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# THE MAMMALIAN FAUNA OF BAROVÁ CAVE (MORAVIAN KARST, THE CZECH REPUBLIC)

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**Abstract:** Barová Cave is located in the central part of the Moravian Karst (the Czech Republic), on the right slope of Josefovské Valley; it is the outflow part of Rudické propadání (Rudice Sink) – Býčí skála (Bull Rock) cave system. Even since its discovery by A. Sobol in 1947, Barová Cave has been known as important palaeontological site, with well-preserved fauna of the Late Pleistocene. In the summer of 2011, a landslide of sediments revealed yet unexamined fossiliferous positions, and started the current research activity. There were discovered skeletal remains of these 21 taxa of vertebrates between 2011 – 2017 in Barová Cave: bear from the cave bear group (*Ursus* ex gr. *spelaeus*), cave lion (*Panthera spelaea*), wolf (*Canis lupus*), cave hyena (*Crocuta crocuta spelaea*), brown bear (*Ursus arctos*), lynx (*Lynx lynx*), wolverine (*Gulo gulo*), fox, probably red (*Vulpes* cf. *vulpes*), marten (*Martes* cf. *martes*), alpine ibex (*Capra ibex*), chamois (*Rupicapra rupicapra*), aurochs or bison (*Bos primigenius*/*Bison priscus*), reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), horse (*Equus* sp.), woolly rhinoceros (*Coelodonta antiquitatis*), hare (*Lepus* sp.), lemming (*Dicrostonyx* sp.), bank vole (*Myodes* sp.), jackdaw (*Corvus monedula*) and probably northern pintail (*Anas* aff. *acuta*). Animal osteological material from sectors 2, 3, 4 and R4 from the Under the Ladder test pit in Barová Cave is analysed in detail in this paper. Bears from the group of cave bears completely dominate, the total sum of bones determined as bear bones make up nearly 95% of all determined material. The cave lion bones comprise nearly 3% of the determined osteological material; bones of a wolf represent about 1.2%, bones of cave hyena approximately 0.5% and bones of ungulates approximately 0.2% of all determined material (Tab. 1). From the MNI point of view the bears from the cave bear group dominate too. Bear bones belonged to at least 40 individuals (70.2% of all minimally present individuals) of all age categories (Tabs 1, 2). The predominance of bones of bears from the cave bear group in Barová Cave shows that the cave was mainly used as a bear wintering site. The presence of bear cub bones proved that the cave also served females as a birthing place. Some bones of bears from the group of cave bears and several bones of cave lions, cave hyenas and wolves also show evidence of bite and gnawing marks by carnivores or scavengers (cave lions, cave hyenas, wolves and perhaps cave bears). This suggests that hibernating bears, and more often the cadavers or isolated bones of dead individuals sometimes served as a food source. The seasonality analysis indicates that the time of death varied most frequently near the end of wintering season (spring/summer). The large amount of bear bone material leads to the consideration that the bears from the cave bear group used Barová Cave over a period longer than thousand years.

**Key worlds:** Quaternary palaeontology, Late Pleistocene, Moravian Karst, Barová Cave, animal assemblage, *Ursus* ex gr. *spelaeus*, wintering site, gnawing marks, hunting and scavenging, seasonality, dental age

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## Introduction

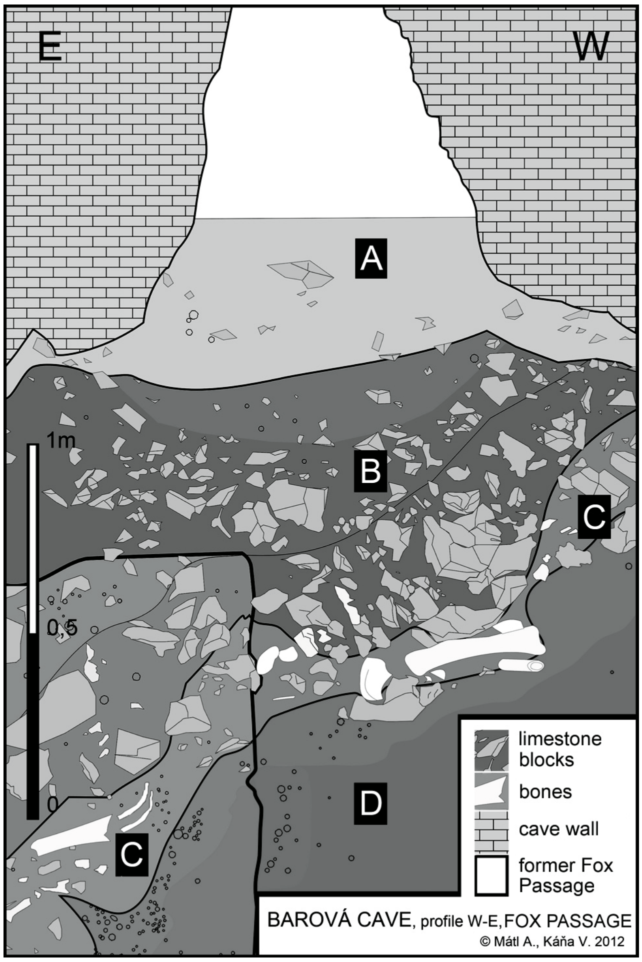
### Cave description and description of its sedimentary filling

Barová Cave is situated in the foot of the Krkavčí skála (Raven Rock), on the right bank of the Křtinský Creek in the Josefovské Valley in the central part of the Moravian Karst of the Czech Republic (Text-fig. 1). It is a part of the cave system Rudické propadání (Rudice Sink) – Býčí skála (Bull Rock) originated in Devonian Josefov and Lažánky limestone of the Macocha formation. Barová Cave forms the active arm of the karst spring area. It is one of the recently discovered caves in the Moravian Karst. It was discovered and described by Antonín Sobol and his colleagues (hence it is sometimes called Sobol's Cave) in 1947, and to a large extent explored in the next five years (Sobol 1948, 1952). Already at that time, fossil bones of Pleistocene fauna were found in sediments between the entrance and the so-called Second Shaft (Strnad 1949).


**Text-fig. 1. Barová Cave, located inside the Czech Republic and the Moravian Karst.**

Barová Cave is an indented polygenetic karst cavity, flowed through by Jedovnický Creek. It comprises three levels (floors) with a total denivelation of about 80 m and a length of approximately 1,000 m. The upper floor is formed by vertical to sub-horizontal spaces of a vadose zone, mainly in directions NE-SW and WNW-ESE. The lower floor is the current creek bed of the Jedovnický Creek in its furthest spring part (in the length of about 200 m). The middle floor connects the other two floors, and is formed by depressions in sediments filling a large, almost monolithic karst cavity. These sediments have a thickness of up to 20 m, and form the bedrock of the studied fossiliferous layers. The origin of the sediments is not yet entirely clear; transport from the surface through chimneys probably prevails, however, waters of the creek were probably also involved in the sedimentation. Lithologically, a major part of the bedrock sediments is composed of clayish and sandy sediments with silicites that correspond to redeposited Mesozoic sediments of the "Rudice layers" type. The immediate bedrock of the sediments with palaeontological content is formed by rusty and gray-yellow clays and sandy clays (henceforth "layer D") of currently unknown age. Natural depressions in the bedrock sediments have formed six dome-like spaces called "Shafts". Bedrock sediments between the First and Second Shaft are covered with a younger debris cone consisting of a layer of Pleistocene and Holocene dusts, sands and clays, with numerous bones of Pleistocene fauna. The sediments of the debris cone (including bones) originate from the entrance area of the cave. The current entrance to the cave is located in the heel of the Krkavčí skála (Raven Rock) at an elevation of 344 m above sea level (40 m above the level of the Jedovnický Creek), and is formed by a top part of one of the chimneys of the upper floor of Barová Cave. Fossil entrances are assumed below, around an elevation of 335 m above sea level. Today they are probably covered and infilled with Holocene debris in the slope of the valley.

Fossiliferous Late Pleistocene sediments between the First and the Second Shaft form a prominent sedimentary tongue or cone at a height of 15–30 m above the creek level (i.e. 320–335 m above sea level), oriented W-E. Its complex structure was noticed by Musil (1959) and Seitl (1988). In general, sediments of the cone can be stratified as follows: above the highest part of the bedrock, a palaeontologically sterile layer D, there is layer C – a relatively thin fossiliferous layer on the basis of the sedimentary tongue. Layer C contains numerous bones of large carnivores, mostly of bears from the group of cave bears, and rarely also bones of other animal species. It reaches a thickness up to one meter, but the average thickness is only ten centimetres. The animal bones are therein concentrated in clusters, rarely in partially anatomical positions. They are deformed and crushed by the pressure of overlying sediments. The sediments of layer C are predominantly clayish, with fragments of fossil sinter, and infrequently with corroded limestone stones. The layer represents the initial stage of the bones' sedimentation, where transport most likely proceeded in only shorter distances (Káňa et al. 2013, Roblíčková and Káňa 2013a, b). Layer B, overlying layer C, is the actual body of the debris cone. It contains massive sharp-edged blocks of limestone and numerous smaller limestone stones.




