and an even weaker correlation in *U. eremus* and *U. ladinicus*, see fig. 8.

Morphodynamic indices

All morphodynamic indices of teeth show a very different behaviour than length and width in showing a

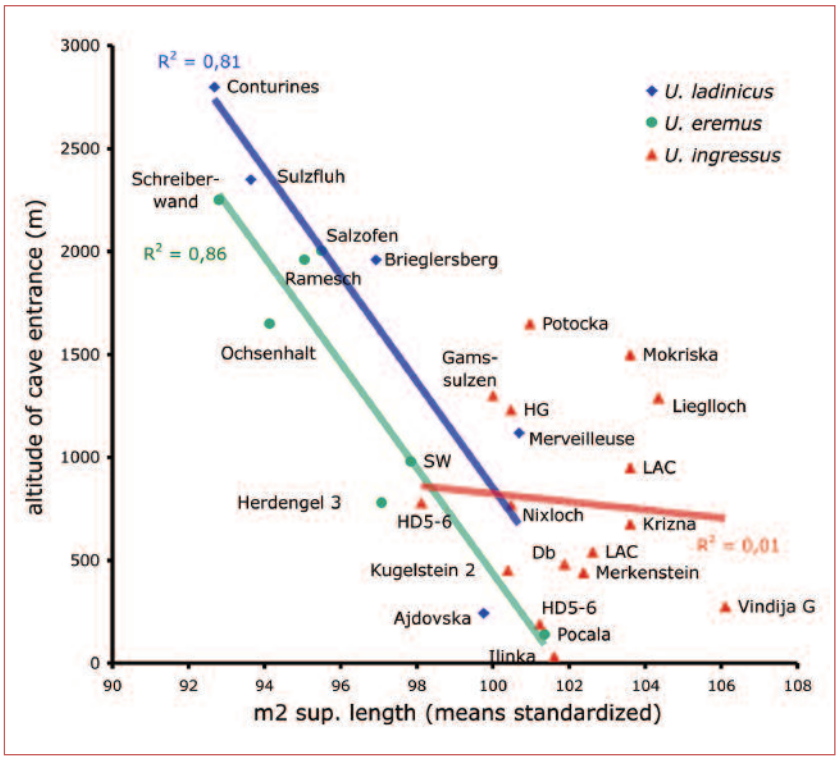


Fig. 3: Scatter-plot showing the correlation of the mean length of the upper M2 and the altitude of the cave entrances.

Die Abhängigkeit der Zahnlänge (Mittelwerte) des Oberkiefer-M2 von der Höhenlage der Höhleneingänge.

positive correlation with the altitude of the site. However, there are differences in the strength of correlation:

p4- and P4-index

There is a slow increase and only a weak correlation between these indices and the altitude of the site in *U. eremus* and *U. ladinicus*, but a strong one in *U. ingressus*. The morphology of the fourth premolars has since a long time been known to reflect the evolution of cave bears. The emergence of additional cusps and edges is basically correlated with the chronology of the fossil bearing strata, a fact that has been shown in the evolution from the Middle Pleistocene *U. deningeri* to the highly evolved *U. ingressus* of the Late Pleistocene.

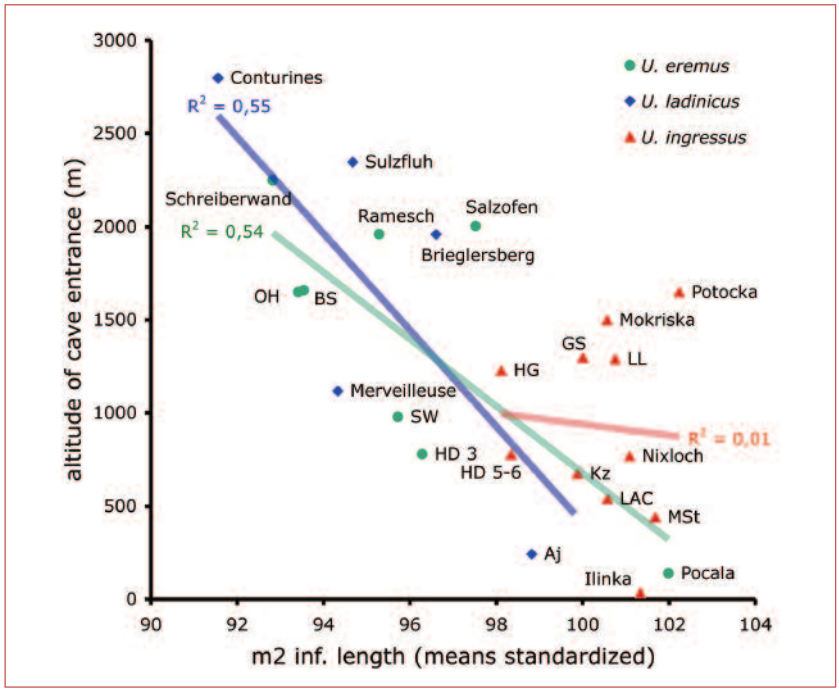


Fig. 4: Scatter-plot showing the correlation of the mean length of the lower m2 and the altitude of the cave entrances. The values are standardized against the mean tooth length of *U. ingressus* from Gamssulzen cave (Lower Austria).

