

Metrics and Evolutionary Level of Teeth of the Bears from Križna jama (Slovenia)

by

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Zusammenfassung

Die metrische Analyse von 44 messbaren Eckzähnen ergab, dass die Križna jama vorwiegend von männlichen Bären als Winterquartier benutzt worden ist – zumindest im Bereich der so genannten “Kittl’s Bärenhöhle”, aus der das untersuchte Material hauptsächlich stammt.

Die metrische und morphologische Aufnahme von 212 Backenzähnen lässt den Schluss zu, dass die Bären der Križna jama der Art *Ursus ingressus* angehören. Das ergibt sich aus den relativ großen Dimensionen und dem hohen morphodynamischen Niveau der 4. Prämolaren und der Molaren M_1 , M_2 und M^2 .

Summary

Metrical analysis of the 44 measurable canine teeth and its results show, that Križna jama was used by male bears as a winter-ground, at least in the area of the so called “Kittl’s Bear-cave” from where the analysed material mainly comes from.

The metrical and morphological uptake of 212 molars comes to the conclusion that the bears of Križna jama belong to the species *Ursus ingressus*. This follows from the relative large dimensions and a high morphodynamic level of the 4th premolars and the molars M_1 , M_2 and M^2 .

Izvešček

Izsledki raziskav 44 medvedjih podočnikov (kaninov) so pokazali, da so pretežno samci prezimovali v Križni jami. Predvsem velja to za »Kittlovo medvedjo jamo«, od

koder izhaja večina preiskanih zob. Meritve in morfološka analiza 212 kočnikov (molarjev) je pokazala, da pripadajo medvedi iz Križne jame vrsti *Ursus ingressus*. Dokaz za to so relativno veliki zobje in visok morfodinamičen nivo 4. Predmeljaka (premolarja) in treh meljakov (molarjev) – M_1 , M_2 in M^2 .

1. Material

All teeth and jaws dealt with herein were unearthed during the excavation campaign from 1999 and 2001. The huge amount of skulls and lower jaws from the old excavations performed by Ferdinand von Hochstetter, formerly housed in the Museum of Natural History in Vienna, disappeared and cannot be included in this analysis. The following numbers of teeth suitable for measuring were used, see Table 1:

Category	Permanent
Canini ^{*)}	44
P ⁴	28
M ¹	31
M ²	32
P ₄	30
M ₁	31
M ₂	27
M ₃	33

Table 1: List of measurable canines and cheek teeth from Križna jama (Slovenia). ^{*)} Due to the fact that it was impossible to distinguish between upper and lower jaw in every single case the canines were treated together.

2. Dimensional Comparison

The comparison in size with other cave bears from alpine regions and also from the lowlands shows that the bear from Križna jama is one of the biggest bears. When

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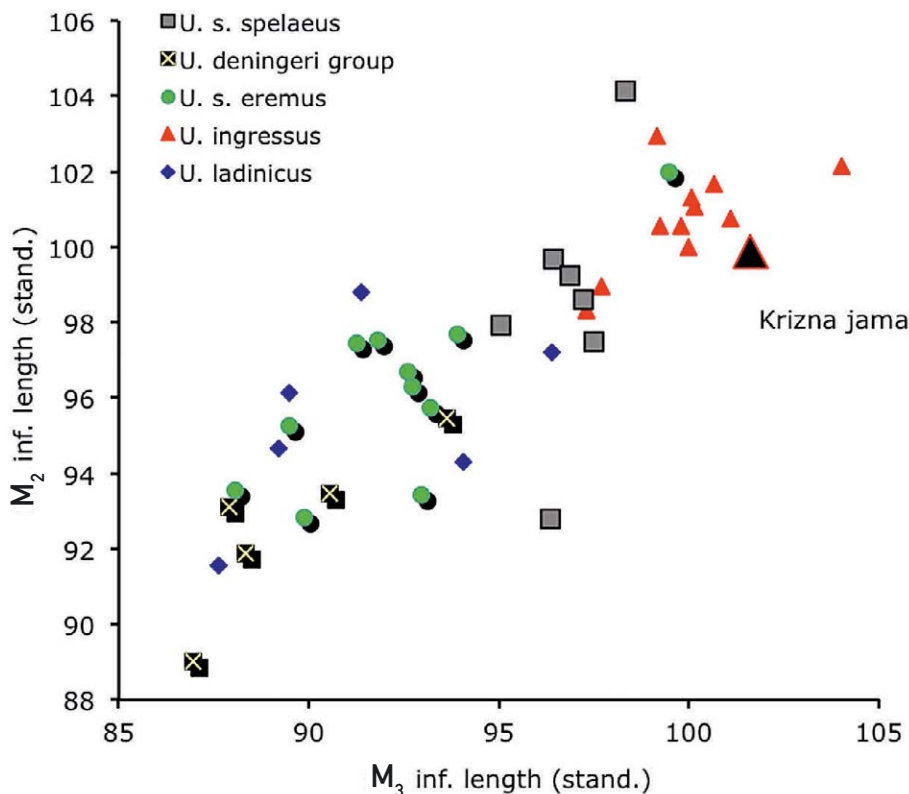