**Text-fig. 2. Profile of the Fox Passage test pit, shape of December 2012. The letters A, B, C mark three fossiliferous layers, the letter D marks a highest part of the palaeontologically sterile bedrock.**

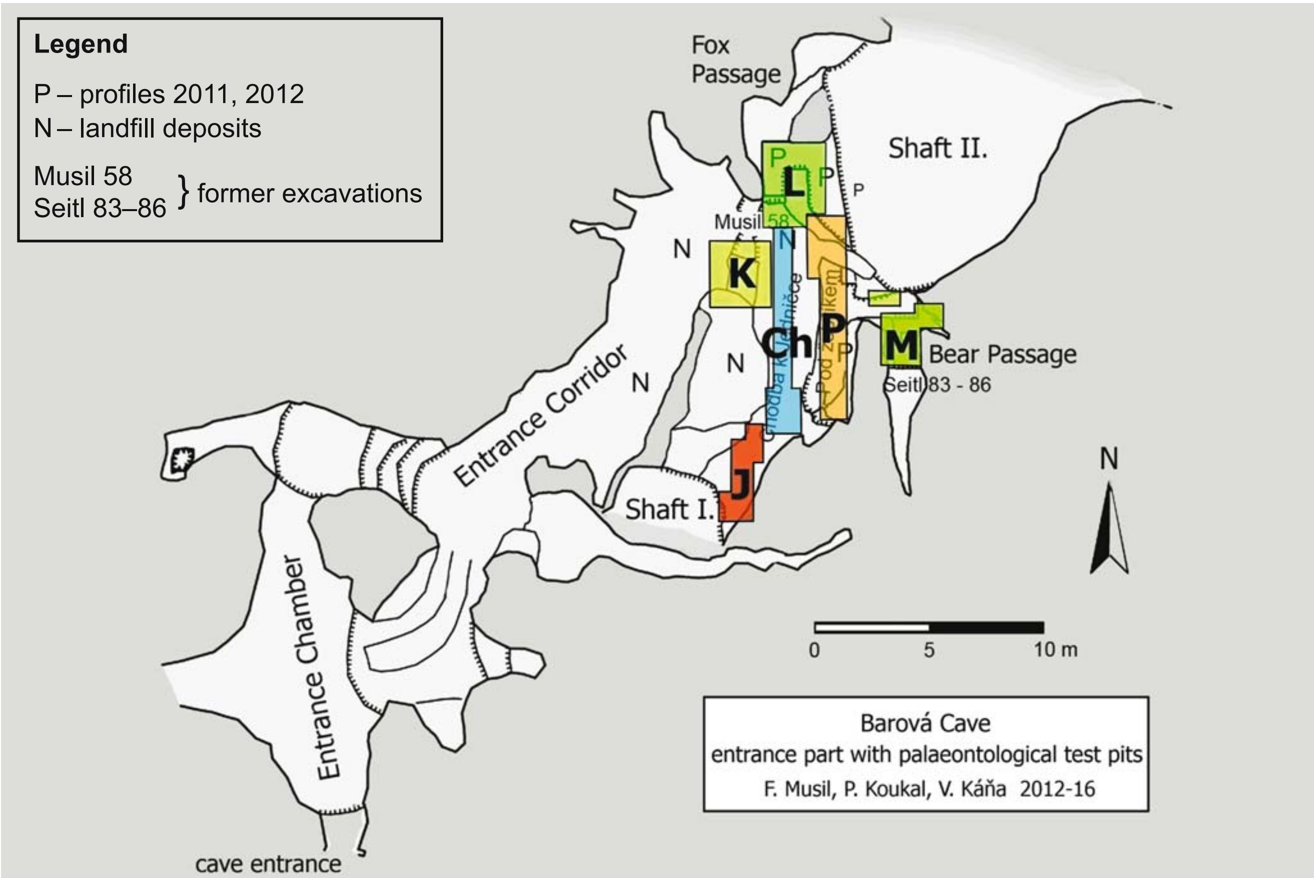
Bone remains of vertebrates are also quite abundant there, but they are scattered, and never in anatomical positions. The bones of layer B are damaged not only by pressure of overlying sediments, but more than the bones of layer C, also by the transport in the sediment or on its surface. The transport presumably proceeded over longer distances. The B-layer sediment consists of grey-yellow silts and clays with interlayers of sands; a considerable part of the matrix resembles a “redeposited loess” according to Musil (1959, 1960). The thickness of layer B in the Under the Ladder test pit reaches up to 150 cm, in the Fox Passage test pit almost four meters. The uppermost layer A is formed mainly by grey-yellow silts and clays, originally overlaid with a sinter plate or a thin sinter layer (Text-fig. 2).

Layer A has been largely destroyed or excavated in previous years (Sobol 1952, Roblíčková and Káňa 2013b).

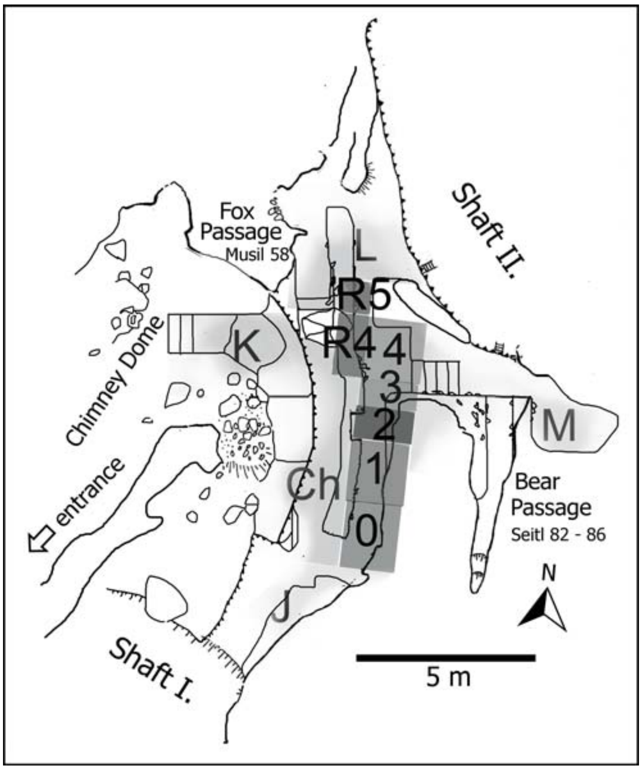
**History of research**

In the sediments of Barová Cave, two waves of palaeontological researches took place before 2011: the excavations by R. Musil in 1958 (Musil 1959, 1960), and the palaeontological-archaeological research by J. Svoboda and L. Seitl in the eighties, during which they also examined sediments of so called “Bear Little Hall”, containing bones of Pleistocene fauna (Seitl 1988). Bones found during these excavations are deposited in the Anthropos Institute of the Moravian Museum (MM) in Brno. Amateur speleologists also intermittently worked in the cave, and their activities to a considerable extent also affected parts of the cave with significant palaeontological content. Their findings were roughly collected, and some of them are deposited in the Anthropos Institute of MM with unknown details (Bartoň in verb. 2012). By summer 2011, the cave was considered to be palaeontologically excavated, individual test pits and trenches were filled with sterile sediment and were completely unrecognizable. A landslide of sediments in the summer of 2011 revealed yet unexamined fossiliferous positions in the Late Pleistocene sediments, and meant the beginning of the current research activity.

Six palaeontological test pits (Fox Passage, Under the Ladder, Bear Passage, Passage to the Shaft I, Shaft I and Chimney Dome; Text-fig. 3) were laid in the fossiliferous sediments of Barová Cave between the First and the Second Shaft during years 2011 – 2016. Older excavated areas were re-located, rid of landfill and reconstructed. In the sediments among trenches of previous researchers, the authors laid a completely new test pit called “Under the Ladder” (Roblíčková and Káňa 2013b), which includes sediments of all three abovementioned fossiliferous layers. Its base is at an elevation of 321 m above sea level. The test pit was divided into technical sectors with a volume of about 1–6 cubic meters of the sediment; size and shape of sectors depends on the shape of the cave ceiling and walls. In the SSW-NNE direction, the sectors are labelled 0, 1, 2, 3 and 4; further in the ESE-WNW direction is sector




**Text-fig. 3. A cut-out of the Barová Cave layout, focused on palaeontological excavations. Single test pits are marked and distinguished by letters. Ch – Passage to the Shaft I test pit, J – Shaft I test pit, K – Chimney Dome test pit, L – Fox Passage test pit, M – Bear Passage test pit, P – Under the Ladder test pit.**




**Text-fig. 4. Layout of the Under the Ladder test pit. Sectors of the Under the Ladder test pit are marked by rectangles with numbers and letters: 0, 1, 2, 3, 4, R4, R5.**


**Text-fig. 5. Photo of a small segment of an instructive profile in the Under the Ladder test pit and the Fox Passage test pit. Visible in the figure are mainly the bones of bears from the cave bear group. Photo by M. Polách.**

R4, and again in the SSW-NNE direction the last sector R5 (Text-fig. 4). The trench is therefore in the shape of an irregular "J", with a length of 5.5 m and a width of 1.5 m (respectively 0.8 m in sector R5). Above sectors 4 and R4, the ceiling of the cave narrows to the chimney 10 m high; the eastern part of these sectors and sector R5 is limited by pendants. In the area of sectors 0–3, sediments reach up to the ceiling or just below. Sector 4 was excavated entirely; in other sectors, part of the sediment was left in the form of a profile, specifically the left or WNW edge (about 20–40% of the total volume). The profile in the Under the Ladder test pit after connecting with the profile in the Fox Passage test pit reaches the length up to 10 m, and is therefore the largest one in the Moravian Karst (Text-fig. 5). This instructive profile is accessible to students and researchers for further research, sampling, etc. (Káňa et al. 2013, Roblíčková and Káňa 2013a, b).

## Methods

Standard methods are used in palaeontological research in Barová Cave. The area with scheduled palaeontological research is first named, and then divided into sectors; the profile is cleaned in its sediments, single layers are distinguished and their interface is located. Sediment excavation is carried out by a dry method, and the sterile sediment is deposited into a pre-defined area. The excavated osteological material is stored in plastic bags separately according to its location, and is always labelled with information about where and when it was found. Maintaining information about the location of findings is essential for retrograde reconstruction of the situation in the cave. Sectors are usually not excavated completely, as the aim is to maintain instructive profiles and enough material for possible revision research. Samples of sediments are usually collected for floating and further analysis. Osteological material is transported to the laboratory of the Anthropos Institute of the Moravian Museum in Brno, where it is further processed (Roblíčková and Káňa 2013a, b).

In the laboratory, the material is first cleaned, conserved if necessary, and fragmentary bones are restored to their original form, provided that their components were found. For taxonomic and anatomical determination of discovered bones, the primary source for comparative analysis is the extensive comparative osteological collection of the Anthropos Institute, but osteological handbooks and atlases (Hue 1907, Lavocat 1966, Pales and Lambert 1971, Schmid 1972, France 2009) are also used. A minimum number of individuals (MNI) of each species is determined using the methodology of Chaplin (1971). The estimation of biological age is based on the stage of development of long bones, and dentition (Kurtén 1958, 1976, Habermehl 1985). The biological age estimation of adult individuals is also based on the degree of dentition abrasion (Kurtén 1958). Pathological changes are observed on the bones, as well as postmortem taphonomic damages, most often predators bite marks or gnawing, or rodents' gnawing (Binford 1981, Lyman 1994). Several samples of osteological material were also successfully dated by radiocarbon method in the Research laboratory for archaeology and the history of art at the University of Oxford (see Chapter Radiocarbon dating).