Die Abhängigkeit der Zahnlänge des Unterkiefer-m2 von der Höhenlage der Höhleneingänge. Als Standard dienen die Mittelwerte von *U. ingressus* aus der Gamssulzenhöhle.

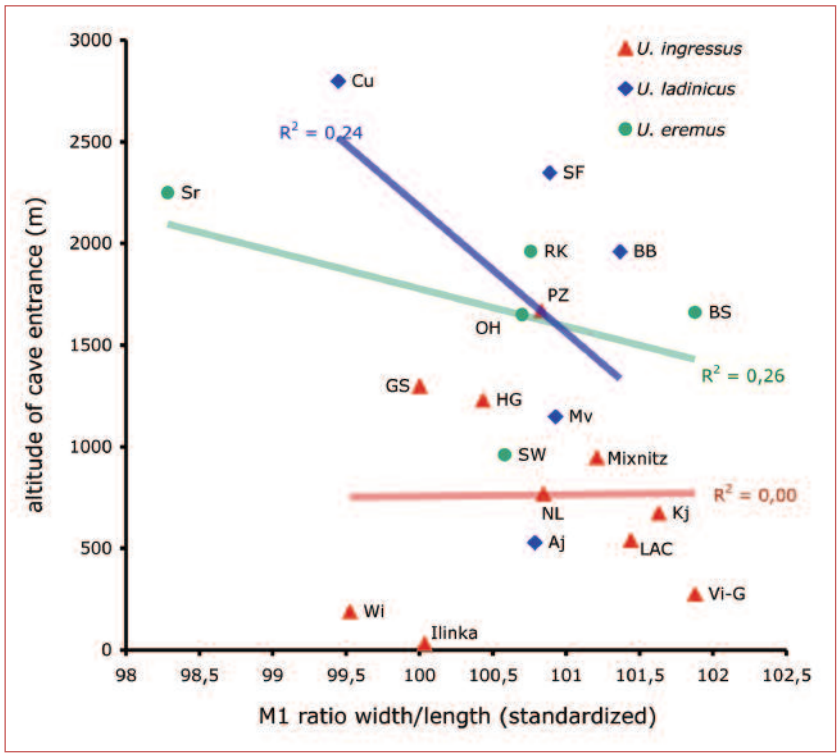


Fig. 5: Scatter-plot showing the correlation of ratio of width and length of the upper M1 and the altitude of the cave entrances.

Das Breiten-Längen-Verhältnis des ersten Oberkiefermolaren und die Höhenlage der Höhleneingänge.

However, what is different is the speed of the evolution in the different cave bear lineages. Moreover, in addition to the temporal correlation, the morphology of the fourth premolar also depends on the altitude of the site; see fig. 9 and 10.

m2-enthypoconid-index

The strongest correlation is observable in *U. ingressus*, with a slightly weaker correlation in *U. eremus*. There is a strange correlation in *U. ladinicus*: while there is only a very weak correlation between this index and the altitude of the site the absolute value exceeds those of all the other bears at different altitudes. The values of enthypoconid-index are astonishingly high in *U. ladinicus* and are the best possibility to morphologically differentiate between this species and *U. eremus*. Until now a conclusive interpretation of this phenomenon is missing, see fig. 11.

M2-metaloph-index

All the species of bears show a positive correlation of this index and the altitude of the site, see fig. 12.

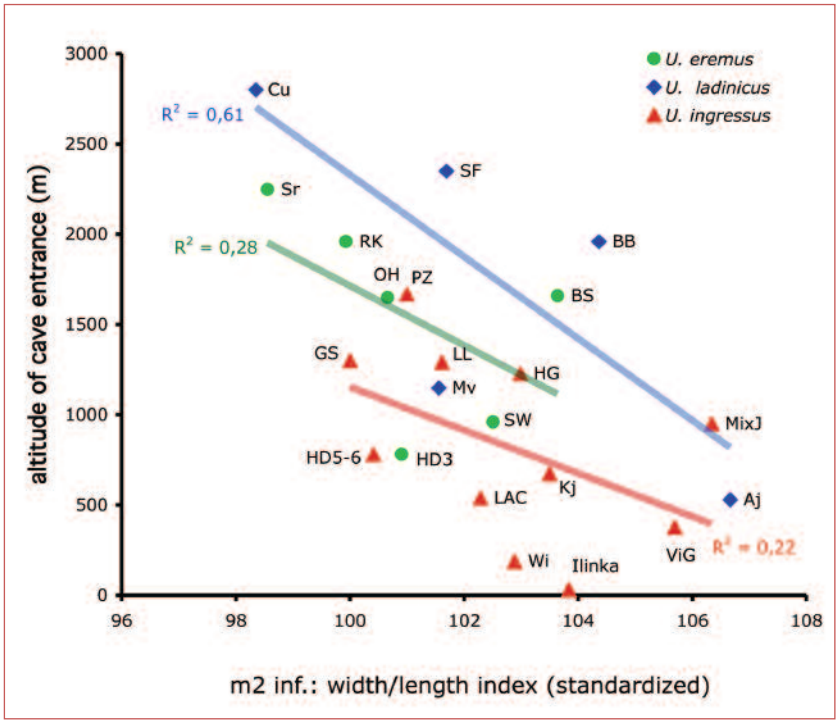


Fig. 6: Scatter-plot showing that the relative width of molars depends only on the altitude of the cave entrance and not on the specific attribution to an evolutionary line.

