

MORPHOMETRICAL FEATURES OF THE CAVE BEAR AND BROWN BEAR HEAD SKELETON: A COMPARATIVE STUDY

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Abstract: The extinct cave bear (CB) is often depicted as a large heavy animal with a prominent, massive skull and severely shortened pelvic limbs. The size and robustness of the CB are comparable to those of the largest living ursids. Great similarities between CB and the brown bear (BB) species prompted our morphometric comparison. The goal of this study was to elucidate the potential differences in the morphometric skull characteristics of CB and BB species. Craniometric measurements were performed on the skulls of both bear species and were compared to identify craniometric features indicative of possible adaptations in both bear species. The results revealed a marked difference in skull size; however, the shape of the CB cranium is generally known to be similar to that of the BB. In CB, the total length of the skull was approximately 1.5 times longer, and the external bony nasal aperture was larger due to the relatively shorter nasal bones. The nose length and median palate length were relatively longer in the CB, and the infraorbital foramen was located more caudally and closer to the zygomatic process. The infraorbital channel of the CB was located over to the second superior molar roots whereas in BB the latter extends beyond the roots of the first to the second superior molar roots. A marked difference was the non-existence of the three most anterior premolars in the maxilla and mandible of the CB, Higher body of the mandible, which, together with the extensive biting surfaces of the cheeks teeth, indicates a predominantly plant-based diet of the CB. The braincase length was considerably shorter in the CB, resulting in a relatively small neurocranium volume. The pronounced frontal fossa in the CB skull continues caudally into a strongly developed frontal area, which gives the CB skull a prominent steep profile. In summary, comparative craniometry showed that CB had a smaller neurocranial volume and had herbivore-adapted jaws and teeth. These metric features of the head skeleton may be related to a lower adaptability to extreme climatic conditions to which they were exposed to during the last Pleistocene glacial period, which may have contributed to their extinction.

Key words: head skeleton; skull; mandible; craniometrical features; bear

Introduction

Bears are members of the *Ursidae* family. It is believed that bears evolved from the canid line during the late Oligocene and early Miocene (1). The family consists of eight extant species which are classified into three subfamilies: *Ailuropodinae* including the giant panda (*Ailuropoda melanoleuca*), *Tremarctinae* including the Andean bear (*Tremarctos ornatus*),

and *Ursinae* which includes six species: brown bear (*Ursus arctos*), polar bear (*Ursus maritimus*), American black bear (*Ursus americanus*), Asiatic black bear (*Ursus thibetanus*), sloth bear (*Melursus ursinus*), and sun bear (*Helarctos malayanus*). The six species in the *Ursinae* diverged in the last five million years (2). The cave bear (CB) (*Ursus spelaeus*) is an extinct species in the *Ursinae* subfamily that was continuously present in the middle and late Pleistocene. CBs were the most common subspecies among the Pleistocene animals (1, 3). The Etruscan bear (*Ursus etruscus*) spread into Eurasia during the early Pleistocene, it gave rise to CBs and was an ancestral to BBs. It was

initially smaller, but continued to trend toward a larger body size (4, 5).

Studies involving mitochondrial and genomic DNA extracted from CB remains showed that it was very closely related to BBs and polar bears but had split from the brown bear lineage before the BBs split from the polar bears (2). The name CB is used because the fossils of this species are usually found in caves that provide a favourable fossilisation environment. There is innumerable and unequivocal evidence of habitation by a number of different species in Eurasian cave sediments. CBs often used caves for hibernation, and for giving birth to cubs. Modern bears can create artificial shelters and hibernation dens; however, they readily hibernate in natural caves when appropriate conditions exist (4). This suggests that CBs may have spent more time in caves than BBs, which use caves occasionally, primarily for hibernation. The preponderance of bear remains found in Pleistocene cave sediments does not necessarily mean that CBs lived exclusively in caves. It may be that the caves provided more favourable conditions for the preservation of remains over a long period of time.

Extensive research and excavations of bone remains have been carried out in almost all important archaeological deposits (6, 7, 8, 9, 10). The CB bone remains are the most numerous of the large mammal species. Bones, teeth, and genetic research have shown that at least four different CB lineages existed before their extinction in the middle Pleistocene (11).

CBs had a wide geographical distribution throughout Europe. Fossil remains have been reported from Spain in the west to Great Britain in the north, in the northern parts of Greece, and as far east as the Urals (12). CBs were also frequent inhabitants of the Alps. In Slovenia, many archaeological sites with CB remains are known, including Potočka zijalka, Mokriška jama, Križna jama, and Divje babe caves, where large quantities of CB bones have been found (13).

The Eurasian brown bear (*Ursus arctos arctos*) is one of the most common subspecies of BB. The BB in the Balkans is a member of this subspecies belonging to the European population (14). Today, Slovenian bears are members of the Alpine-Dinaric-Pindos population, which occupies the area from the Eastern Alps in Austria and north-eastern Italy, to the Pindos Mountains in Greece (15) and extends over the territory of Austria, Italy,

Slovenia, Croatia, Bosnia and Herzegovina, North Macedonia, Montenegro, Serbia, Kosovo, Albania, and Greece. The Dinaric-Pindos BB population number is assessed at 2100–2800 bears (16, 17). Slovenia is located on the north-western edge of the most densely populated area of the Dinaric bear population and is thus the westernmost part of the BB population in Central Europe (18).