### Estimation of MNI and age of bear individuals from the cave bear group

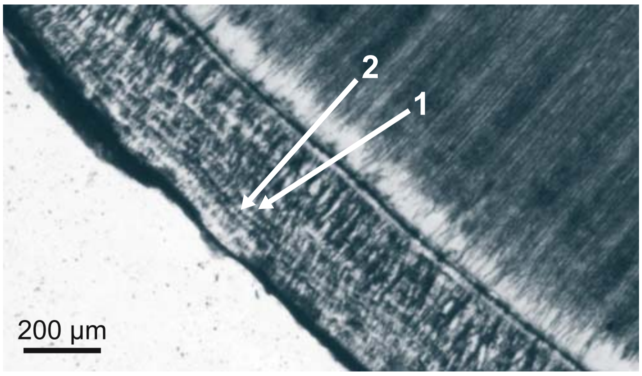
Minimum number of adult and subadult individual cave bears was determined based on the frequency of permanent premolars and molars (the most frequent were upper second molars). Minimum number of juvenile individuals without developed permanent premolars and molars was determined according to the number of long bones of adequate size and development. The age of adult or subadult individuals at the time of their death/killing is estimated based on the stage of the abrasion of the permanent teeth, the age of juveniles is estimated according to the length of long bones of the limbs (Kurtén 1976). Individuals aged 1–2 years at the time of death/killing were estimated on the basis of the development of the molar roots or the length of long bones (Kurtén 1958, 1976).

Differences in age at the time of death/killing in bears older than 2–3 years were estimated based on the degree of the abrasion of occlusal surfaces of permanent molars. The following categories were set on the basis of author's observation:

1. If the upper first molars (M1) or lower first molars (m1) had no or very mild abrasion (only tips of tubercles are moderately abraded), and crowns of upper second molars (M2) or lower second (m2) or third (m3) molars had no abrasion, the individuals were categorized as very young adults (or adolescents, subadults). The development of these molar roots was usually impossible to study, because the roots were hidden in jaws. In case of single molars, the roots of M1 and m1 were fully developed and closed; the roots of M2, m2 and m3 were either also closed or just closing.
2. If molars M1, m1 had mild abrasion (all tubercles are distinctly abraded), and molars M2, m2, m3 had very mild abrasion, the individuals were categorized as young adults.
3. If molars M1, m1 had mild to moderate abrasion (occlusal surface is abraded more or less to flat), and molars M2, m2, m3 had mild abrasion, the individuals were categorized as young to middle-aged adults.
4. If molars M1, m1 had moderate abrasion (height of molar is moderately reduced) and molars M2, m2, m3 had mild to moderate abrasion, the individuals were categorized as middle-aged adults.
5. If all molars had a moderate to heavy abrasion (height of molar is distinctly reduced), the individuals were categorized as middle-aged to old adults.
6. If all molars had a heavy abrasion (height of molar is heavily reduced), but were not worn to the roots, the individuals were categorized as old adult bears.
7. The last category is composed of bears with very heavily worn molars (height of molar is very heavily reduced), alternatively worn to the root. These individuals were categorized as very old adult individuals.

**Seasonality and dental age determination**

Eight permanent teeth of various mammals from Barová Cave were used to determine seasonality and dental age – seasons of the time of death and age of the given individual. The method is based on the analysis of increments of the cementum on teeth roots. Preparation of samples for this analysis is not complicated, and uses methods used in other disciplines, such as geology and pedology (e.g. Fancy 1980, Stallibras 1982, Beasley et al. 1992, Burke 1993, Debeljak 1996, 2000, Ábelová 2005, Nývltová Fišáková 2007, 2013). A transverse cut is made in the first third of the root (Text-fig. 6), which is subsequently studied under a polarizing microscope using crossed Nicols at a magnification of 4× – 10× (Ábelová 2005, Nývltová Fišáková 2007, 2013). The resulting image is recorded by a digital camera.




**Text-fig. 6. Photo of cave lion lower premolar p4 root cut. The approximate age of individual is 9.5 years (No 3 in Tabs 6, 7). The thin layers on the edge of root are the dental cement increments; number 1 marks winter increment, number 2 marks summer increment. Photo by M. Nývltová Fišáková.**

The principle of the method for determining seasonality is based on increment of the cementum on the roots of teeth of mammals in the course of an individual's life, and therefore any kind of a permanent tooth can be used for this analysis. The method exploits the fact that the rate of increment of the cement is not the same in various seasons. The increment is more intense during the growing season (May to October – summer increment), and less intense during the dormant season (November to April – winter growth). Moreover, the summer growth is bright and the winter growth is dark, due to different activity of cementoblasts (Text-fig. 6). The thickness of the last increment indicates the time elapsed since the beginning of its formation, i.e. from May or November. It is possible to determine in which part of the year the subject died, if we assess whether the last increment of the cementum is the summer or winter one, and what is its thickness (Lieberman et al. 1990, Carlson 1991, Lakota-Moskalewska 1997, Curci and Tagliacozzo 2000, Debeljak 2000, Ábelová 2005, Hillson 2005, Nývltová Fišáková 2007, 2013). To calculate dental age by the method of cement increments, it is necessary to add to the number of summer (or winter) increases the time elapsed between the birth of the studied individual and the eruption of the particular analysed permanent tooth (Hensel and Sorensen 1980, Matson et al. 1993, Debeljak 1997, Van Horn et al. 2003, Medill et al. 2009, Beke 2010, White et al. 2016).

## Palaeontological analysis

So far there have been discovered skeletal remains of nine taxa of carnivores, seven taxa of ungulates, one taxon of hares, two taxa of rodents and two taxa of birds during the palaeontological research in Barová Cave during 2011 – 2017. About 18,000 pieces of mostly fragmentary animal bones has been found in the course of these excavations until now, but not all osteological material has been analysed yet. Bears from the cave bear group (*Ursus* ex gr. *spelaeus*) completely dominate among carnivores. Thousands of pieces of their bones have been found. Other carnivores found in the cave include cave lions (*Panthera spelaea*) and wolves (*Canis lupus*), with hundreds of bones, and cave hyenas (*Crocuta*

*crocuta spelaea*) with tens of pieces of bones. Osteological remains of other five taxa of carnivores have been found to date, but only in pieces: brown bear (*Ursus arctos*), lynx (*Lynx lynx*), wolverine (*Gulo gulo*), fox, probably red (*Vulpes* cf. *vulpes*) and marten (*Martes* cf. *martes*). There were found several, mostly fragmentary bones of seven taxa of ungulates: alpine ibex (*Capra ibex*), chamois (*Rupicapra rupicapra*), aurochs or bison (*Bos primigenius*/*Bison priscus*), reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), horse (*Equus* sp.) and woolly rhinoceros (*Coelodonta antiquitatis*). Hares (*Lepus* sp.) were represented only by several bones, and a very small number of findings also come from two rodent species: lemming (*Dicrostonyx* sp.) and bank vole (*Myodes* sp.). Regarding the remains of birds, so far there have been discovered bones of a jackdaw (*Corvus monedula*), 30 fragmentary bones of a single skeleton, and one bone of a duck, probably northern pintail (*Anas* aff. *acuta*).

**Animal bones from sectors 2, 3, 4 and R4 of the Under the Ladder test pit**

Animal osteological material from sectors 2, 3, 4 and R4 from the Under the Ladder test pit (Text-fig. 4) was analysed in detail. 7,585 pieces of bone were found, largely fragments of bones, in these sectors; 5,116 pieces of them were identified to their taxa (Tab. 1). The largest number of bones found in these sectors came from bears from the cave bear group (*Ursus* ex gr. *spelaeus*); 3,663 pieces of bone were assigned to this taxon (Tab. 1). Due to the high fragmentation of osteological material from Barová Cave, a fairly high number of mostly tiny, badly identifiable fragments remained identified only as very likely from bears of the cave bear group (in Table 1 labelled *Ursus* cf. ex gr. *spelaeus*, there were mostly fragments of ribs and vertebrae). These fragments also can be perceived as remains of bears from the cave bear group, and the total sum of bones determined as *Ursus* ex gr. *spelaeus* and *Ursus* cf. ex gr. *spelaeus* make up nearly 95% of all determined material from the monitored sectors of the Under the Ladder test pit (Tab. 1). Six bone fragments were assigned only to the genus bear (*Ursus* sp.); it was not possible to specify if these were the remains of a cave bear or a brown bear, and no bone was positively determined as a brown bear (*Ursus arctos*) in these sectors of the Under the Ladder test pit. The cave lion (*Panthera spelaea*; Tab. 1) was, after cave bear, the second most abundant species in the monitored sectors, but with a large quantitative distance. Its bones comprise nearly 3% of the determined material. Bones

**Table 1. Numbers of determined bones of individual animal taxa from all explored sectors (2, 3, 4 and R4) of the Under the Ladder test pit. This number of osteological finds of individual animal taxa is also expressed as a percentage both of total quantity of found animal bones and of total quantity of determined animal bones. The table also shows minimal number of individuals (MNI) of single animal taxa.**

| Taxon | Pieces of bones | % | % from determined | MNI | % MNI |
|---|---|---|---|---|---|
| *Ursus* ex gr. *spelaeus* | 3,663 | 48.29 | 71.60 | 40 | 70.18 |
| *Ursus* cf. ex gr. *spelaeus* | 1,196 | 15.77 | 23.37 | | |
| *Ursus* sp. | 6 | 0.08 | 0.12 | | |
| cf. *Ursus* sp. | 1 | 0.01 | 0.02 | | |
| *Panthera spelaea* | 147 | 1.94 | 2.87 | 4 | 7.02 |
| *Canis lupus* | 58 | 0.76 | 1.13 | 2 | 3.51 |
| *Canis* cf. *lupus* | 3 | 0.04 | 0.06 | | |
| *C. crocuta spelaea* | 27 | 0.36 | 0.53 | 3 | 5.26 |
| Mustelidae | 1 | 0.01 | 0.02 | | |
| | | | | | |
| *Rupicapra rupicapra* | 5 | 0.07 | 0.10 | 1 | 1.75 |
| *Cervus elaphus* | 2 | 0.03 | 0.04 | 2 | 3.51 |
| *Rangifer tarandus* | 1 | 0.01 | 0.02 | 1 | 1.75 |
| *Rangifer* cf. *tarandus* | 1 | 0.01 | 0.02 | | |
| *Equus* sp. | 1 | 0.01 | 0.02 | 1 | 1.75 |
| *Dicrostonyx* sp. | 1 | 0.01 | 0.02 | 1 | 1.75 |
| *Myodes* sp. | 1 | 0.01 | 0.02 | 1 | 1.75 |
| | | | | | |
| *Corvus monedula* | 1 | 0.01 | 0.02 | 1 | 1.75 |
| Aves | 1 | 0.01 | 0.02 | | |
| | | | | | |
| Total of determined bones/total of MNI | **5,116** | **67.45** | **100.00** | **57** | **100.00** |
| Undetermined bones | 2,469 | 32.55 | | | |
| | | | | | |
| **Total of bones** | **7,585** | **100.00** | | | |

of wolves (*Canis lupus*), along with three bones determined most likely as wolf (*Canis* cf. *lupus)* represent about 1.2% of the determined findings; bones of cave hyenas (*Crocuta crocuta spelaea*) represent approximately 0.5% of the findings. The last determined carnivore skeletal remain from sectors 2, 3, 4 and R4 from the Under the Ladder test pit is a rib fragment of an individual from the family Mustelidae (Tab. 1). There were found also several skeletal remains of ungulates, specifically chamois (*Rupicapra rupicapra*), red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) in the aforementioned sectors. However, bones of ungulates comprise only 0.2% of the determined animal bones from the monitored sectors. There were found two rodent lower jaws, from a bank vole (*Myodes* sp.) and a lemming (*Dicrostonyx* sp.), about thirty bones from one skeleton of a jackdaw (*Corvus monedula*), and one unspecified bird humerus (Aves; Tab. 1). Sediments of the Under the Ladder test pit were not floated, therefore the occurrence frequency of small mammals (rodents) and birds, as well as bear cubs may be underestimated.