Die relative Breite der Unterkiefermolaren ist abhängig von der Höhenlage der Höhlen und nicht von der Zugehörigkeit zu einer bestimmten Evolutionslinie.

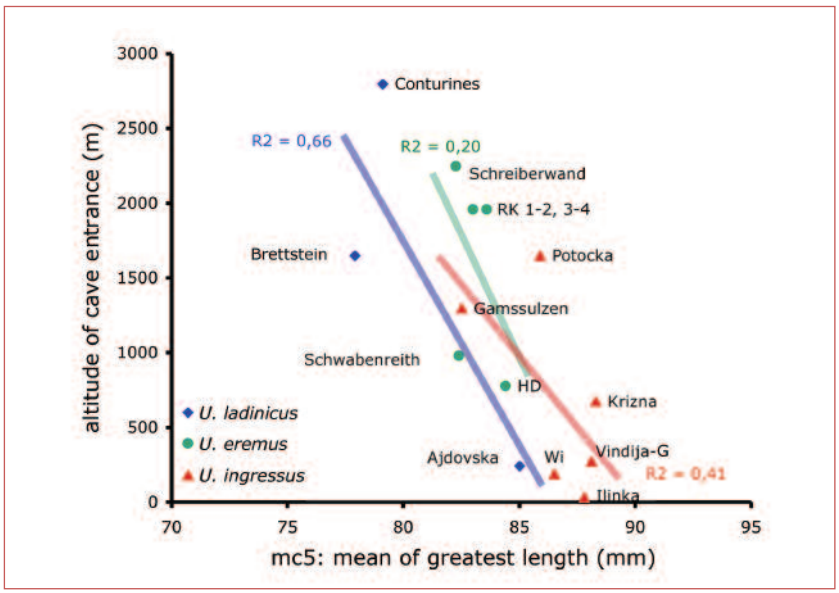


Fig. 7: Scatter-plot showing the correlation of greatest length of the 5th metacarpal bone and the altitude of the cave entrances.

Der Gesamtlänge des 5. Metacarpale und die Höhenlage der Höhlenfundstellen.

Distribution of sexes versus altitude of site

The hypothesis that the different means of metric parameters of sites in the alpine region and in the lowlands can be explained by unequal distribution of sexes was published by Spahni (1954). This was disproved by Rabeder (2001) using material from high-alpine sites (Conturines cave and Ramesch Knochenhöhle) and by means of analyses of fossil DNA; see Hofreiter et al. (2004) and Rabeder et al. (2004). Seventeen caves have enough canines to obtain realistic and thus correct results. When reading the literature one can find two different terms for the distribution of sexes: sex ratio and sex index.

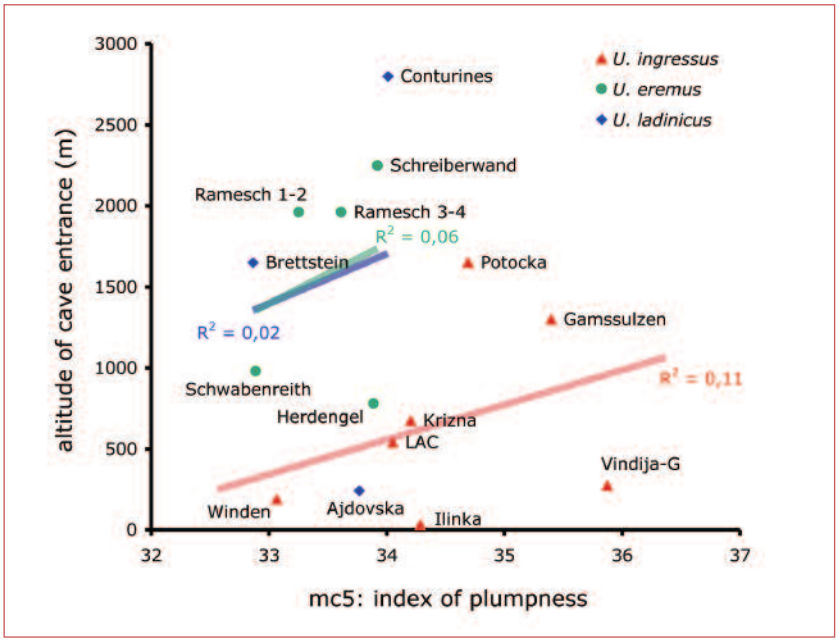


Fig. 8: Scatter plot showing the correlation of plumpness index of 5th metacarpal bone and the altitude of the cave entrances.

Der Plumpheitsindex des 5. Metacarpale und die Hoehenlage der Hoehlenfundstellen.

Table 2: Distribution of sexes, size of cave bears and altitude of the sites in use.