During the Pleistocene ice age, the climate was too cold for BBs to survive in Europe, except in some places in Russia, Spain, and the Balkans, while the CB became extinct. The southern European BB is a relic from the late Pleistocene in comparison to the north-east European bear population, and spread throughout Europe only at the beginning of the Holocene (19).

In recent decades, many metric studies have been conducted on bears (20, 21, 22, 23, 24). Generally, the *Ursidae* represent the largest terrestrial carnivores, with a robust body, short tail, and short but powerful limbs. They are quadrupedal plantigrades. The head is large and robust with erect rounded ears, small eyes, grasping lips, and a particularly long tongue. The extinct CB is often depicted as a large heavy animal with a distinctive bulky skull and strongly shortened pelvic limbs in comparison to the thoracic ones. The size and robustness of the CB body are comparable to those of the largest extant ursids. The CB is thought to resemble a very large and cumbersome BB that fed mostly on plants (25). Therefore, we assumed that the CB and the modern BB shared similar morphological characteristics, which prompted our comparative craniometric study.

Craniometric characteristics have typically been used to describe the morphological characteristics of individuals to compare groups and to evaluate skull dimensions. Skulls differ in size and shape among the mammalian species. Considering that craniometry is becoming increasingly important in the characterisation of certain species, breeds and crosses, we compared the main metric features of the head skeleton of an extinct CB with that of a modern BB.

Material and methods

Two fossil skulls and three fossil mandibles of adult CBs, found at the archaeological site of Križna jama cave in Slovenia and owned by the palaeontological collection of the Natural History Museum of Slovenia were studied. The data

were compared to those of two adult BB skulls, including the mandibles, owned by the Anatomical Museum of the Veterinary Faculty University of Ljubljana. Craniometry was performed on the skulls and mandibles (Figures 1–5).

Several craniometric points and landmarks on the skull were determined for linear measurements. Firstly, the most important craniometrics points, shown in Figure 1, were marked: *akrokranium* (A), the most caudal point of the cranium vertex in the median plane; *prosthion* (P), the most rostral point of the interincisive suture; *basion* (B), the point in the middle of the ventral margin of the foramen magnum; *synsphenion* (S), the midpoint in the intersphenoid suture; *nasion* (N), the median point of the naso-frontal suture; *frontal midpoint* (F), the median point of the line joining both the most lateral points of the frontal bone on the occipital side of the orbit *ectorbitale* (Ect); *rhinion* (Rh), the median point of the line joining the most rostral points of the nasals; *staphylion* (St), the most caudal point of the palatine bone in the median plane; *palatinoorale* (Po), the median point of the palatine maxillary suture; *otion* (Ot), the most lateral point of the mastoid region; *zygion* (Zy), the most lateral point of the zygomatic arch; *entorbitale* (Ent), the naso-medial indentation of the orbit that corresponds with the inner angle of the living animal; *euryon* (Eu), the most lateral points of braincase; *coronion* (Cr), the highest point of the coronoid process; *infradentale* (Id), the most prominent median point at the rostral border of the alveoli of the mandible incisors.

The craniometric measurements of each skull were taken according to the scheme provided by von den Driesch (26) and are given in millimetres. The measurements were taken with a curved calliper in millimetres and a sliding calliper with an accuracy of 0.1 mm.

The following craniometric measures were taken for each skull (Table 1, Figure 1a, -b, -c): *the total length* (L1) from A to P; *the condylobasal length* (L2) from the caudal border of the occipital condyles to P; *the basal length* (L3) from B to P; *the basicranial axis* (L4) from B to S; *the basifacial axis* (L5) from S to P; *the neurocranium length* (L6) from B to N; *the upper neurocranium length* (L7) from A to F; *the viscerocranium length* (L8) from N to P; *the facial length* (L9) from F to P; *the greatest length of the nasal bone* (L10) from N to Rh; length of braincase; *the inner length of the cranial cavity* (L11) from B to cribriform plate; *the nose length*

(L12) from medial orbital border to P; *the median palatal length* (L13) from St to P; *the length of the horizontal part of the palatine bone* (L14) from St to Po; *the length of the cheektooth row* (L15); *the alveolus M² to alveolus C length* (L18) of the caudal border of alveolus of M² to rostral border of alveolus of C; *the length of the molar row* (L16); *the length of the premolar row* (L17); *P¹ to M² length* (L19); *the greatest diameter of the auditory bulla* (D) from the most caudal point of the bulla on the suture with the jugular process up to the external carotid foramen; *the greatest mastoid breadth* (W23) the distance between left and right Ot; *the breadth dorsal to the external auditory meatus* (W24); *the greatest breadth of the occipital condyles* (W25); *the greatest breadth of the bases of the paracondylar process* (W26), *the greatest foramen magnum breadth* (W27); *the foramen magnum height* (H28); *the greatest neurocranium breadth* (W29) between left and right Eu; *the zygomatic breadth* (W30) Zy-Zy; *least postorbital breadth of skull at the postorbital constriction* (W31); *the frontal breadth*, Ect-Ect (W32); *the least breadth between the orbits* Ent-Ent (W33); *the greatest palatal breadth* (W34); *the least palatal breadth behind the canines* (W35); *the breadth at the canine alveoli* (W36); *the greatest inner height of the orbit* (H37); *the skull height* (H38); *the skull height without the sagittal crest* (H39); *the height of the occipital triangle* (H40); *the neurocranium capacity* (C42).