*The bear from the cave bear group*

Bones of the bears from the cave bear group from sectors 2, 3, 4 and R4 of the Under the Ladder test pit (if we add to the determined bones those that were determined as *Ursus* cf. ex gr. *spelaeus*, due to their heavy fragmentation, it is a total of 4,859 bones and fragments of bones) belonged to at least 40 individuals (MNI = 40; Tab. 1).

Fragments of cranial bones together with mostly fragmentary upper and lower jaws and with isolated teeth predominate among the anatomical elements of cave bear skeleton in the studied sectors; these fragmentary cranial bones with jaw fragments and loose teeth constitute 1,264 pieces of all 4,859 determined bones of bears from the cave bear group. The vertebrae and rib fragments of bears from the cave bear group were also common in sectors 2, 3, 4 and R4 of the Under the Ladder test pit (807 pcs of vertebrae, 687 of ribs). Fragments of scapulae (174 pcs) and pelvic bones (162 pcs) were more frequent among the limb bones, followed by femurs, humeri and tibias. The bigger amount of phalanges (199 pcs), metacarpal and metatarsal bones (83 and 56 pcs) were also found. Some cave bear bones remained anatomically undetermined.

The age structure of these at least 40 bears is as follows: one newborn or fetus, two individuals several weeks (a month) old, two individuals 2–3 months old. Two bears based on the found bones were one year old at the time of death/killing; two individuals were 1–2 years old. Another two bears died/were killed at two years of age, as adolescents (Tab. 2). Thirteen individuals were classified as very young adults (or adolescents), based on tooth abrasion, another six as young adults. Four individuals were included in the category of young to middle-aged adult bears, another four in the category of middle-aged adults. Two, probably the oldest individuals, based on the degree of molar abrasion, were categorized as old adult bears (Tab. 2). Thorough metric analysis of the bones and teeth of the bears from Barová Cave has not yet been conducted, so we cannot determine the ratio between the number of males and females living in the cave. Nevertheless, based on the size of the teeth, it appears that the number of wintering females slightly prevailed over males. Deciduous bear teeth, with the exception of two deciduous canines, were not found in the monitored sectors, probably due to the fact that the most part of sediments was not floated.

**Table 2. The age structure of bears from the cave bear group (*Ursus* ex gr. *spelaeus*) at their time of death (estimated on the basis of animal osteological material from 2, 3, 4 and R4 sectors of the Under the Ladder test pit).**

| **Age categories** | **MNI** | **Illustrative age (in years)** |
|---|---|---|
| newborn (foetus) | 1 | |
| approx. 1 month | 2 | |
| 2–3 months | 2 | |
| approx. 1 year | 2 | |
| 1–2 years | 2 | |
| approx. 2 years | 2 | |
| very young adult (or adolescent) | 13 | 2–4 |
| young adult | 6 | 5–7 |
| young to middle aged adult | 4 | 8–10 |
| middle aged adult | 4 | 11–14 |
| middle aged to old adult | 0 | 15–18 |
| old adult | 2 | 19–22 |
| very old adult | 0 | >22 |
| **Total of individuals** | **40** | |

*The cave lion*

A total of 147 bones/fragments of cave lions from sectors 2, 3, 4 and R4 of the Under the Ladder test pit represent the

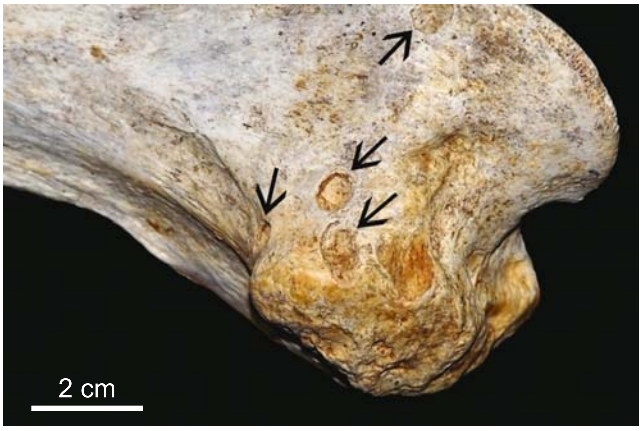

**Text-fig. 7. Photo of a skull with lower jaw of a cave lion subadult female (registration number is Ok-139786), discovered in layer C of sector 4 of the Under the Ladder test pit. Photo by V. Káňa.**

remains of at least four individuals (MNI = 4; Tab. 1); two of them were probably males and two females. Ageing and sexing of these lions is based on cranial characters and/or the postcranial bone size (humeri, metacarpal and metatarsal bones; after Turner 1984, Diedrich 2011). The first of the individuals is a subadult female, which is represented above all by a complete skull with a lower jaw (Text-fig. 7; its registration number is Ok-139786, the skull is deposited in Anthropos Institute, Moravian Museum). The skull of this adolescent female was found in anatomical position with five cervical vertebrae in layer C of sector 4, and based on the position and biological age, another 74 pieces of lion bones from sectors 4 and R4 that presumably come from the same individual were preliminary assigned to the skull. The second of the lions is an adult male, represented by a braincase and fragments of upper jaws, and several teeth found in sector R4. To its skeleton we can, due to the degree of bone development and size, provisionally assign at least 17 additional bones from sectors 4, R4 and R5. A premolar of this individual was used to analyse seasonality (see below). The third individual from sector R4 is probably an adult female, detected primarily on the basis of a humerus found at the interface of layers B and C. Individual cave lion bones were found also in sector 2. These bones can, but due to the nature of the fossilization and the distance of the deposition do not have to, come from the third individual. Bones from sectors 2 and 3 belong to another adult male, which is clearly not identical with the male represented by the braincase. It is therefore the fourth individual.

*Wolf and cave hyena*

Wolf bone remains (61 pieces) from sectors 2, 3, 4 and R4 from the Under the Ladder test pit originate from at least two adult individuals (MNI = 2; Tab. 1). Teeth of the first one have very little wear; therefore it was a young individual. Upper M2 that probably originates from the other (second) individual has slight abrasion. The second of at least two wolves died (was killed?) at an older age than the first one.

The number of the cave hyena bones from sectors 2, 3, 4 and R4 from the Under the Ladder test pit (27 pieces) is lower than the total number of the wolf bones. Yet the hyena bones originate from more individuals than the wolf bones, presumably from at least three individuals (MNI = 3; Tab. 1). Based on the fragments of right ulnas, there were two larger adult individuals and the third individual was smaller but also adult. A more precise estimation of the two larger individuals is difficult, because the tips of the crowns of the upper left canines (C) and incisors (I3) with corresponding size are broken off, most likely during life, and the degree of the abrasion cannot be determined. Only one upper incisor I3 from a larger individual did not have the tip of the crown broken off, and so showed abrasion. There was found a smaller lower right molar m1 that could belong to the third above-mentioned smaller individual. This molar had abrasion. Due to the sexual dimorphism of hyenas, it can be considered that the found hyena bones originate from two adult, not quite young females (the larger individuals) and one adult, again not quite young male (the smaller individual).




**Text-fig. 8. Photo of gnawing marks on the distal joint of humerus of a bear from the cave bear group (*Ursus* ex gr. *spelaeus*). Photo by V. Káňa.**

*Remaining animal taxa from sectors 2, 3, 4 and R4 from the Under the Ladder test pit*

Five chamois bones (two phalanges, a talus, a fragment of tibia and a metacarpal bone) originate from at least one adult individual (MNI = 1; Tab. 1). In the case of the red deer, there were found only two bone remains: the lower left permanent molar m2, and a fragment of the right lower jaw with the premolar p4 and molar m1. It could be therefore the remains of a single deer; nevertheless the lower left molar m2 is abraded more heavily, while the teeth of the right lower jaw have only a moderate degree of abrasion. Found bone remains of deer therefore likely come from two differently aged adults (MNI = 2; Tab. 1). One carpal and a fragment of the metacarpal bone of the reindeer originate from at least one adult individual, and one minimally represented horse was probably adult at the time of death/killing. The findings of rodents also always come from one adult, as well as the finding of a jackdaw skeleton.

*Summary*

Determined osteological material from sectors 2, 3, 4, and R4 from the Under the Ladder test pit originate from at least 57 individuals, however, especially in case of the taxa that are represented by a greater number of found bones, it is more than likely that the actual number of individuals was higher. Even on the basis of a minimum number of individuals the bears from the group of cave bears are clearly the dominant taxon (Tab. 1). Cave lions are the second most numerous animal occurring on the basis of MNI, although according to the situation in sectors 2, 3, 4 and R4 of the Under the Ladder test pit, Barová Cave was visited ten times less by lions than by bears. Interestingly, the smaller number of the hyena bones still represent more individuals than twice greater number of wolf bones (Tab. 1). The question therefore is, which one of these two carnivores was the more frequent visitor in the cave. A few bones of ungulates, rodents and birds always represent one individual, except for the deer (Tab. 1).