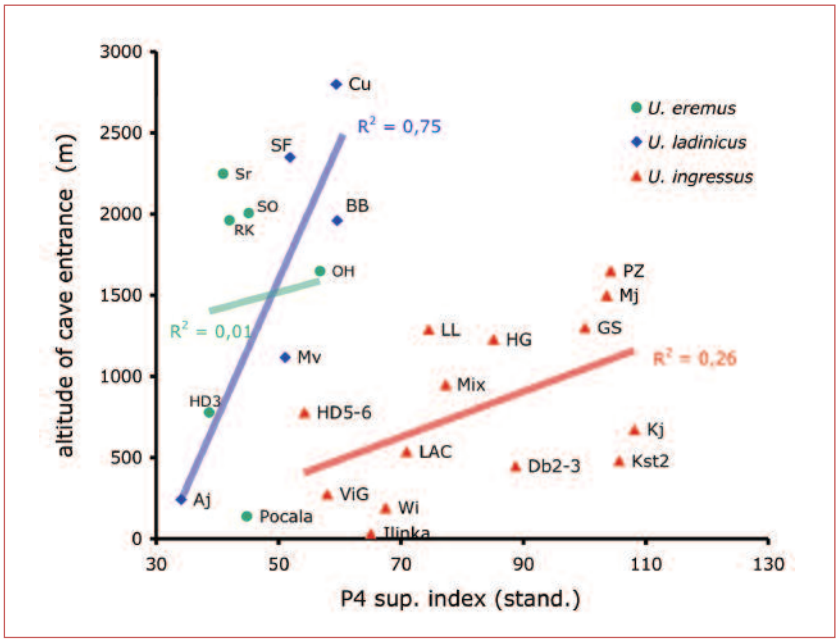
Fauna	Canines		n	Sex-ratio	Sex-index	Altitude in m a.s.l.	m1-length standard.	Species
	Female	Male						
Ajdovska	12	12	24	1.00	50.00	244	95.46	*eremus*
Brieglersberg	22	7	29	3.14	75.86	1960	96.09	*ladinicus*
Conturines	33	33	66	1.00	50.00	2800	93.02	*ladinicus*
Divje babe	322	288	610	1.12	52.79	450	100.56	*ingressus*
Gamssulzen	61	22	83	2.77	73.49	130	100.00	*ingressus*
Herdengel	24	30	54	0.80	44.44	780	97.63	*eremus*
Herkova jama	22	16	38	1.38	57.89	511	88.03	*deningeri*
Križna jama	11	34	45	0.32	24.44	670	100.82	*ingressus*
Loutraki	181	63	244	3.44	74.18	540	99.44	*ingressus*
Mixnitz	~3000	~9000	~12000	0.33	25.00	959	103.34	*ingressus*
Mokriška jama	273	477	750	0.57	36.40	1500	100.36	*ingressus*
Ochsenhalt	46	41	87	1.12	52.87	1650	96.32	*eremus*
Pocala	326	410	736	0.80	44.29	139	102.71	*eremus*
Potočka zijalka	16	47	63	0.34	25.40	1650	103.07	*ingressus*
Ramesch	83	71	154	1.17	53.90	1960	93.05	*eremus*
Repolust	23	29	52	0.79	44.23	525	88.45	*deningeri*
Schreiberwand	15	16	31	0.94	48.39	2250	92.86	*eremus*
Schwabenreith	51	28	79	1.82	64.56	960	96.00	*eremus*
Σ without Mixnitz	**1450**	**1593**	**3043**	**0.91**	**47.65**	—	—	—

Sex ratio means the quotient of female and male canines, i.e. sex ratio = f/m where f is the number of female and m the number of male canines.

The sex ratio follows a hyperbolic function where r_{sex} = f/m. A more suitable parameter is the sex index which is calculated as i_{sex} = f/(f+m) x 100 and represents the relative abundance of females in percent.

Table 2 gives the usable sites along with the number of canines and the means of the length of the lower first molar.

Fig. 13 is a scatter-plot of sex index against altitude of the site and fig. 14 is a scatter-plot of sex index against m1-length as an indicator of body size, including the specific attribution. In both diagrams, it is obvious that there is no or only a weak correlation at all. Fig. 14 shows only a weak correlation between the length of the m1 and the sex index for *U. ingressus*, which means that the slightly higher values from Mixnitz, Križna jama and Potočka zijalka can be explained by a domination of males. Within *U. eremus* the correlation is even weaker. There are alpine faunas with a female predomination, Brieglersberg cave for instance, and such with a male predomination, as it is the case in Potočka zijalka and such caves with an approximately equal distribution of