Figure 1: Comparison of size of molars of Pleistocene cave bear faunas in Europe.

comparing the averaged lengths of M^2 and M_3 the bears from Križna jama supersede most of the other cave bears, see Figure 1. The distribution of length and width of all teeth shows congruence with the bears from Gamssulzen cave, Herdengel cave (layer 5–6), Hartelsgraben cave, Drachenhöhle von Mixnitz, Merkenstein cave, Nixloch, Liegloch, (Austria), from Mokriška jama and Potočka zijalka (Slovenia) as well as with the big sized cave bears from Germany (Zoolithenhöhle, Erpfingen, Hohle Stein) and Spain (Ekaïn, Arrikutz, Toll and Reguerillo). All the other cave bear faunas are attributable to the *U. deningeri*-group (Hundsheim, Jagsthausen, Petershöhle, Hunas, Repolusthöhle and Herkova jama), to *U. ladinicus* (Concurines cave, Brieglersberg cave, Sulzfluh cave, Ajdovska jama, Grotte de Prélétang and Grotte de Merveilleuse) and to *U. eremus* (Ramesch-Knochenhöhle, Salzofen cave, Ochsenhalt cave, Schwabenreith cave und Herdengelt cave (layer 3) show by far smaller dimensions of the molars, with only one exception: the bears from Grotta di Pocalà (CALLIGARIS et al., 2005) which come close to the bears from Križna jama but genetically belong to *U. eremus*.

Data from: CALLIGARIS et al. (2005), PACHER et al. (2004, 2011), RABEDER (1995, 1999), RABEDER et al. (2008), TORRES (1988) and original.

Sexual dimorphism: Based on the distribution of size, the canines form two distinctly separated clusters, which probably represent sexes, see RABEDER & WITHALM (this volume: Fig. 2). There are only 11 canines attributable to females contrasting with 34 canines representing the males. Thus the sex index (number of females/total number $\times$ 100) is 24.44 and the sex ratio (number of females/number of

males) equals 0.32. The cave bear fauna from Križna jama was – at least in Kittl's Bärenhöhle – dominated by males, only one quarter of the analysed canines was probably female. A similar distributional pattern with a male domination is observable in the cave bear fauna from Potočka zijalka, the only difference is that the separation is not so strict as in Križna jama, see PACHER et al. (2004).

A totally different relation of sexes can be observed in Gamssulzenhöhle: females dominate this fauna, for comparisons see RABEDER (1995). Moreover, within the male canines from Gamssulzenhöhle the really big teeth with a width wider than 23 mm are missing. This results in a much bigger variability in the bears from Križna jama when comparing to the two other sites. By means of comparison of these three cave bear faunas a possible explanation for the sex ratio of Potočka bears was found, see Table 2.

3. Morphodynamic Analysis

P^3

No P^3 -alveolus could be found in the 13 upper jaws or upper jaw fragments respectively.