**Table 3. Number of bones of bears from the cave bear group (*Ursus* ex gr. *spelaeus*) with provable predatory bite and gnawing marks in layer B (Under the Ladder test pit; 2, 3, 4 and R4 sectors). The table shows percentage share of gnawed, chewed or bitten bones among the single kinds of bear bones or anatomical parts of bear skeleton. Cave bear bones without anatomical determination remained unutilized.**

| Skeleton parts | Number of bones (100%) | Bones with gnawing marks | Bones with gnawing marks in % | Bones with probable gnaw-ing marks | Bones with probable gnawing marks in % | Bones with gnawing marks – total in % |
|---|---|---|---|---|---|---|
| skulls + lower jaws | 228 | 3 | 1.32 | 3 | 1.32 | **2.64** |
| vertebrae + ribs | 308 | 8 | 2.60 | 8 | 2.60 | **5.20** |
| shoulder blades | 34 | 0 | 0 | 5 | 14.71 | **14.71** |
| humeri | 21 | 4 | 19.05 | 5 | 23.81 | **42.86** |
| radii + ulnas | 34 | 1 | 2.94 | 6 | 17.65 | **20.59** |
| pelvic bones | 26 | 4 | 15.38 | 4 | 15.38 | **30.76** |
| femurs + patellas | 40 | 6 | 15.00 | 9 | 22.50 | **37.50** |
| tibias + fibulas | 42 | 3 | 7.14 | 7 | 16.67 | **23.81** |
| wrist + ankle bones | 25 | 3 | 12.00 | 1 | 4.00 | **16.00** |
| metacarpal and metatarsal bones + phalanges | 73 | 0 | 0 | 0 | 0 | **0** |
| **Total** | **831** | **32** | **3.85** | **48** | **5.78** | **9.63** |

## Traces of feeding activity on animal bones from the Under the Ladder test pit

### *Traces of feeding activity on the bones of bears from the cave bear group*

Some bones of bears from the cave bear group from sectors 2, 3, 4, and R4 of the Under the Ladder test pit show evidence of feeding activity of carnivores or scavengers. There are teeth marks on the bear bones, bite and gnawing marks by wolves, cave hyenas, cave lions and maybe even cave bears (Text-fig. 8). Traces of biting on the bear bones might be a result of fighting and the subsequent consumption of the prey in case the lions, or perhaps hyenas, tried to hunt the overwintering bear and the attempt was successful. It is assumed, however, that a larger amount of gnawing occurred after the death of bears, when the hyenas, wolves, lions and maybe even bears tried to feed on cadavers or skeletons of already dead individuals. Bones are often chewed off at one of the joints, edges and protrusions of joint parts are chewed off or gnawed, gnawing traces are found on the broken off edges of the compact parts of the bones. Grooves from the teeth of a carnivore or scavenger caused by gnawing of meat, tendons, periosteum etc. are also visible on bones. However, bite marks were not found on all of the bear bones; on the contrary, the number of bones with definite or probable gnaw marks is rather low in comparison with the total number of bones.

**Table 4. Number of bones of bears from the cave bear group (*Ursus* ex gr. *spelaeus*) with provable predatory bite and gnawing marks in layer B + C (Under the Ladder test pit; 2, 3, 4 and R4 sectors). The table shows percentage share of gnawed, chewed or bitten bones among the single kinds of bear bones or anatomical parts of bear skeleton. Cave bear bones without anatomical determination remained unutilized.**

| Skeleton parts | Number of bones (100%) | Bones with gnawing marks | Bones with gnawing marks in % | Bones with probable gnaw-ing marks | Bones with probable gnawing marks in % | Bones with gnawing marks – total in % |
|---|---|---|---|---|---|---|
| skulls + lower jaws | 372 | 0 | 0 | 9 | 2.42 | **2.42** |
| vertebrae + ribs | 364 | 5 | 1.37 | 19 | 5.22 | **6.59** |
| shoulder blades | 30 | 1 | 3.33 | 1 | 3.33 | **6.66** |
| humeri | 23 | 1 | 4.35 | 2 | 8.70 | **13.05** |
| radii + ulnas | 31 | 2 | 6.45 | 2 | 6.45 | **12.90** |
| pelvic bones | 41 | 1 | 2.44 | 1 | 2.44 | **4.88** |
| femurs + patellas | 26 | 1 | 3.85 | 5 | 19.23 | **23.08** |
| tibias + fibulas | 35 | 0 | 0 | 2 | 5.71 | **5.71** |
| wrist + ankle bones | 26 | 0 | 0 | 2 | 7.69 | **7.69** |
| metacarpal and metatarsal bones + phalanges | 131 | 0 | 0 | 3 | 2.29 | **2.29** |
| **Total** | **1,079** | **11** | **1.02** | **46** | **4.26** | **5.28** |

**Table 5. Number of bones of bears from the cave bear group (*Ursus* ex gr. *spelaeus*) with provable predatory bite and gnawing marks in layer C (Under the Ladder test pit; 2, 3, 4 and R4 sectors). The table shows percentage share of gnawed, chewed or bitten bones among the single kinds of bear bones or anatomical parts of bear skeleton. Cave bear bones without anatomical determination remained unutilized.**

| Skeleton parts | Number of bones (100%) | Bones with gnawing marks | Bones with gnawing marks in % | Bones with probable gnaw-ing marks | Bones with probable gnawing marks in % | Bones with gnawing marks – total in % |
|---|---|---|---|---|---|---|
| skulls + lower jaws | 644 | 1 | 0.16 | 3 | 0.47 | **0.63** |
| vertebrae + ribs | 530 | 15 | 2.83 | 27 | 5.09 | **7.92** |
| shoulder blades | 95 | 4 | 4.21 | 5 | 5.26 | **9.47** |
| humeri | 25 | 1 | 4.00 | 4 | 16.00 | **20.00** |
| radii + ulnas | 34 | 1 | 2.94 | 2 | 5.88 | **8.82** |
| pelvic bones | 89 | 4 | 4.49 | 7 | 7.87 | **12.36** |
| femurs + patellas | 34 | 7 | 20.59 | 2 | 5.88 | **26.47** |
| tibias + fibulas | 33 | 1 | 3.03 | 4 | 12.12 | **15.15** |
| wrist + ankle bones | 60 | 2 | 3.33 | 1 | 1.67 | **5.00** |
| metacarpal and metatarsal bones + phalanges | 151 | 1 | 0.66 | 0 | 0 | **0.66** |
| **Total** | **1,695** | **37** | **2.18** | **55** | **3.24** | **5.43** |

On the bear bones from layer B, definite and probable gnaw marks have been only found on 9.63% of these bones (Tab. 3). There are interesting differences in the frequency of gnaw marks on different types of bones. Carnivores' gnaw marks were most often found on humeri, taking into account the total number of bear humeri found in layer B (Tab. 3). Gnaw marks were also often observed on femurs, including patellas, and pelvic bones. To a lesser extent, gnaw marks were found on radii, ulnas, tibias and fibulas. Very few traces of feeding activity of carnivores or scavengers were found on bones of skulls, lower jaws, vertebrae and ribs. No gnaw marks were found on metacarpal bones, metatarsal bones and phalanges from layer B (Tab. 3). Most often, those bones that were gnawed were the nutritionally more advantageous ones.

**Table 6. The list of animal teeth used for seasonality and dental age analysis from Barová Cave; determination and location of these teeth.**

| No | Tooth | Species | Location |
|---|---|---|---|
| **1** | P4 sin | *Panthera spelaea* | Under the Ladder test pit, sector R4, layer C |
| **2** | P3 dex | *Panthera spelaea* | Bear Passage, discovered by L. Seitl |
| **3** | p4 dex | *Panthera spelaea* | Under the Ladder test pit, sector 3, layer B + C |
| **4** | C sin | *C. crocuta spelaea* | Bear Passage, discovered by L. Seitl |
| **5** | c sin | *C. crocuta spelaea* | Bear Passage test pit, sector 3, layer C |
| **6** | C sin | *Ursus* ex gr. *spelaeus* | Under the Ladder test pit, sector 4, layer C |
| **7** | m1 dex | *Canis lupus* | Under the Ladder test pit, sector 3, layer B + C |
| **8** | m2 sin | *Cervus elaphus* | Under the Ladder test pit, sector 4, layer B |

**Table 7. The results of seasonality and dental age analysis. Analysed teeth come from Barová Cave, see Table 6.**

| No | Tooth | Species | Seasonality | Approximate age |
|---|---|---|---|---|
| **1** | P4 sin | *Panthera spelaea* | winter/spring | 11 years |
| **2** | P3 dex | *Panthera spelaea* | winter/spring | 3 years |
| **3** | p4 dex | *Panthera spelaea* | autumn/winter | 9.5 years |
| **4** | C sin | *C. crocuta. spelaea* | spring/summer | 5 years |
| **5** | c sin | *C. crocuta spelaea* | spring/summer | 9 years |
| **6** | C sin | *Ursus* ex gr. *spelaeus* | spring/summer | 14.5 years |
| **7** | m1 dex | *Canis lupus* | spring/summer | 5 years |
| **8** | m2 sin | *Cervus elaphus* | spring/summer | 8 years |

On the other hand, it must be stated that the aforementioned limb bones (humeri, femurs, etc.) are, due to their size, generally well preserved, which perhaps makes it easier to identify the traces of feeding activities on them.

In layer B + C gnawing marks (definite and probable together) were found on 5.28% of bear bones (Tab. 4). Layer B + C is singled out on the contact of layers B and C, animal bones are classed into it if they pass smoothly from layer C to layer B, and it is not possible to decide which of the two layers these bones belong to. Layer B + C is also singled out in those locations where it was not possible to distinguish layer B from layer C. The highest quantity of bones with traces of carnivore feeding activity in layer B + C was found among bear femurs, including patellas (23%); gnawing marks on humeri, radii and ulnas were also common. In comparison with layer B, fewer gnawing marks were found on bear pelvic bones, tibiae and fibulae of layer B + C; on the contrary, there were more often gnawed bones of wrists and ankles, vertebrae and ribs. The least frequent in layer B + C there were gnawed bones of skulls and lower jaws, metacarpal and metatarsal bones and phalanges (Tab. 4). Also in layer B + C, gnawing marks were concentrated rather on bear bones to which more muscles are attached (primarily the femur), however, the results are not as unequivocal as in layer B.

The number of bones of bears from the group of cave bears on which there were found the traces of feeding activity of carnivores is similar in layer C to layer B + C; 5.43% of bear bones were gnawed (Tab. 5). Most frequently in layer C there were gnawed femurs, including patellas (26.5% of femurs were gnawed) and humeri; a number of gnawed bones were also found among tibias, fibulas and pelvic bones. On the contrary, the fewest carnivore tooth marks were noted on bones of skulls, lower jaws, metacarpal and metatarsal bones, and phalanges (Tab. 5). Similarly to in previous layers, the most gnawing marks were found on bones richly covered with muscles (femurs and humeri).

Finally, definite and probable gnawing marks are observable on 6.35% of all anatomically determined bones of bears from the cave bear group (*Ursus* ex gr. *spelaeus*) that were found in sectors 2, 3, 4 and R4 of the Under the Ladder test pit.