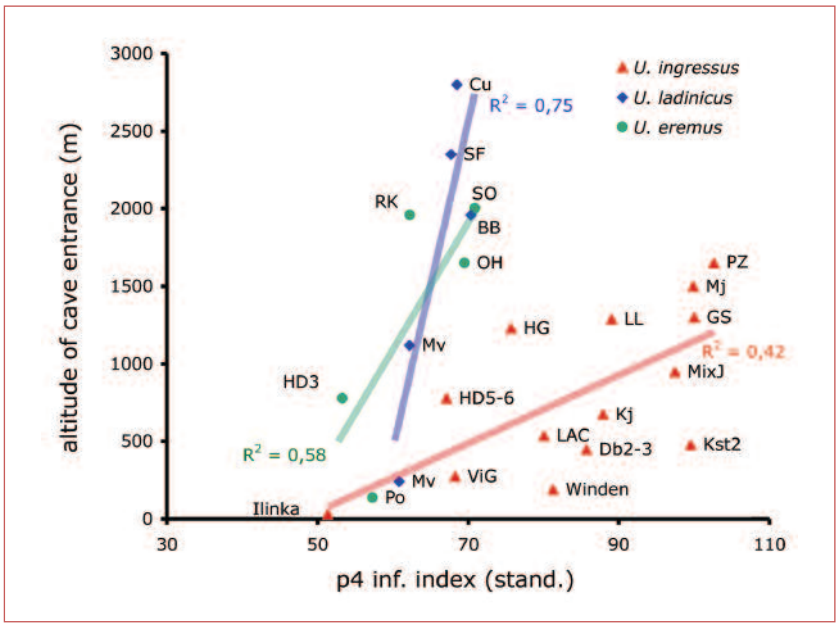


Fig. 9, 10: Scatter-plot showing the correlation of the morphologic indices of the 4th premolars and the altitude of the cave entrances.

Die morphologischen Indices der 4. Prämolaren im Vergleich zur Höhenlage der Höhleneingänge.

the sexes. Examples of the latter are Conturines cave, Ramesch Knochenhöhle and Ochsenhalt cave.

Fig. 14 deals with the correlation between the sex index and the mean body size. When the faunas with *U. ingressus* are taken into account one would tend to confirm a correlation between sex index and mean body size: the faunas from Potočka zijalka and Križna jama are dominated by males and show slightly higher means than their female dominated counterparts – Gamssulzen cave and Loutraki Aridea cave. The *U. ladinicus*-faunas on the other hand show that the influence of the altitude exceeds that of the sex index. It is obvious that the female-dominated fauna from Brieglersberg cave displays higher means of m1-length than that of the Conturines cave. At this point it should be mentioned that the ratio of male and female bears could be affected by a lack of data. For more information on this topic see Rabeder (2001).

However, it is remarkable that unbalanced sex ratios were found only in *U. ingressus*-faunas whereas most of the faunas of the two other two cave-bear lineages show roughly equal numbers of sexes.

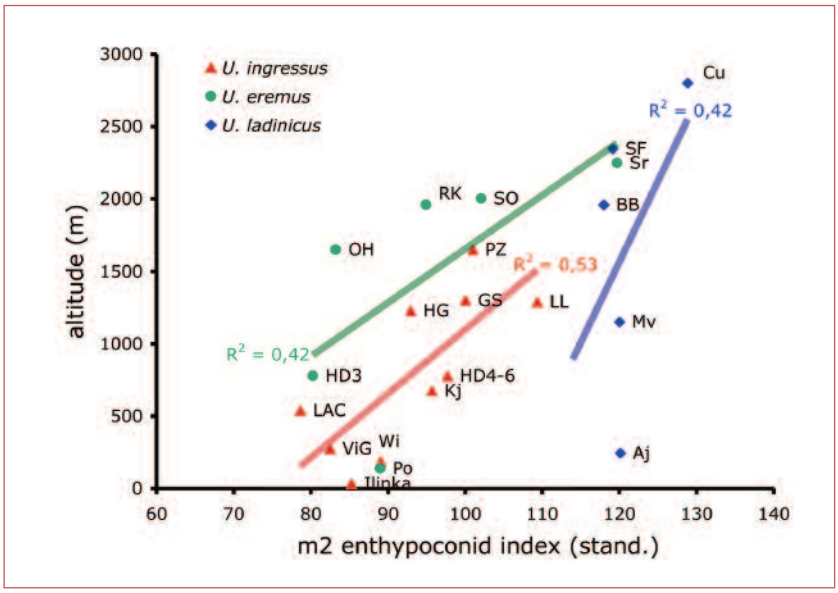


Fig. 11: Scatter-plot showing the correlation of the enthypoconid-index of the lower m2 and the altitude of the cave entrances.

Die Abhängigkeit des m2-Enthypoconid-Index von der Höhenlage der Bärenhöhlen.