The neurocranium capacity is based on the cranial cavity volume. The cranial cavity openings were closed with cellulose wadding, and the neurocranium was subsequently filled with fine seeds of rice through the foramen magnum and repeatedly shaken to remove eventual air pockets. Finally, the seeds were tipped into a measuring cylinder and the content volume was read.

The measurements for each mandible were taken as follows (Table 2, Figure 1d): *the total length* from condylar process to Id (L1*); *the length from the angular process to Id* (L2*); *the length from the notch between the condylar process and angular process to Id* (L3*); *the length from the condylar process to the caudal border of the canine alveolus* (L4*); *the length from the notch between the condylar process and angular process to the canine alveolus* (L5*); *the length from the angular process to the caudal border of the canine alveolus* (L6*); *the length of the caudal border of the M₃*

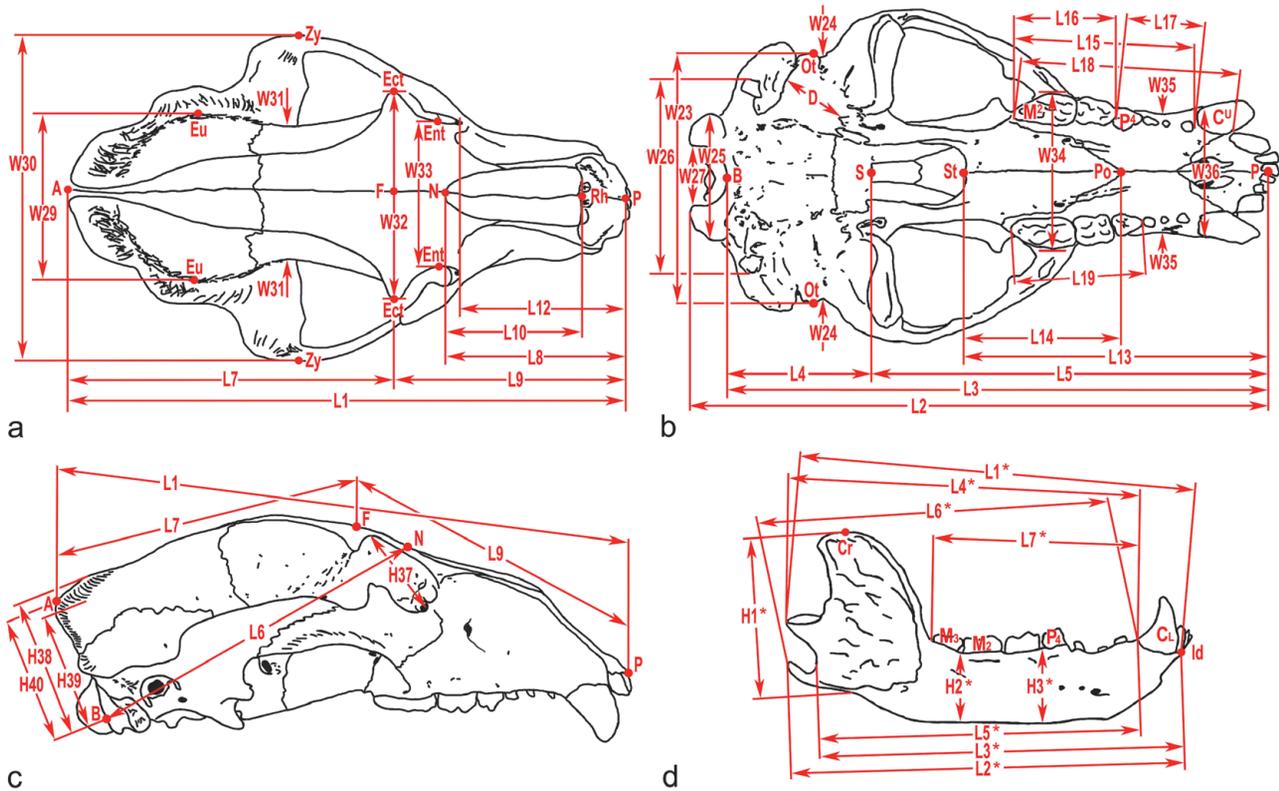


Figure 1: Craniometric measurements of the *Ursus* cranium, (a) dorsal, (b) ventral and (c) right side view and the *Ursus* mandible, (d) right side view