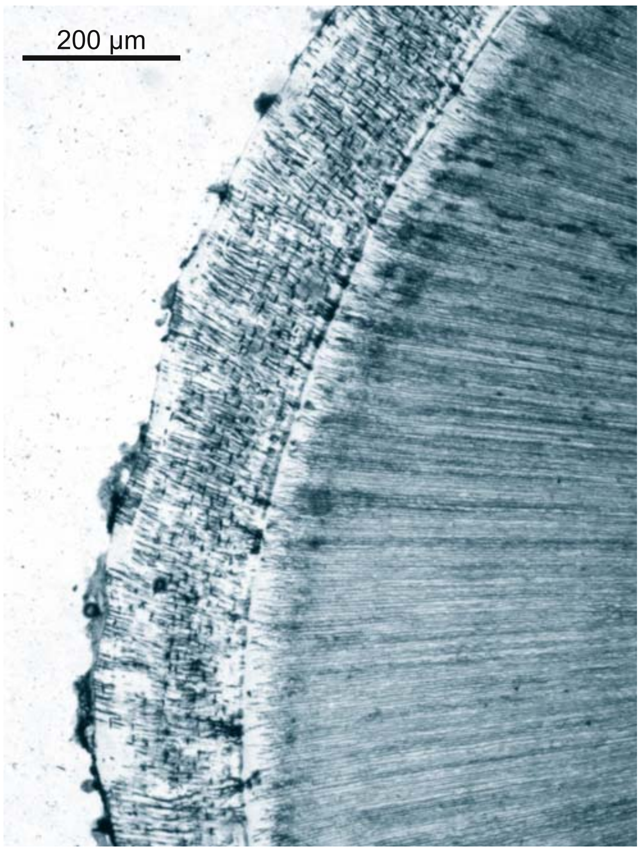
*Traces of feeding activity on the bones of other carnivores*

Traces of feeding activity by another carnivore or scavenger were occasionally found on some bones of cave lions. Of 147 lion bones excavated from sectors 2, 3, 4, and R4 of the Under the Ladder test pit, gnawing marks were found in seven, i.e. on 4.76% of the bones. Traces of feeding activity by a carnivore the size of a wolf to a hyena occurred in four bones out of 74 bones, probably belonging to the aforementioned subadult lioness. Specifically, gnawing marks were found on both proximal joints of humeri, and on two tail vertebrae (Roblíčková and Káňa 2013b, Káňa and Roblíčková 2014). Other traces of gnawing of lion bones were found in the monitored sectors, again on humerus, patella and tibia. On the pelvis fragment of the male lion from the sector adjacent to the examined ones, there were found tooth marks, whose size and position do not exclude feeding activity of a hyena, or lion cannibalism.

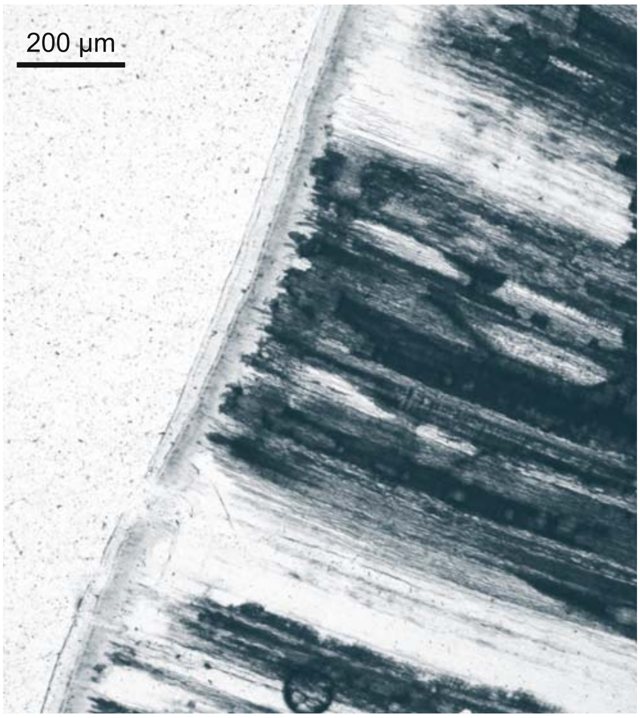
Traces of gnawing were also noted on several wolf bones. Two tibias were gnawed, in both cases the gnawing marks were found at edges of compact parts of the bones. Furthermore, there was found a humeral head that could have been chewed off, based on the marks at the edges. The last gnawed wolf bone could be a cervical vertebra, with probable tooth marks. Regarding the cave hyena, on the bones from sectors 2, 3, 4, and R4 of the Under the Ladder test pit, there were detected gnawing marks in two cases. A fragment of an ulna was found with clearly detectable tooth marks, and there was also found a part of a radius, of which the missing residue was probably gnawed off.

**Seasonality and dental age**

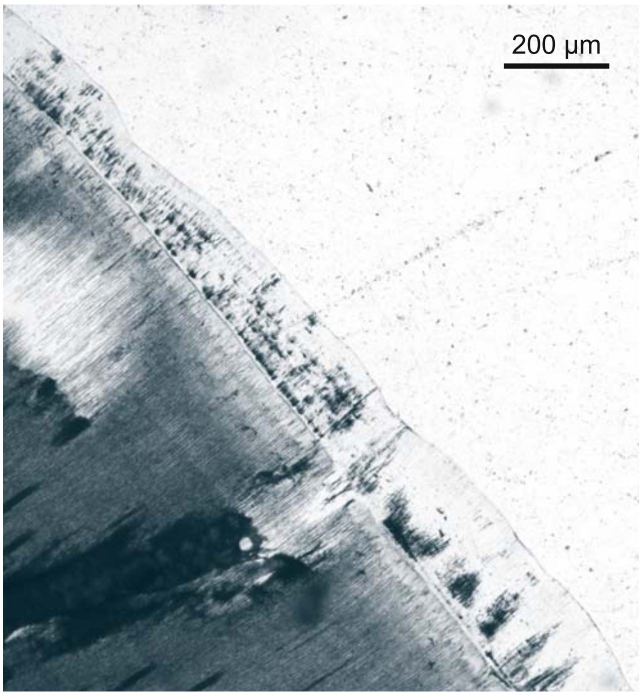
From Barová Cave, five teeth of various species of mammals from the Under the Ladder test pit and three teeth from the Bear test pit, a total of 8 teeth, have been analysed so far for determination of seasonality and dental age. Three of the studied teeth belonged to a cave lion, two to a cave hyena, one each to a bear from the cave bear group, to a wolf and red deer (Tab. 6). The first of three studied premolars of a cave lion comes from the aforementioned male lion represented mainly by the braincase. Based on the number of increments of dental cementum, it was an 11 year old individual that died at the turn of winter and spring, as the winter growth increment was more or less finished (Text-fig. 9; No 1 in Tab. 7). The second analysed lion premolar also did not have completely finished winter increment, therefore




**Text-fig. 9. Photo of a cave lion (*Panthera spelaea*) upper premolar P4 root cut. The approximate age of individual is 11 years (No 1 in Tabs 6, 7). Photo by M. Nývltová Fišáková.**

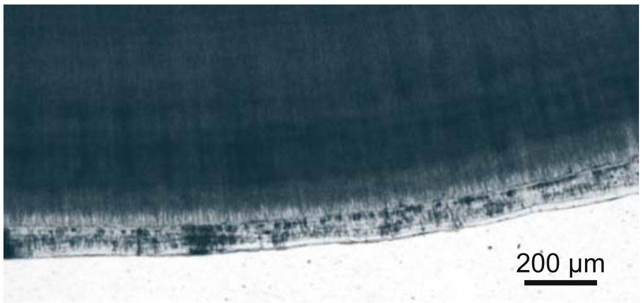



**Text-fig. 10. Photo of a cave lion (*Panthera spelaea*) upper premolar P3 root cut. The approximate age of individual is 3 years (No 2 in Tabs 6, 7). Photo by M. Nývltová Fišáková.**

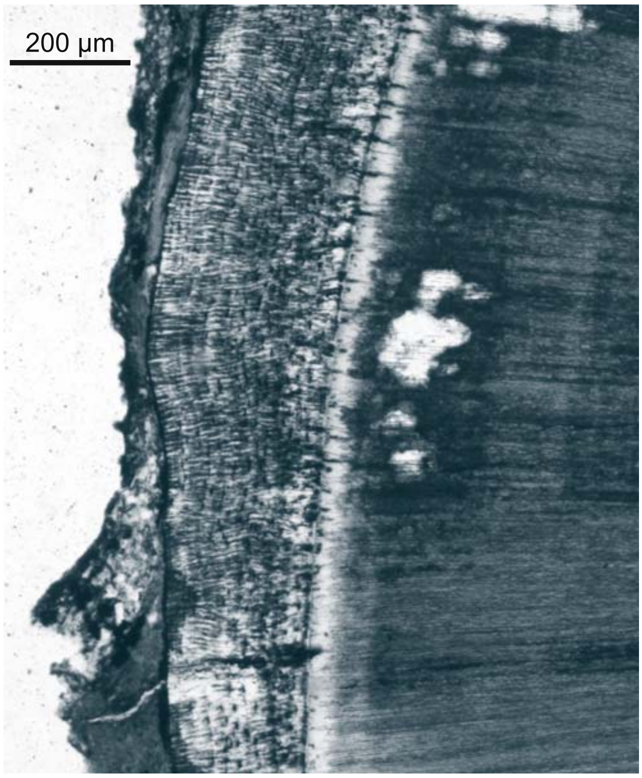



**Text-fig. 11. Photo of a cave hyena (*C. crocuta spelaea*) upper canine root cut. The approximate age of individual is 5 years (No 4 in Tabs 6, 7). Photo by M. Nývltová Fišáková.**

this individual probably also died at the turn of winter and spring, and according to the number of increments, at an age of 3 years (Text-fig. 10; No 2 in Tab. 7). The third studied premolar belonged to the lion 9.5 years old, according to the number of increments. Growth of the summer increment




**Text-fig. 12. Photo of a cave hyena (*C. crocuta spelaea*) lower canine root cut. The approximate age of individual is 9 years (No 5 in Tabs 6, 7). Photo by M. Nývltová Fišáková.**