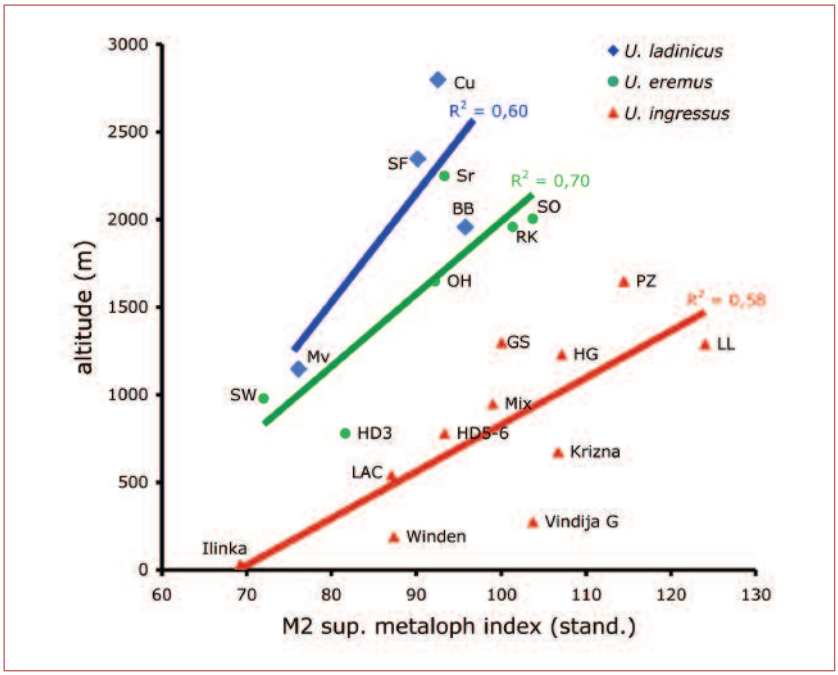


Fig. 12: Scatter-plot showing the correlation of the metaloph-index of the upper M2 and the altitude of the cave entrances.

Die Abhängigkeit des M2-Metaloph-Index von der Höhenlage der Bärenhöhlen.

DISCUSSION

The reduction of body size in high-alpine cave bears (alpine nanism) is commonly seen as an adaptation to the less favourable climate, i.e. short summers and long winters. It is easier for smaller animals to find enough food and thus it is easier for them to fulfil the needs of metabolism during winter. For two lineages of cave bears, *U. eremus* and *U. ladinicus*, it is possible to follow the hypothesis of Ehrenberg (1929) because there are no contradictory data. Ursus ingressus on the other hand, found another way of adapting to the (high-) alpine conditions: an improved performance of mastication is visible in all morphodynamic indices and is obviously aimed at an increased daily food intake during the vegetation period and thus at a sufficient fat storage before autumn. The variability of morphologic parameters is very high in *U. ingressus*, especially those of the indices of the fourth premolars, which is much higher than in the other taxa. A possible explanation for this phenomenon can be found in the fast adaptation of *U. ingressus*-group to high-alpine habitats. This strategy was obviously successful: *U. ingressus* survived

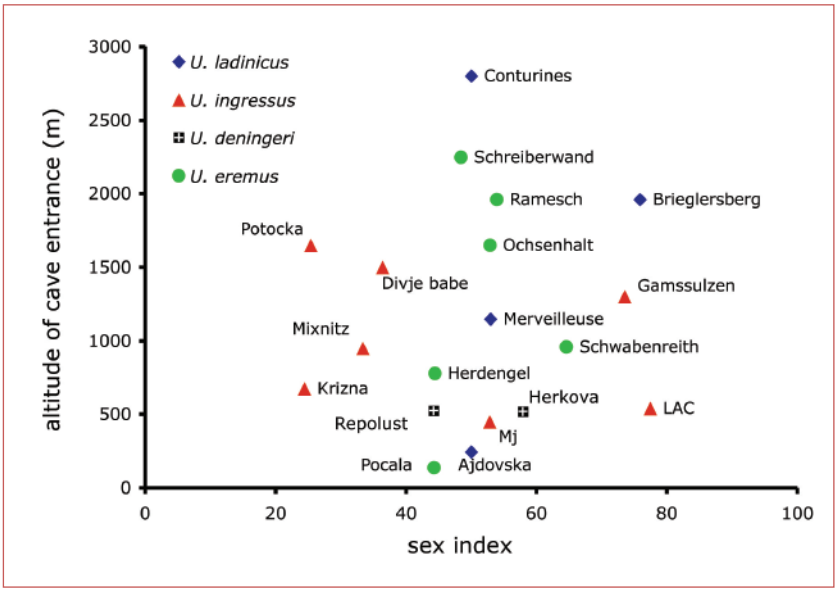


Fig. 13: The sex ratio of cave bears in relation to the altitude of the cave entrances.

Das Geschlechterverhältnis der Höhlenbären im Bezug zur Höhenlage der Fundstellen.

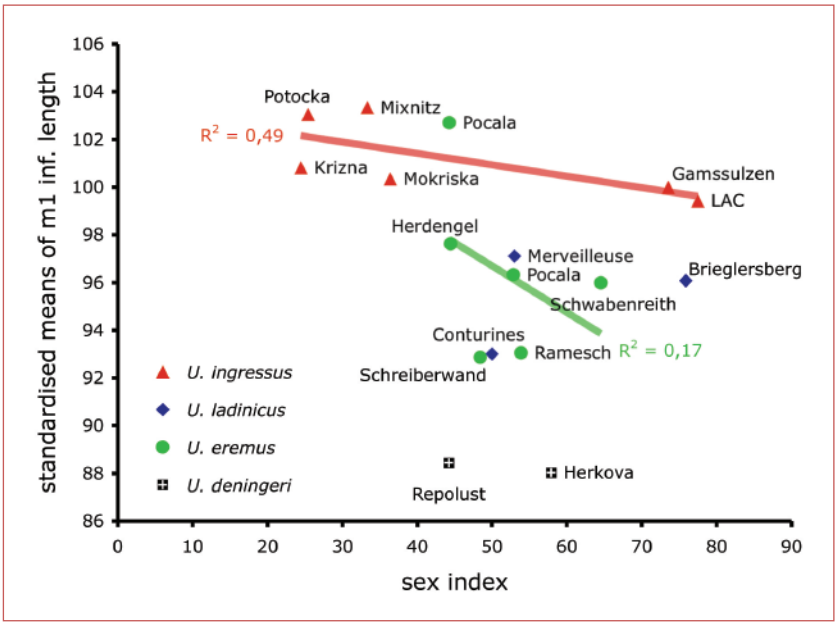


Fig. 14: The sex ratio of cave bears in relation to the length of the lower m1.