A akrokranium; B basion; Ect ectorbitale; Ent entorbitale; Eu euryon; F frontal midpoint; P prosthion; N nasion; O otion; S synsphenion; Zy zygion; L length, D diameter; W breadth; H height; Id infradentale; Cr coronion; C^U upper-, C_L lower- canine tooth; M² second upper-, M₁ first lower-, M₂ second lower-, M₃ third lower- molar tooth; P₄ fourth lower premolar tooth total L1; condylobasal L2; basal L3; basicranial axis L4; basifacial axis L5; neurocranium L6; upe neurocranium L7; viscerocranium L8; facial L9; greatest nasals L10; braincase L11; nose L12; greatest median palatal L13; horizontal part of the palatine L14; cheektooth row L15; molar row L16; premolar row L17; L18 from caudal border of alveolus of M² to rostral border of alveolus of C^U; L19 from P₄ to M₂; auditory bulla D; mastoid W23; dorsal to the external auditory meatus W24; occipital condyles W25; the bases of the paracondylar process W26; foramen magnum greatest W27; greatest neurocranium W29; zygomatic W30; least skull W31; frontal W32; between the orbits least W33; greatest palatal W34; least palatal W35; at the canine alveoli W36; greatest inner H37 of the orbit; skull H38; skull H39 without the sagittal crest; occipital triangle H40; total L1*; L2* from the angular process to infradentale; L3* from the notch between the condyle process and angular process to infradentale; L4* from the condyle process to caudal border of the canine alveolus; from the notch between the condyle process and angular process L5* to caudal border to the C_L alveolus; L6* from the angular process to caudal border of the canine alveolus; L7* from the caudal border of the alveolus of M₃ to caudal border of the C_L alveolus; mandible ramus H1*; H2* of the mandible behind M₂; H3* of the mandible between P₄ and M₁

alveolus of to the caudal border of the canine alveolus (L7*); the height of the vertical ramus from the basal point of the angular process to Cr (H1*); the mandible height behind M₂, measured on the buccal side (H2*); the mandible height between P₄ and M₁ (H3*).

Owing to large differences in craniometric values between the two bear species, we normalised the CB skull measurements to the average of the total length of the BB skull. The average values of the BB measurements were used as a standard for comparison (100% value). The relative deviations of the CB normalised values were considered an expression of species dimorphism.

Similarly, the mandible measurements of the CBs were normalised to the average measurements of the BB mandibles.

Results and discussion

The bear species measurements are summarised in Table 1. The relative deviations for each craniometric parameter of the CB compared with the BB are graphically presented.

Several relative skull length parameters, such as the condylobasal length (L2), basal length (L3), upper neurocranium length (L7), facial length (L9), length of the cheektooth row

(L15), length of the caudal border of M² alveolus to the rostral border of the C alveolus (L18), the molar row length (L16), and the distance of the P⁴ to M² (L19) showed less than 5% size-based deviations between the BB and CB skulls. The relative values of some width parameters, such as (W30) zygomatic breadth, (W34) greatest palatal breadth, and (W36), the breadth at the canine alveoli deviated even less.

The relative neurocranium length (L6) of CB was 6% shorter than that in BB, while the relative basicranial axis (L4) was 8% shorter.

The relative length of basifacial axis (L5), and certain relative values of the skull facial part, such as nose length (L12) and median palatal length (L13), were about 8%-10% longer in the CB than that in BB. Additionally, the relative length of the horizontal part of the palatine bone (L14) was 12% longer in the CB.

Some dimensions, such as the greatest mastoid breadth (W23), the greatest breadth of the occipital condyles (W25), zygomatic breadth (W30), the greatest palatal breadth (W34), the breadth of the canine alveoli (W36), skull height (H38), and height of the occipital triangle (H40), showed less than 5% relative deviations in the CB skull.

Some measured parameters, mainly of the cranial part of the head skeleton, such as the greatest breadth (W27), height of the foramen magnum (H28), the greatest breadth of the neurocranium (W29), and frontal breadth (W32), showed 13%-15% lower values in the CB. Additionally, some individual values of the skull facial part, such as the least breadth between the orbits (W33), the least palatal breadth (W35), and the greatest inner height of the orbit (H37), were 15-20% shorter in CB, and the greatest length of the nasal bones (L10), and the length of the braincase (L11) were also shorter by more than 15%.

The largest deviation was observed in the greatest diameter values of the auditory bulla (D), which was approximately 21% shorter, and of the least breadth of the skull (W31), which was 24% narrower in CB. Accordingly, the measured length of the braincase was 16% shorter. In the CB, this is reflected in the relatively smaller volume of the neurocranium capacity (C42). This is important because the brain fits into the cranial cavity. Therefore, it is obvious that a larger neurocranium cavity volume can accommodate a larger brain. Therefore, a larger brain in relation

to body size could be considered an advantage for the individual with respect to behavioural adaptability (27), which is crucially important when an individual is exposed to new or changing environmental conditions. Furthermore, in a new environment, the survival rate of mammals with larger brains to their body weight is supposed to be higher than that of mammals with smaller brains. Because of the relatively small CB brain, this conjecture did not support the survival of CB species under the extreme conditions of the last Pleistocene glacial period. We can speculate that a smaller brain may be one of the crucial factors leading to reduced adaptability to extreme conditions, and thus one of the reasons for the CB extinction.