Morphotypes of the P^4

The distribution of P^4 -morphotypes within the Križna material is shown in Table 3. Due to the fact that most of the P^4 (95%) show a fully developed metaloph the resulting index is high. Approximately 60% show also a protoloph. The number of usable teeth is reduced because 38% of all fourth upper premolars are too heavily worn. This limits also the worth of the analysis itself.

Table 2: Analysis of canines from three different bear caves.

			Range of canine width (mm)		n
	Sex index (%)	Sex ratio	Male	Total	
Potočka zijalka	25.40	0.34	4.8	8.9	63
Križna jama	24.44	0.32	5.5	10	45
Gamssulzenhöhle	73.50	2.70	4.2	8.9	83

Morphotype	f_i	Metaconulus	Metaloph	Protostyle	Protoloph	w_i	$f_i \cdot w_i$
A/D	1	0	1	0	0	1	1.00
B/D	1	1	0.5	0	0	1.5	1.50
D	5	1	1	0	0	2	10.00
D/F	6	1	1	0	1	3	18.00
E	1	1	1	1	0	3	3.00
E/F	1	1	1	1	0.5	3.5	3.50
E/F-F	1	1	1	1	0.75	3.75	3.75
F	3	1	1	1	1	4	12.00
n	19					$\Sigma(f_i \cdot w_i)$	52.75

$$P^4\text{-index} = \Sigma(f_i \cdot w_i) \times 100/n = 277.63. \text{ Index standardized} = 108.5 \text{ (GS standard} = 255.7)$$

Table 3: Weighting of P^4 morphotypes and calculation of morphodynamic indices. f – (frequency) number of morphotypes, w – (worth) morphodynamic factor = sum of single valued steps, GS standard = P^4 -index of Gamssulzen cave (see RABEDER, 1995; 1999).

Morphotype	f_i	Paraconid	Metaconid	Metastylids	Hypoconid	Metalophid	Hypolophid	w_i	$f_i \cdot w_i$
B/C1	2	0.5	0.25	0	0	0	0	0.75	1.50
C1	4	0.5	0.5	0	0	0	0	1	4.00
C1/2	3	0.5	0.5	0	0.5	0	0	1.5	4.50
C1-C1/2	1	0.5	0.5	0	0.25	0	0	1.25	1.25
C1-E1	3	0.5	0.5	0	0	0.5	0	1.5	4.50
C1-E1/2	2	0.5	0.5	0	0.5	0.25	0	1.75	3.50
C2	4	0.5	0.5	0	1	0	0	2	8.00
D1	3	0.5	0.5	0.5	0	0	0	1.5	4.50
D1/2	1	0.5	0.5	0.5	0.5	0	0	2	2.00
D2	2	0.5	0.5	0.5	1	0	0	2.5	5.00
D2/F2	1	0.5	0.5	0.5	1	0	1	3.5	3.50
E1	2	0.5	0.5	0.5	0	0.5	0	2	4.00
E1/2	2	0.5	0.5	0.5	0.5	0.5	0	2.5	5.00
n	30							$\Sigma(f_i \cdot w_i)$	51.25

$$P_4\text{-index} = \Sigma(f_i \cdot w_i) \times 100/n = 170.83. \text{ Index standardized} = 86.19 \text{ (GS standard} = 198.2)$$

Table 4: Weighting of P_4 morphotypes and calculation of morphodynamic indices. f – (frequency) number of morphotypes, w – (worth) morphodynamic factor = sum of single valued steps, GS standard = P_4 -index of Gamssulzen cave (see RABEDER, 1995; 1999).

Morphotypes of the P₄

The distribution of P₄-morphotypes within the Križna material is shown in Table 4. The following pattern is applied for the taxation of additional occlusal(?) elements: Elements of the Trigonid like fully developed cuspids and lophids (paraconid, metaconid, metastylid and metalophid) equal a factor of 0.5, the elements of the talonid equal a factor of 1. An explanation for the comparably high index of the p4 from Križna jama can be found in a lack of the primitive morphotypes A and B1 as well as in the presence of a hypoconid in approximately 25% of the teeth. Traces of a metalophid are visible in 27%, and some are even fully developed whereas a hypolophid is seldom. All in all there is a domination of the highly developed morphotypes.