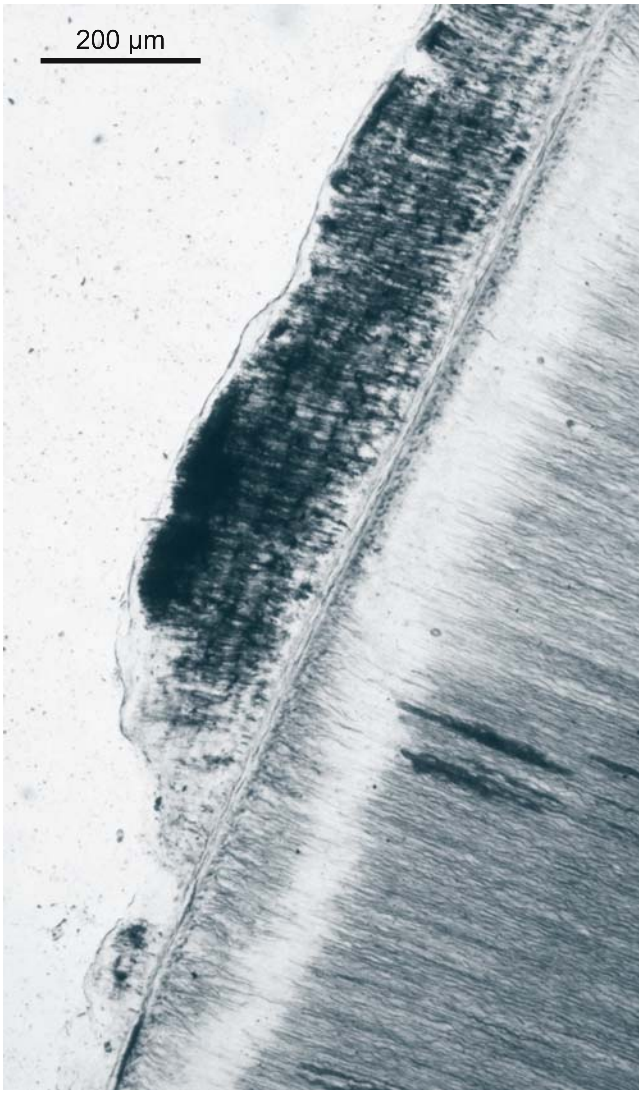

**Text-fig. 13. Photo of an upper canine root cut of a bear from the cave bear group (*Ursus* ex gr. *spelaeus*). The approximate age of individual is 14.5 years (No 6 in Tabs 6, 7). Photo by M. Nývltová Fišáková.**

was finished and the winter one had not yet started, therefore the individual died at the turn of autumn and winter (Text-fig. 6; No 3 in Tab. 7). In both analysed canines of the cave hyenas, the development of winter growth was completed, but the summer growth had not started, therefore both individuals from which the canines come died at the turn of spring and summer. According to the number of increments of the dental cementum, one hyena individual died aged 5 years (Text-fig. 11; No 4 in Tab. 7) and another aged 9 years (Text-fig. 12; No 5 in Tab. 7). The examined bear canine had a completely developed winter increment, and the summer one had not started to form. The owner of this tooth therefore died at the turn of spring and summer, according to the number of increments approximately at the age of 14.5

years (Text-fig. 13; No 6 in Tab. 7). In the wolf, increments of dental cementum of the molar root were analysed; the individual died at the turn of spring and summer (the winter increment was finished and the summer one had not started to form) at the age of 5 years (Text-fig. 14; No 7 in Tab. 7). The molar was analysed also in the case of the red deer. The winter increment on its root was fully developed, but the summer one had not begun to form, therefore the deer died at the turn of spring and summer at the age of 8 years, according to the number of increments (Text-fig. 15; No 8 in Tab. 7).

**Radiocarbon dating**

Our numerous efforts to obtain some radiocarbon data from osteological material of Barová Cave were often unsuccessful, due to lack of collagen. Attempts at radiocarbon dating of animal bones from Barová Cave have so far yielded the following uncalibrated data: from the sample of the tooth and bone of bears from the cave bear group, data >44,300 $^{14}$C BP (OxA-29570) and >44,600 $^{14}$C BP (OxA-29571) were obtained. The cave lion bone sample provided a date >45,800 $^{14}$C BP (OxA-34342), and a single two-sided bordered date of 46,300 ± 2,600 $^{14}$C BP (OxA-33450) was obtained from the sample of the horse bone.

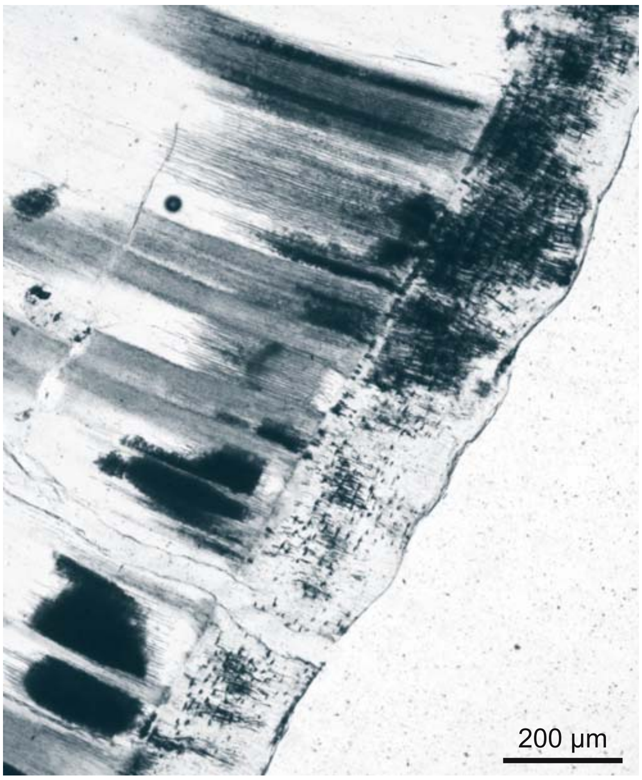



Text-fig. 14. Photo of a wolf (*Canis lupus*) lower molar m1 root cut. The approximate age of individual is 5 years (No 7 in Tabs 6, 7). Photo by M. Nývltová Fišáková.

## Discussion and conclusions

The bones of bears from the cave bear group, which accounted for 95% of all determined material, completely dominated in the excavated osteological material in sectors 2, 3, 4 and R4 of the Under the Ladder test pit. In terms of the minimum numbers of individuals (MNI) that are determined based on the found animal bones, bears considerably predominated over the MNI of other animal taxa (the minimum number of individual bears from the group of cave bears was 70.18% of all the minimally present individuals; Tab. 1). The situation discovered in the Under the Ladder test pit is not unique in Barová Cave; on the contrary, the absolute predominance of the bear bones is documented in the Fox Passage test pit (Roblíčková and Káňa 2013a), and is preliminarily documented in all test pits excavated so far. Similar results were obtained by previous researchers (Musil 1959, 1960, Seitl 1988). The unequivocal predominance of the bones of bears from the cave bear group in Barová Cave has only one explanation: the cave was mainly used as a bear wintering site. The bones of dead bears were deposited in the cave and later formed fossiliferous sedimentary layers.

Both male and female bears of various ages wintered in the cave; females apparently mildly prevailed over the males (according to the size of the teeth found). The bone remains of the five youngest individuals, the bear cubs who




Text-fig. 15. Photo of a red deer (*Cervus elaphus*) lower molar m2 root cut. The approximate age of individual is 8 years (No 8 in Tabs 6, 7). Photo by M. Nývltová Fišáková.

died or were killed at the age of the newborn to maximally 3 months (see Chapter The bear from the cave bear group in Palaeontological analysis) and did not survive the first winter of their life proved that the cave served females as a birthplace. The cave bear cubs were probably born between November and February during the wintering, and they left the cave with their mothers during the spring or at the beginning of summer, in April, May or June (Kurtén 1976). Another six young bears died in Barová Cave in the period from their second to the third winter (included), that means, one to two years old. In individuals of this age, determination of their age is still possible, based on the exchange of deciduous teeth for permanent ones, growing and closing of the permanent teeth roots, and growing limb bone lengths (Kurtén 1958, 1976, Musil 2014). It is worth mentioning that none of the bones found clearly belonged to an individual aged between 3–4 months and about 1 year. This means the bones belonged to bear cubs that died during their first wintering, and then the bones of the cubs that died/were killed during their second wintering were found. The fact that there were no bones of bear cubs in the cave that verifiably died in the summer months (e.g. from half-year to three quarters-year-old individuals) can be seen as an indication that the bears did not use caves much during the summer. On the other hand, it was probably easier to catch some ungulate prey during the summer months, so predators possibly did not try to steal bear cubs from their mothers, because of danger connected with such actions, and these young animals stayed alive during summertime. This assumption is not in conflict with use of the cave as a refuge during the summer.

In bears older than 2 to 3 years, when determining the age, only the degree of abrasion of a crown of premolars and molars can be used. In the methods, we set up 7 age categories of bears based on the degree of abrasion of the molars, ranging from very young adults or adolescents with not at all or very slightly worn crowns to old or very old individuals with heavily worn teeth, in some cases to the root. However, the information about the age of individuals obtained this way is relative. Kurtén (1976) does not assume that the bears from the cave bear group lived for more than 20 years; Musil (2014) states that the average age of the bears fluctuated between 20 and 30 years, and according to the age-determining method based on the number of incremental lines of the dental cementum, bears even lived 25–30 years, exceptionally up to 35 years (Musil 2014). If we stick to the midpoint of the two opinions, and assume that bears lived for about 25 years, then the first age category "very young adult (or adolescent)" could be 2 to 4 years of age, the second category "young adult" 5 to 7 years, the third category "young to middle-aged adult" 8 to 10 years, the following category "middle-aged adult" 11 to 14 years, "middle aged to old adult" 15 to 18 years, the age category "old adult" 19 to 22 years and the last category "very old individual" over 22 years of age (Tab. 2). However, this definition of age categories based on tooth abrasion should be seen as illustrative, because the degree of the tooth abrasion does not depend only on the individual's age, but to a large extent on the type of food that the individual predominantly fed on. Moreover, assessment of the abrasion degree of a tooth is highly individual, and depends on the opinion of each researcher, unless we quantify exactly the height of the crown of the examined teeth in particular abrasive and thus perhaps age stages. Quantification of the height of the molar crown in particular stages of abrasion is, however, very problematic, due to the jaggedness of the crown surface, and also due to the possible differences in the original height of the crowns of unworn young permanent molars, depending on the size and morphological variability of the individual bear.