The dorsal surface of the skull facial part is formed by the dorsal surfaces of the nasal, incisive, and maxillary bones and the nasal processes of the frontal bones. In CB, the prominent feature is the unpaired and more extensive external bony nasal aperture. This is mainly due to the relatively shorter length of the nasal bones, which form the caudodorsal edge of the bony opening and relatively longer terminal line passing along the nasal processes of the incisive bones. According to the nose length (L12) or the median palatal length (L13), which were relatively longer in the CB, the external nasal aperture has an oblique caudodorsal position in the CB. In BB, the nasal opening is smaller and set more vertically.

The nasal process of the incisive bone is connected medially to the nasal bone, laterally to the maxilla, and in both bear species, to the frontal bone at the base level of the frontal process of the maxilla. The maxilla has a roughly pyramidal shape with its apex directed cranially and its wide base on the caudal side of the bone. There is a prominent elliptical infraorbital foramen for the passage of the infraorbital nerve and the vessel on the facial surface. In BB, this opening is located more rostrally and lies at a level above the anterior root of the M¹, whereas in the CB, the infraorbital foramen is located more caudally and closer to the zygomatic process, located nearly in front of the zygomatic arch and at a level above the interalveolar septum between M¹ and M² teeth. In BB, the alveolar process of the maxilla contains alveoli dentales for the roots of the canine tooth and six cheek teeth, four premolars, and two molars. Hence, the dental formula in the upper jaw of the BB is 3, 1, 4, 2. In contrast, in the CB

Table 1: The size-based dimorphism between the brown bear and the cave bear skulls, the deviations (%) of the CBn are graphically displayed

	BBa	CBa	CBn	DEVIATIONS of the CBn from BBa (%)
L1	306.5	445.0	306.5	0.0
L2	284.5	426.0	293.4	3.1
L3	266.0	398.0	274.1	3.0
L4	75.5	101.0	69.6	-7.9
L5	193.0	301.5	207.7	7.6
L6	174.5	237.0	163.2	-6.5
L7	167.0	241.0	166.0	-0.6
L8	138.0	220.0	151.5	9.8
L9	163.0	240.0	165.3	1.4
L10	82.0	101.0	69.6	-15.2
L11	128.0	157.0	108.1	-15.5
L12	118.0	185.0	127.4	8.0
L13	149.0	236.5	162.9	9.3
L14	73.5	119.0	82.0	11.5
L15	91.0	135.8	93.5	2.8
L18	111.8	164.0	113.0	1.1
L16	53.0	76.0	52.3	-1.2
L17	38.3	59.5	41.0	7.1
L19	66.5	94.1	64.8	-2.6
D	28.0	32.0	22.0	-21.3
W23	128.0	187.0	128.8	0.6
W24	124.0	191.0	131.6	6.1
W25	60.5	84.0	57.9	-4.4
W26	91.5	143.0	98.5	7.6
W27	30.0	37.0	25.5	-15.1
H28	20.5	26.0	17.9	-12.6
W29	97.5	122.0	84.0	-13.8
W30	173.0	248.0	170.8	-1.3
W31	68.5	76.0	52.3	-23.6
W32	91.0	120.0	82.7	-9.2
W33	66.5	88.0	60.6	-8.9
W34	78.0	110.0	75.8	-2.9
W35	51.0	65.0	44.8	-12.2
W36	67.0	98.0	67.5	0.7
H37	44.5	55.0	37.9	-14.9
H38	79.0	120.0	82.7	4.6
H39	67.0	105.0	72.3	7.9
H40	74.0	113.0	77.8	5.2
C42	332.5	375.0	258.3	-22.3

BBa - the average values of the brown bear skulls craniometric features used as the standard of comparison;

CBa - the cave bear skull average data;

CBn - the cave bear skull normalized data

maxilla, the three anterior premolars are absent and only the fourth molar, P⁴, is present, giving the upper jaw dental formula: 3, 1, 1, 2. There is a distinct alveolar-free dorsal border between the canine and P⁴, called the interalveolar margin, *margo interalveolaris*, or diastema.

In BB, the first three premolars usually appear in a rudimentary form with no real function. Often, they do not grow or may fall out later. Small interdental spaces were found between each premolar in the BB. In the CB, the alveolar juga of both canine alveoli were the most prominent above the diastema on the facial surface of the maxilla.

Table 2: The size-based dimorphism between the brown bear and the cave bear mandibles, the deviations (%) of the CBn are graphically displayed

	BBa	CBa	CBn	DEVIATIONS of the CBn from BBa (%)
L1*	206.0	329.7	206.0	0.00
L2*	210.3	329.7	206.0	-2.02
L3*	196.5	313.7	196.0	-0.25
L4*	178.0	287.7	179.8	0.99
L5*	168.0	270.3	168.9	0.55
L6*	181.3	287.0	179.3	-1.05
L7*	106.8	163.7	102.3	-4.20
H1*	83.3	148.7	92.9	11.48
H2*	46.3	86.7	54.2	17.09
H3*	40.3	76.0	47.5	17.99

BBa - the average data of the BB mandibles measurements used as the standard of comparison,

CBa - the cave bear mandible average data,

CBn - the cave bear mandible normalized data

The absence of the three anterior premolars in both the upper and lower jaws, a rather long diastema, and the blunt morphology of the molar cusps with broad occlusal surfaces indicate their function in grinding plant food.