The P4/4-index: The P4/4-index is the geometric mean of P⁴- and P₄-index and is calculated in the following way:

$$\text{P4/4-index (geometric mean of 277.63 and 170.83)} = 217.78. \text{ Standardised} = 96.74$$

Morphotypes of the M²: The most obvious evolutionary change concerns the occlusal surface of the M² – the development of the metaloph, i.e. the connection of the metacone and the inner ridge with a row of cusps or even by a single edge. This metaloph corresponds to the distal margin of the M₂. Also within the material from Križna jama there is a variation of this character from morphotype A (unordered) and B (misarranged) to morphotype C (strictly ordered). Morphotype D (a single edge) was not found at all. The numbers from 1 to 3 characterize the position of the metaloph; 1 – the row is situated between meta- and hypocone, 3 – between meta- and protocone and 2 is somewhere in between. The curvature of the metaloph towards mesiolingual is interpreted as an adaptation to the form of the distal M₂. Within the material from Križna jama there is a domination of morphotype C3 (< 60%), on the other hand there are also three samples without an ordered metaloph (morphotype A). An explanation for the high M²-metaloph index of the Križna jama bears can be found in the high abundance of

Morphotype	f _i	Cusp row	Course of cusp row	w _i	f _i · w _i
A	3	unordered	No course at all	1	3
B1	3	misarranged	Towards hypocone	2	6
B2	2	misarranged	Towards a point between proto- and hypocone	3	6
B3	1	misarranged	Towards a point between proto- and hypocone	4	4
C1	2	strictly ordered	Towards protocone	3	6
C2	1	strictly ordered	Towards a point between proto- and hypocone	4	4
C3	13	strictly ordered	Towards protocone	5	65
D3	0	cutting ridge	to protocone	6	0

$$\text{M}^2\text{-metaloph index} = \sum (f_i \cdot w_i) \times 100/n = 376.00. \text{ Index standardized} = 100.27 \text{ (GS standard} = 375.0)$$

Table 5: Weighting of metaloph morphotypes of M² and calculation of morphodynamic indices. f – (frequency) number of morphotypes, w – (worth) morphodynamic factor = sum of single valued steps, GS standard = M²-metaloph index of Gamssulzen cave (see RABEDER, 1999).

Posteroloph morphotype	f _i	Cusp row between metastyle and hypocone	w _i	f _i · w _i
0	0	No cusps	0	0
1	0	With cusps, not transversally ordered	1	0
1/2	1	Cusps partially ordered transversal	1.5	1.5
2	5	Cusp row misarranged or imperfect	2	6
2/3	1	Transversal cusp row not complete	2.5	2.5
3	13	Cusp row complete	3	39
n	18		$\sum (f_i \cdot w_i)$	49

Table 6: Weighting of posteroloph morphotypes of M² and calculation of morphodynamic indices. f – (frequency) number of morphotypes, w – (worth) morphodynamic factor = sum of single valued steps, GS standard = M² posteroloph index of Gamssulzen cave (see RABEDER, 1999).

$$\text{M}^2\text{-posteroloph index} = \sum (f_i \cdot w_i) \times 100/n = 265.00. \text{ Index standardized} = 126.79 \text{ (GS standard} = 209.0)$$

Table 7: Weighting of M_1 and M_2 enthyoconid morphotypes and calculation of morphodynamic indices. **f** – (frequency) number of morphotypes, **w** – (worth) morphodynamic factor = sum of single valued steps, GS standard = m_1 resp. M_2 enthyoconid index of Gamssulzen cave (see RABEDER, 1999).