Geschlechterverhältnis der Höhlenbären im Bezug zur m1-Länge.

the Plenigacial in the alpine regions and only became extinct approximately 15 ka bp. In contrast, *U. eremus* became extinct approximately 30 ka bp and *U. ladinicus* even earlier.

In *U. ingressus* there is also a high degree of variability in the metric parameters, but they are not correlated with the altitude of the habitat. The factors that influence this development are to date unknown. It could be possible that there are differences in the diet of the cave bear lineages which could be unveiled by means of stable isotope analysis (^{13}C, ^{15}N, ^{18}O). Actually, the information on stable isotopes is available for only two alpine cave bear sites. Future projects will be targeted on this subject.

ACKNOWLEDGEMENTS

We are deeply indebted to Prof. David K. Ferguson for the correction of the manuscript. We are also grateful for the reviews of our colleagues Alain Argant (Grenoble), Gennady Baryshnikov (St. Petersburg) and Vida Pohar (Ljubljana). Moreover, we would like to thank Bernard Rafienna (St. Pierre de Chartreuse, France) for the possibility to study the fossil bears from the caves of the Massif Vercors.

This study is part of the project F.A.C.E. (Fossil Animals of Caves in Europe) Austria of the Commission of Quaternary Research, Austrian Academy of Sciences and was partly financed by the Department of Cultural Affairs of the Government of Lower Austria (Project LNOe0038).

REFERENCES

Abel, O. & Kyrle, G., (1931): Die Drachenhöhle bei Mixnitz. – Speläolog. Monogr., 7-9, Wien.

Calligaris, R., Rabeder, G, & Salcher, T. (2006): Neue paläontologische Grabungen in der Grotta Pocala bei Triest. – [in:] Ambros, D., Gropp, C., Hilpert, B. & Kaulich, B. (eds.) Neue Forschungen zum Höhlenbären in Europa. – Naturforsch. Ges. Nürnberg, Abh., 45/2005:49–56, Nürnberg.

Debeljak, I. (2002a): Mortality Dynamics and Paleoecology of Cave Bear from Divje babe I Site. – Ph. D. Thesis, Faculty of Natural Sciences and Engineering, University of Ljubljana.

Debeljak, I. (2002b): Fossil population structure of the cave bear from Divje babe I site, Slovenia: Preliminary results. – Abh. zur Karst- und Höhlenkunde (München), 34: 41–48.

Döppes, D. & Rabeder, G. (eds.) (1997): Pliozäne und pleistozäne Faunen Österreichs. Ein Katalog der wichtigsten Fossilfundstellen und ihrer Faunen. – Mitt. Komm. Quartärforsch. Österr. Akad. Wiss., Wien, 10: 267.

Ehrenberg, K. (1929): Die Ergebnisse der Ausgrabungen in der Schreiberwandhöhle am Dachstein. – Paläont. Z., 11 (3):261–268.

Hofreiter, M. (2005): Evolutionsgeschichte alpiner Höhlenbären aus molekulargenetischer Sicht. – Mitt. Komm. Quartärforsch. Österr. Akad. Wiss., 14: 67-72.

Hofreiter, M., Rabeder, G., Jaenicke, V., Withalm, G., Nagel, D., Paunovic, M., Jambr si , G. & Pääbo, S. (2004): Evidence for reproductive isolation between cave bear populations. – Current Biology, 14 (1): 40–43.

Hofreiter, M., Münzel, S., Conard, N., Pollack, J., Weiss, G. & Pääbo, S. (2007): Sudden replacement of cave bear mitochondrial DNA in the Late Pleistocene. – Current Biology, 17 (4).

Nordmann, A. von, (1858): Palaeontologie Südrusslands. Helsingfors.

Pacher, M., Pohar, V. & Rabeder, G. (eds.) (2004): Potočka zijalka. Palaeontological and archeological results of the campaigns 1997-2000. – Mitt. Komm. Quartärforsch. Österr. Akad. Wiss., 13: 1–245.

Pohar, V. (1981): La faune pléistocene de la cavité de jama pod Herkovimi pecmi. – Geologija 24(2): 241–284.

Pohar, V., Rabeder, G. Kralj, P. & Misic, M. (2002): Cave sediments and fossil mammal remains in Križna jama, Southern Slovenia. – [in:] Rosendahl, W. Morgan, M. & Lopez Correa – Abh. Karst- Höhlenkde, München, 34: 49–51.

Rabeder, G. (1991): Die Höhlenbären von Conturines. Entdeckung und Erforschung einer Dolomiten-Höhle in 2800 m Höhe. – (Athesia-Verl.), Bozen.