Compared to the BB, the upper margin of the nasal dorsum is relatively horizontal in the CB. In the BB, it runs caudodorsally and continues without a sharp boundary into the frontal area. In the CB, there is a distinct unpaired midsagittal depression at the transition from the nasal to the frontal region. The frontal fossa (*fossa frontalis*) extends caudally on the frontal bones from the nasal bones to a strongly developed frontal area. This feature gives it a distinctive and characteristic steep profile in the lateral view, which is not present in the BB (Figure 2).

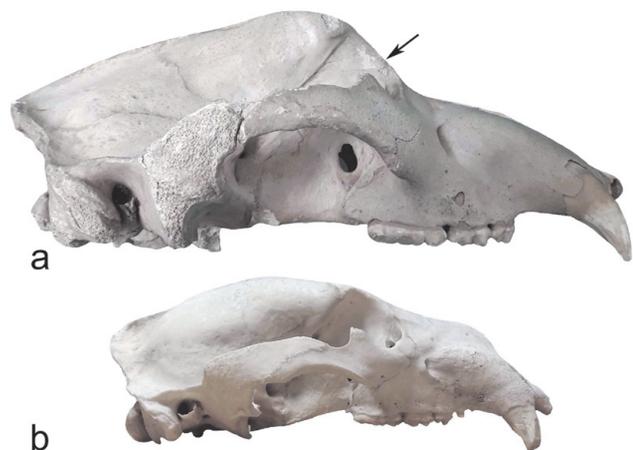


Figure 2: Cave bear (a) and brown bear (b) cranium, right side view

Note that the characteristic steep profile of the cave bear skull and strongly developed frontal area (arrow) is not present in the brown bear

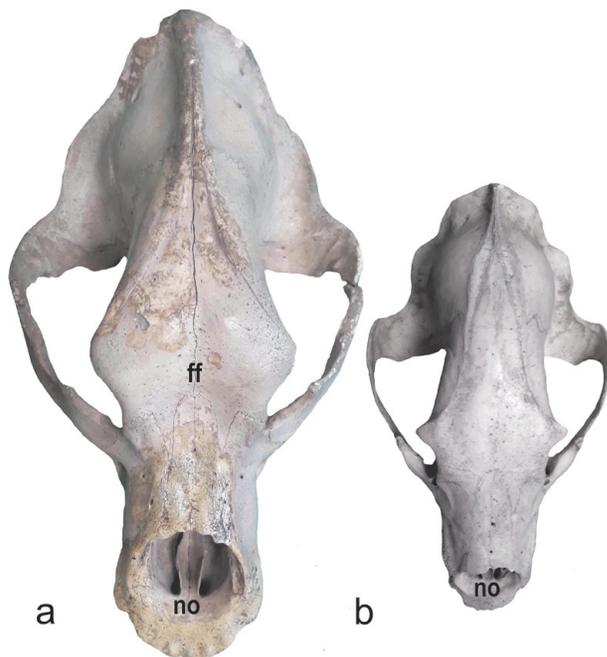


Figure 3: Cave bear (a) and brown bear (b) cranium, dorsal view

An extensive bony nasal opening (no) and the frontal fossa (ff) extending from the nasal bones to the frontal bones are characteristic of the cave bear skull

The prominent dorsal part development of the CB skull, especially in the frontal area, indicates a relatively high extent of the frontal sinus between the ecto- and endo-calvar laminae, whereas in BB, the frontal sinus is narrower. According to Torres Pérez-Hidalgo, the CB frontal bones are extremely thick; possibly because of their large size and protecting function, they are pneumatized to reduce their weight (28) and may have functioned as shock absorbers to protect the brain. The CB had a larger olfactory tract than BB (4, 28). Thus, the enlargement of the frontal sinuses could have been a pleiotropic effect of the turbinates development into the nasal cavity (29). The anterior part of the powerful masticatory temporal muscle was attached to an enlarged frontal region. The sinuses also serve as a reservoir for gases such as nitric oxide and hydrogen sulphide, which play an important role in hibernation control by lowering the heart rate and body temperature. The extensive sinuses may have contributed to a longer hibernation duration in the CB, which would have been beneficial during the long winters of the late Pleistocene. It is possible that death from starvation owing to prolonged hibernation could be one of the factors contributing to their extinction (30).