Enthyoconid morphotype	fi		Enthyoconid consists of	w_i	fi . wi	
	M_1	M_2			M_1	M_2
A	0	0	No cusps	0.0	0	0
B	6	0	1 cusp	0.5	6	0
B/C	2	6	1 cusp and a second imperfect one	1.0	3	9
C	0	3	2 cusps	1.5	0	6
C/D	3	2	2 cusps and a third imperfect one	2.0	7.5	5
D	0	0	3 cusps	2.5	0	0
n	11	11		3.0	16.5	20

M_1 index = $\Sigma (fi.wi).100/n = 150.00$. Index standardized = 114.50 (GS standard = 131.0)

M_2 index = $\Sigma (fi.wi).100/n = 181.82$. Index standardized = 98.12 (GS standard = 185.3)

	mean	GS standard	standardised	deviation	max	min	number
female canines length	22.09	21.13		—	24.0	20.6	11
female canines width	15.72	15.36	102.33	—	16.5	14.0	11
male canines length	28.27	26.45	106.87	2.73	34.3	22.7	33
male canines width	21.46	19.63	109.33	1.43	24.0	18.5	33
P^4 length	20.03	20.13	99.49	1.43	22.2	17.3	28
P^4 width	14.27	14.21	100.39	1.04	16.6	12.1	2
P^4 Index	276.39	255.70	108.09	—	4.0	1.5	18
$P4/4$ index	217.75	225.12	96.72				
P_4 length	15.42	15.24	101.18	0.99	17.3	13.9	30
P_4 width	10.69	10.32	103.62	0.82	12.3	9.4	30
P_4 index	175.83	198.20	88.72	—	3.0	0.75	30
M^1 length	28.57	28.73	99.38	1.12	32.0	26.7	31
M^1 Width	19.93	19.75	100.76	1.14	22.5	18.0	31
M^2 length	46.00	44.40	103.61	2.97	50.4	39.9	32
M^2 Width	23.20	22.55	102.90	1.12	25.4	21.1	32
M^2 metaloph index	400.00	375.00	106.67	—	6.0	1.0	22
M^2 posteroloph index	265.00	209.00	126.79		3.0	1.0	18
M_1 length	30.47	30.22	100.82	1.26	33.0	27.5	31
M_1 width	15.33	14.50	105.72	1.14	19.3	13.8	31
M_1 enthyoconid index	140.91	131.00	107.56	—	2.5	1.0	11
M_2 length	30.56	30.63	99.88	1.44	33.6	27.6	31
M_2 width	18.86	18.25	103.32	1.17	21.1	17.0	29
M_2 enthyoconid index	192.00	185.3	103.44	—	2.5	1.5	12
M_3 length	28.01	27.56	101.63	2.05	30.7	22.4	33
M_3 width	19.93	19.11	104.28	1.29	21.6	15.5	33
M^2/M^1 length ratio	161.04	154.54	104.26				
M_3/M_2 length ratio	91.56	89.98	101.75				

Table 8: Measurements of canines and cheek teeth of *Ursus ingressus* from Križna jama (Slovenia).