Rabeder G., (ed.) (1995): Die Gamssulzenhöhle im Toten Gebirge. – Mitt. Komm. Quartärforsch. Österr. Akad. Wiss., 9: 1–133.

Rabeder, G. (1999) Die Evolution des Höhlenbärengebisses. – Mitt. Quartärkomm. Österr. Akad. Wiss., 11: 1–102.

Rabeder, G. (2001) Geschlechtsdimorphismus und Körpergröße bei hochalpinen Höhlenbärenfaunen. – Beitr. Paläont., 26: 117–132.

Rabeder, G. (2004) Die Höhlenbären der Sulzfluh-Höhlen. – Vorarlberger Naturschau (Dornbirn), 15: 103-114.

Rabeder, G., (2005): Neue paläontologische Daten von der Bärenhöhle im Hartelsgraben (1714/1), Gesäuseberge, Steiermark. – Die Höhle, 56 (1): 44–46.

Rabeder, G. & Hofreiter, M. (2004): Der neue Stammbaum der Höhlenbären. – Die Höhle 55, (1-4): 58–77.

Rabeder, G., Hofreiter, M. Nagel, D. & Withalm G. (2004): New Taxa of Alpine Cave Bears (Ursidae, Carnivora). – Cahiers scientif. / Dép. Rhône - Mus. Lyon, Hors série, n° 2 (2004): 49–67.

Rabeder, G., Hofreiter, M. & Wild, E. (2005): Die Bären der Brieglersberghöhle (1625/24). Die Höhle 56, (1): 36-43.

Rakovec, I. (1976): The cave bear from the Mokrica cave in the Savinja Alps (Slovenia, Yugoslavia).) – Razpr. IV. razr. SAZU 10:123–203.

Spahni, J.-C. (1954) : Les gisements à ursus spelaeus de l'Autriche et leurs problèmes. – Bull. Soc. Préhist. Franc. (Le Mans), LI, 7:346–367.

Tsoukala, E. & Rabeder, G. (2006): Cave bears and Late Pleistocene associated faunal remains from Loutraki Aridea (Pella, Macedonia, Greece). – [in:] Ambros, D., Gropp, C., Hilpert, B. & Kaulich, B., (eds.). Neue Forschungen zum Höhlenbären in Europa. – Naturforsch. Ges. Nürnberg, Abh., 45/2005: 225–236.

Turk, I. (ed.) (2007): Divje babe I – Upper Pleistocene Palaeolithic site in Slovenia; Part I: Geology and Palaeontology, ZRC SAZU (opera instituti archaeologici Sloveniae), Ljubljana.

Wild, E., Paunovic, M., Rabeder, G., Steffan I. & Steier, P. (2001): Age determination of fossil bones from the Vindija Neandertal site in Croatia. – Radiocarbon, 43, 2B: 1021–1028.

Withalm, G. (2001): Die Evolution der Metapodien in der Höhlenbären-Gruppe (Ursidae, Mammalia). – Beitr. Paläont., 26: 126–249.

DISKUSSION

Die Verkleinerung der Körperdimensionen bei hochalpinen Bären („Gebirgsnanismus") wird allgemein als Anpassung an das ungünstigere Klima (kurze Sommer, lange Winter) gedeutet. Kleinere Tiere können ihren Bedarf an Nahrung und damit an Energie leichter decken als große. Für die beiden Linien von *Ursus eremus* und von *Ursus ladinicus* kann diese Hypothese beibehalten werden, weil keine widersprüchlichen Daten vorliegen. Die Bären der *Ursus ingressus*-Gruppe hingegen haben einen anderen Weg der Gebirgsanpassung beschritten. Eine Verbesserung der Kauleistung ist von allen morphodynamischen Indices abzulesen und zielt darauf ab, die Menge der pro Vegetationstag aufgenommenen Nahrung zu steigern und damit auch eine größere Fettspeicherung bis zum Herbst zu gewährleisten. Bei *U. ingressus* variieren die morphologischen Werte, besonders die Indices der Prämolaren, wesentlich stärker als bei den anderen Arten. Möglicherweise ist dies auf die höhere Evolutionsgeschwindigkeit zurück zu führen, mit denen sich die Bären der *U. ingressus*-Gruppe an das Gebirgsleben angepasst haben. Offensichtlich war diese Strategie erfolgreich: *U. ingressus* überlebte in den Alpen das Hochglazial und starb erst vor etwa 15.000 Jahren BP aus, während *U. eremus* schon vor ca. 30.000 Jahren verschwunden ist, *U. ladinicus* wahrscheinlich schon früher.

Auch bei *U. ingressus* streuen die metrischen Daten beträchtlich, sie sind aber nicht höhenabhängig, sondern werden offensichtlich von Faktoren gesteuert, die noch unbekannt sind. Es wäre möglich, dass es auch Unterschiede in der Ernährung gibt, die man eventuell durch die Analyse der stabilen Isotopen (^{13}C, ^{15}N, ^{18}O) herausfinden könnte. Derzeit sind nur die Isotopenverhältnisse von zwei alpinen Höhlen bekannt. Geplante Projekte sollen dieser Fragestellung nachgehen.