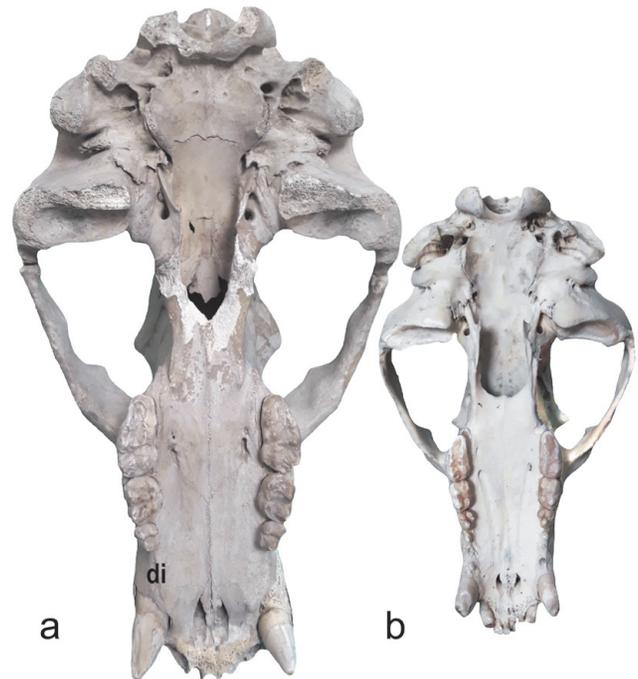


Figure 4: Cave bear (a) and brown bear (b) cranium, basal view

Note the absence of the first three upper premolars and the presence of the maxillary diastema (di) in the cave bear skull

On the lateral surface of the cranial part of the skull are the orbit and the prominent zygomatic arch. The latter is a laterodorsally convex bridge formed by a laterally compressed zygomatic bone and a dorsoventrally compressed zygomatic process of the temporal bone.

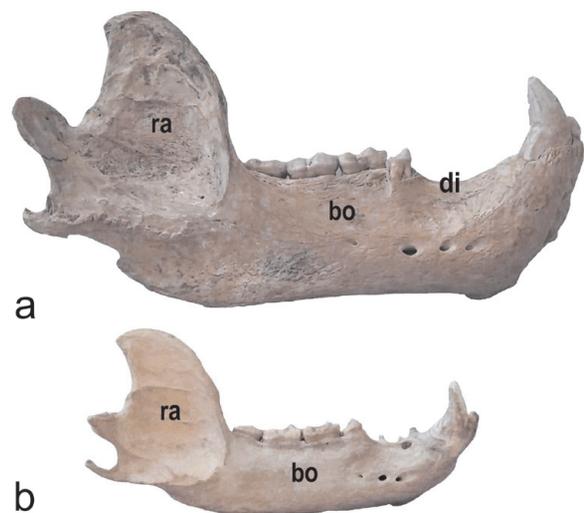


Figure 5: Cave bear (a) and brown bear (b) mandible, right side view

Note a more pronounced and higher ramus (ra) and body (bo) and the absence of the first three premolars with a pronounced diastema (di) in the cave bear mandible

The zygomatic breadth (W30) of these two species did not differ. In both species, it represented 56% of the total skull length. The ratio of the zygomatic breadth to the total length of the skull determines the shape of the skull, which is very similar in both species. This is consistent with the data of Grandal-d'Andlague & López-González 2005 (29), who reported that the cranium shape of *U. spelaeus* was generally extremely similar to that of *U. arctos*.

Owing to the relatively deep frontal fossa and the steep transition of the nasal area into the frontal region, the upper part of the face is positioned more caudally in the CB than in the BB. According to the total length of the skull, this is reflected in the approximately 10% longer viscerocranium length (L8) and 8% longer nose length (L12) in CB. The width of the greatest palatal breadth (W34) measured across the outer borders of the alveoli and the breadth of the canine tooth alveoli (W36) did not show any discernible differences between the two species. The least palatal breadth (W35), measured behind the canine teeth, was 12% narrower in the CB. This is visually reflected in the slight narrowing of this part of the nose.

Both palatal lengths, the median palatal length (L13) and length of the horizontal part of the palatine bone (L14), were 9%–12% longer in CB, while the length of the cheektooth row (L15) did not differ considerably. The premolar row length (the length of P⁴, including diastema) seemed to be longer in the CB, because most of its anterior part is a toothless diastema. Therefore, all cheek teeth, P⁴, M¹ and M², were located behind the lip opening, *rima oris*. The more caudal placement of the cheek teeth in the oral cavity indicates their primary chewing function, presumably biting plant food, as clearly shown by their wide occlusal surfaces.

In the CB, the bony opening of the intrapharyngeal ostium above the caudal border of the hard palate was circular in cross-section, while in BB, it was transversely oval. In both species, the unclosed orbital margin was slightly irregular in shape, while the orbits in the CB were closer together. The distance of the least breadth between the orbits (W33) was 9% narrower in CB, and so was the distance between the zygomatic process of the frontal bone (W32). The greatest inner height of the orbit (H37) was approximately 15% lower in the CB than in the

BB, suggesting that the eyeballs may have been smaller in the CB.

The orbital opening faces more rostrally in the CB skull. The shorter distance between the orbits (W33) may indicate that the CB had a larger binocular visual field. A dorsally convex ventral orbital crest (*crista orbitalis ventralis*) of the frontal bone, which is more prominent in the CB, indicates a well-developed pterygoid muscle. The crest demarcates the medial boundary between the orbital and the ventrally positioned pterygopalatine fossa. The rostral end of the fossa funnels down to the infraorbital channel, which is located dorsal to the roots of the second superior molar, while in BB, the position of the entire infraorbital channel is more rostral over almost the entire length of M¹. M² was the only upper cheek tooth in CB, which was according to the total length of the skull 7% longer than that in BB. All other maxillary cheek teeth were shorter, according to the total skull length in the CB.