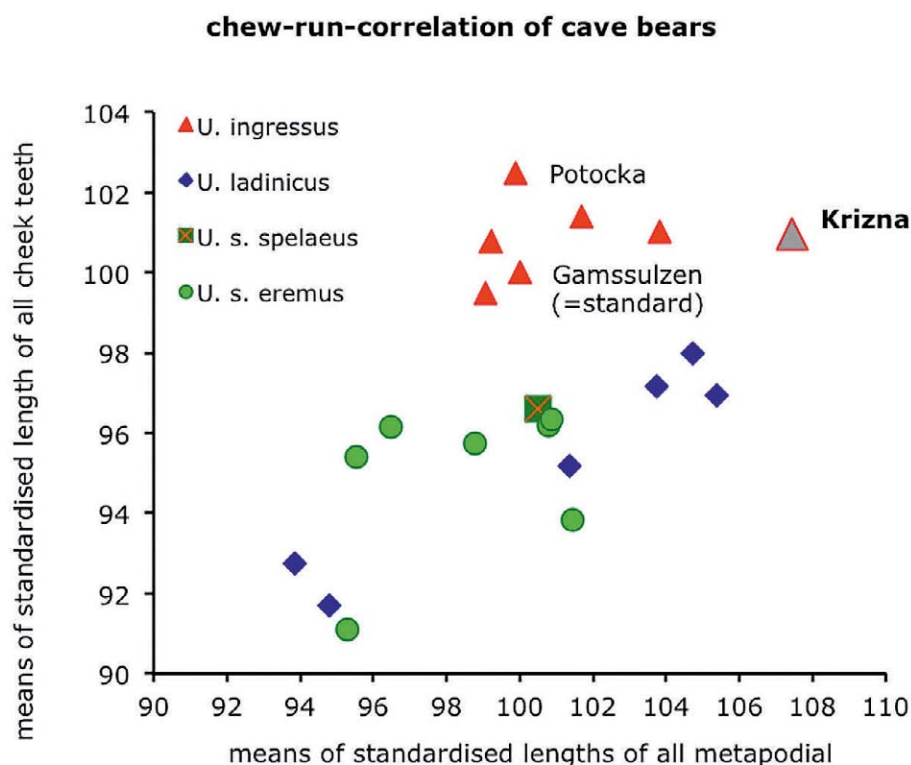


Figure 2: Correlation between length of metapodial bones and length of cheek teeth of the cave bear faunas (compare to RABEDER & WITHALM, 2011: diagram 2–3)

morphotype C3. A second row of little accessory cusps is situated distally to the metaloph, reaching from metastyle to the hypocone. It is called posteroloph. Within the material from Križna jama there are only 18 teeth showing this character, but these teeth show an exceptionally high-developed posteroloph. 13 upper M^2 from Križna jama show the highest developmental level which is called morphotype “3” and counts three. A not so well ordered or incomplete row of cusps is called morphotype “2” and was found only three times in Križna jama. Last but not least there are two more teeth with an intermediate developmental level between morphotype “1”, which shows cusps that are not transversally ordered, and “2” and “3” respectively. The M^2 -metaloph index is given in Table 5, the M^2 -posteroloph index is given in Table 6.

Functional Analysis: An explanation for the function of meta- and posteroloph can be found in their position in respect of the molars of the lower jaw as well as by the abrasional patterns. The M^2 -metaloph fits perfectly well in the incision between M_2 and M_3 and follows the distal margin of the M_2 , the latter runs with several cusps from hypoconid to the entoconid. The posteroloph functions as an antagonist of the highly variable structure of the M_3 -protoconid.

4. The Enthypoconid-Index of M_1 and M_2

The formation of the enthypoconid can be explained as an adaptation to the pressure of mastication and the related abrasion of the M^1 paracone and the M^2 paracone as well. It is calculated by the number of cusps the

enthypoconid consists of and proved to be a good tool because it helps to distinguish between the different evolutionary lines of cave bears. The number of usable M_1 and M_2 is pitifully low as most of the teeth are heavily worn, but the few usable teeth show a high evolutionary level which is comparable to those of the bears from Gamssulzen cave, see Table 7.

5. Conclusion

The metric values of the studied teeth, see Table 8, lay with few exceptions (length of P^4 , M^1 and M_2) above the volumes of standard fauna of *Ursus ingressus* RABEDER et al., 2004 from the Gamssulzen cave (RABEDER, 1995, 1999). The „mean of standardised length of all cheek teeth“ is a significant index for the discrimination of cave bear species (see RABEDER & WITHALM, 2011:75–76: diagram 2 and 3). The cluster of *Ursus ingressus* is defined specially with high means of cheek teeth measurements. The means of standardised values (length: 100.86, width: 103.00) of Križna jama are the greatest ones of all cave bears (see Fig. 1).

In the „chew-run-diagram“ the mean of all standardised lengths of cheek teeth are related to the mean of all standardised length of metapodial bones. The fauna of Križna jama falls clearly in the cluster of *Ursus ingressus* (see Fig. 2).

The most values of all important morphodynamic indices (P^4 index, enthypoconid index of M_1 and M_2 , metaloph index and posteroloph index of M^2 , M^2/M^1 index and M_3/M_2 index) are higher than the Gamssulzen values with

one exception: the P_4 index fits under the Gamssulzen level. The high values of morphodynamic indices argue for a affiliation to *Ursus ingressus* also.

6. References

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