There is a prominent external sagittal crest on the dorsal surface of the neurocranium, which is longer in the CB. It is located along the entire length of the interparietal suture from the level of the least breadth of the skull (W31) and runs caudally, where it is limited by the transverse nuchal crest, which marks the transition between the dorsal and caudal surfaces of the skull. The BB braincase is almost hemispherical. The relatively short external sagittal crest in the BB is limited only at the position of the interparietal bone and the parietal part of the occipital bone. The width of the least breadth of the skull (W31) at the neurocranium is approximately 24% lower in the CB. Additionally, the greatest neurocranium breadth (W29) between the Eur points is 13% lower in the CB. The right and left temporal lines diverge from the sagittal crest and continue rostrally to the zygomatic process.

The temporal fossa is the area on both sides of the sagittal crest and ventrolateral from the temporal lines. In BB, this is a relatively convex surface on each side of the dorsal part of the skull, whereas in CB, it is rather flat because of the narrower neurocranium. The skull is narrow and high in the CB. These features may have accounted for a more powerful masticatory musculature, especially the temporal and masseter muscles in the CB. As pointed out by Mazza et al. (31), anterior parts of the temporal

muscles are inserted into the high, broad, and robust frontal bones. Consistent with the masticatory muscles arrangement in the CB, the masticatory force must have been stronger in the posterior part of the jaw, where the strongest molars are located. The upper second molar acted against the lower second and third molars. The amount of food that could be processed between the CB teeth was probably small, as the gap size was more limited than that in carnivores that crushed food with the premolars.

Considering the size of the CB mandible (Table 2), all mandibular length data were not considerably different from the comparative norm, while the mandibular ramus was approximately 11% higher than in BB. The mandibular body was also 17%–18% higher in the CB. These findings of expanded mandibular ramus and body further support the hypothesis that CB had better developed masticatory muscles than BB, especially the masseter and pterygoid muscles. Therefore, the tongue must have been larger as well, which is also implied by the relatively deep intermandibular space. All these facts further confirm the assumption that CB was primarily a herbivorous species.

In summary, the comparative craniometry of the CB and BB skulls revealed that CB had a smaller neurocranial cavity volume and thus a smaller brain size, which may reflect a lower adaptability to extreme climatic changes to which they were exposed to during the last Pleistocene glacial period. Additionally, herbivore-adapted jaws and teeth were not an evolutionary advantage in the vegetation-poor era. All these facts might have led to the extinction of the CB.

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MORFOMETRIČNE ZNAČILNOSTI SKELETA GLAVE JAMSKEGA IN RJAVEGA MEDVEDA: PRIMERJALNA ŠTUDIJA

M. Uršič

Izvleček: Izumrli jamski medved je pogosto upodobljen kot robustna, težka žival z masivno lobanjo in izrazito skrajšanima medeničnima okončinama. Po velikosti ga lahko primerjamo z največjimi vrstami današnjih medvedov. Domnevne podobnosti med jamskim in rjavim medvedom so spodbudile našo primerjalno študijo, s katero želimo pojasniti morebitne razlike v morfoloških značilnostih lobanj, iz česar je mogoče sklepati na možne prilagoditve pri obeh vrstah. Oblika lobanje je pri jamskem medvedu precej podobna obliki pri rjavem medvedu, ugotovili pa smo izrazito razliko v velikosti. Pri jamskem medvedu je celotna dolžina lobanje približno 1,5-krat daljša, zunanja koščena odprtina vhoda v nosno votlino pa je zaradi razmeroma krajših nosnih kosti obsežnejša. Dolžina nosu in mediana nebna dolžina sta pri jamskem medvedu daljši. Podočnična odprtina leži nekoliko kavalneje in bližje ličnemu loku. Posledično se podočnični kanal pri jamskem medvedu nahaja le nad koreninami drugega molarja, medtem ko slednji pri rjavem medvedu sega še nad korenine prvega molarja. Razlika je bila opazna tudi v neizraslih prvih treh premolarjih tako v zgornji kot spodnji čeljusti jamskega medveda ter izrazitejšem telesu spodnje čeljustnice. Vse to, vključno z obsežnimi griznimi ploskvami molarjev, nakazuje pretežno rastlinsko prehrano. Dolžina možganske votline je pri jamskem medvedu opazno krajša, kar se odraža v sorazmerno majhni prostornini. Globoka čelna jama se kavalno strmo nadaljuje v močno razvito čelno področje. Manjša prostornina možganske votline, rastlinski hrani prilagojene čeljusti in površine zob ter nekatere druge metrične značilnosti okostja glave bi lahko bile vzročno povezane z nižjo prilagodljivostjo ekstremnim podnebnim razmeram, katerim je v zadnjem pleistocenskem ledeniškem obdobju jamski medved neuspešno kljuboval in kar bi lahko znatno prispevalo k njegovemu izumrtju.

Ključne besede: okostje glave; lobanja; spodnja čeljustnica; kraniometrične lastnosti; medved