However, if we use the above-mentioned age categories, then most of the individuals (13 in total) died/were killed in the age of abrasion/age category of very young adult (or adolescent), i.e. 2 to 4 years old, and a larger number of bears (6 in total) died/were killed also in the age category of the young adult, at an approximate age of 5 to 7 years (Tab. 2). These results indicate a high mortality rate among young bears, which corresponds to Musil's opinion (2014) that there is a period of increased mortality between the fourth and the fifth year of age of bears from the cave bear group. Musil (2014) even states that in most bear caves, findings of bones of such young individuals can reach up to 70%. In the monitored sectors of the Under the Ladder test pit in Barová Cave, there were found remains of a total of at least 40 individuals of bears from the cave bear group, 19 of them died/were killed in the age category of 2 to 4 years and 5 to 7 years, i.e. 47.5%. None of the bear molars found in sectors 2, 3, 4 and R4 of the Under the Ladder test pit was very heavily worn, or worn up to the root, so utterly senile individuals were probably rare in the cave. To the discussion about the age of the bears at the time of their death, it is also worth pointing out that the only canine of a bear from the cave bear group (from the sector 4, layer C of the Under the Ladder test pit) examined for the tooth cementum annulation comes from an individual approximately 14.5 years old. Based on seasonality, this bear died near the turn of spring and summer, probably at the end of wintering (No 6 in Tabs 6 and 7; Text-fig. 13). The cause of its death may have been natural – lack of fat supplies and exhaustion after winter.

The minimum number of cave lion individuals, determined on the basis of lion bones found in sectors 2, 3, 4 and R4 of the Under the Ladder test pit corresponds to ten percent of the MNI of the cave bears. At least four lions comprise about 7% of the minimally fifty-seven individuals of all taxa present in the cave (see Tab. 1). However, just in this part of the Under the Ladder test pit, the palaeontological content of which is the subject of the paper, the largest concentration of lion bones in the cave (or their undevastated parts) was found so far, so the ratio between the lion and bear individuals is overvalued in favor of the lions. Sectors 4 and R4, together with sector R5 (not included in this work), belong to the richest, regarding the representation of lion bones. The upper left premolar P4 of the male represented mainly by its braincase (see Chapter The cave lion in Palaeontological analysis) was examined for the incrementation of the cementum, with the resultant finding that this lion died near the turn of winter and spring at the approximate age of 11 years (Text-fig. 9; No 1 in Tab. 7). The season of its death suggests that it could have died in an unsuccessful attempt of predation of bears shortly before the bears, weakened after wintering, left the cave. In today's wildlife, an age higher than 10 years is in big cats their common age of death; in the case of males, death is not unusual even at a younger age (Schaller 1972, Smuts et al. 1978). Today's big cats are past the peak of their life force after 8 years of age. Similarly, when predating wintering bears or trying to use carcasses or bones of dead bears at the end of the winter, another lion could lose its life, dying again at the turn of winter and spring, based on the results of seasonality (Text-fig. 10; No 2 in Tab. 7). The third lion, whose premolar was examined, died at the turn of autumn and winter at the beginning of wintering (Text-fig. 6; No 3 in Tab. 7). It is also possible to contemplate the death/killing of this lion in connection with its feeding activities. The only juvenile lion female found in Barová Cave is represented mainly by the skull, with the registration number Ok-139786 (see Chapter The cave lion in Palaeontological analysis; Text-fig. 7). The death of this young, inexperienced lioness can again be associated with an unsuccessful attempt to hunt a bear or a bear cub. Failed predation was perhaps a more frequent cause of lion deaths in caves than older findings and their interpretations would suggest. The skeletal remains of the sub-adult lioness, as well as the resulting age categorization of the analysed teeth of the cave lions (11 years, 9.5 years and 3 years), suggest that feeding activities in "bear caves" could be an emergency solution for the old or the young, inexperienced lion individuals. But we cannot omit other options. The lion could take shelter in the cave and die because of an illness, injury, or an accident preventing it from leaving the cave. However, lions probably did not use the cave as a place of a permanent or breeding shelter; at least, no bones of lion cubs have been found in Barová Cave (unlike e.g. the Výpustek Cave).

In the case of the cave hyenas, it cannot be ruled out that the cave was used as a permanent or breeding shelter. As a fact supporting this theory, we could accept the sporadic occurrence of bone remains of ungulates in the fossil layers as remains of hyena prey (unless they were leftovers of prey of lions or wolves). However, bones of cubs were not found in sectors 2, 3, 4 and R4 of the Under the Ladder test pit even in the case of the cave hyenas. The two canines of two different cave hyena individuals examined in terms of seasonality showed that both individuals died near the turn of spring and summer (Text-figs 11, 12; Nos 4 and 5 in Tab. 7). It can be supposed that it happened when trying to find food in the cave – the carcasses or bones of dead bears, or even to catch a hibernating bear or a bear cub – at the end of the cold season or just at the beginning of warmer season. In sectors 2, 3, 4 and R4 of the Under the Ladder test pit, no bones of wolf cubs were found (see Chapter Wolf and cave hyena in Palaeontological analysis). The wolf molar, studied for seasonality, revealed that the owner died near the end of the cold season (Text-fig. 14; No 7 in Tab. 7), perhaps for reasons similar to those described in lions and hyenas.

The above-mentioned reflections on supposed attempts of the cave lions and perhaps hyenas to catch wintering bears, and efforts of carnivores, including the wolf, to feed on cadavers or bones of the dead bears, are not based so much on the predominant season of the death of the carnivores based on the seasonality, but mainly on found bite and chewing marks on the bones of bears from the cave bear group (see Chapter Traces of feeding activity on animal bones from the Under the Ladder test pit). Predation by cave lions and hyenas was clearly not the primary cause of death of the bears in the cave, because more than 90% of the bear bones do not have any bite or chewing marks. Still, a rather steady, even though small, portion of the chewed bones suggests that this food source was of some importance to the carnivores. Chewing marks were observed on 9.63% of the bear bones found in layer B, 5.28% of the bear bones from layer B + C, and 5.43% of the bones from layer C. In all three layers (most notably in layer B), the bones to which a greater amount of muscle mass is attached, namely the femur and the humerus were chewed more frequently (see Tabs 3, 4, 5). This is not a surprising finding, because muscles have a high nutritional value. On the other hand, even if a carnivore did not feed on fresh prey, but chewed the carcasses or bones of dead bears, the femurs, humeri and the other long bones of the limbs were probably the most beneficial. The joint heads of the bones of the limbs from the previously deceased individuals probably still contained blood in the spongiosa, and could still be covered with nutritious cartilage and tendons. Larger and longer bones are also more graspable for the animal, and provide the sufficient leverage to produce force for cracking the bone or chewing off the spongiosa. However, it should not be omitted that the massive long bones of the limbs are better preserved in the sediment and less eroded, so it is possible that the chewing marks are better preserved on them.

Approximately as often as on bear bones, traces of the other carnivores' feeding activity were also found on the lion, hyena and wolf bones; their frequency was therefore quite low. Chewing marks were again noticed mostly on long bones of the limbs. Traces of feeding activity on the bones of lions, hyenas and perhaps wolves can be explained as remnants of unsuccessful attempts by these carnivores to catch a bear or a bear cub that ended fatally for the carnivore. But they could also originate after the death of the individual, when another carnivore chewed loose bones or a carcass. Even cannibalism, which means feeding on the bones of its own kind, cannot be ruled out. In the cave, degradation of organic matter is slower, due to the constant lower temperature; bones or skeletons of dead animals have apparently been loose for longer periods of time on the surface of the sediment, or they were covered with only a thin sedimentary layer. For carnivores, therefore, it was not difficult to get them.

The palaeontologically most important sedimentary layers of Barová Cave, layers B and C, contain in sectors 2, 3, 4 and R4 the bone remains of identical animal taxa (except for occasional minor deviations), and the bone remains' percentage of individual taxa is similar. It can therefore be assumed that these layers do not represent different time periods of the presence of large mammals. The bones in layer C can be interpreted as shifted over a shorter distance. They can be considered as the remains of individuals that died in the cave at places farther from the entrance. The transport distance of these bones to the place of their final placement was probably quite short in the horizontal direction. Mainly it was gravitational subsidence into lower positions. Traces of corrosion on the surface of the C-layer bones lead to the idea that the bones fell onto the slightly aquiferous bedrock. They could lie in puddles or on damp soft sediments, into which they were gradually pushed by the weight of the overlying rock. The contemporary layer C is composed of reddish clay, similar to the underlying layer D. Animal bones in layer C do not necessarily come from individuals that died in the cave earlier, but rather from those individuals that died in the parts of the cave more distant from the entrance. Some of the C-layer bones were also found in a partially anatomical position, which proves transport over a short distance, possibly in an articulated state.

Layer C, compared to layer B, is moderately enriched with cave lion bones. Cave lion bones comprise 0.7% of all determined osteological material in layer B, while lion bones represent 5.0% of the determined findings in layer C. The total sum of bones determined as cave lion make up nearly 2.9% of all determined material from the monitored sectors of the Under the Ladder test pit (Tab. 1). Lion bones occur frequently at the interface of these two lithologically different layers. The larger representation of cave lion bones in layer C is due to the above-mentioned skeleton of a juvenile lioness, since 70 of the total of 74 bones of this individual were found in layer C.

The already deposited C-layer sediments covered the B-layer sediments. These sediments (including the animal bones) can be characterized as clearly allochthonous, shifted over a greater distance, in tens of meters. Their origin is in the vicinity of the cave entrance, possibly even in the illuminated zone. Into the lower, and from the entrance more distant parts of the cave, B-layer sediments were transported gravitationally (cryogenic processes cannot be entirely excluded). The transfer of animal bones and the B-layer sediments to their current location can be imagined as a long-term process, compared to the transfer of the C-layer bones. Because of the longer transport, the B-layer animal bones were more accessible to carnivores, probably for longer period than the bones of layer C. This theory is supported by the almost double frequency of feeding activity traces on the B-layer bones, compared to layer C bones. The animal bones of layer B do not have to be the remains of individuals that died later, but they are rather the bones that underwent longer-term transport.

The $^{14}$C data place using of Barová Cave by bears and other fauna in the MIS 3 period. The deposition of animal bones in the B-layer and C-layer sediments of the 2, 3, 4 and R4 sectors of the Under the Ladder test pit, together with the $^{14}$C dating results, put the local cave bears, lions and all other fauna in the same period of the cave settlement. The found bone remains form logical thanatocoenosis. Taking into account the total number of animal bones picked up from Barová Cave, both during our ongoing research and during the previous exploitation activities (Musil 1959, 1960, Seitl 1988), and adding to it an estimated amount of the osteological material remaining in the cave, we get to the number of several tens of thousands of bones. This tremendous amount of especially bear bone material leads to the consideration that bears from the cave bear group wintered in Barová Cave over a period longer than thousand years. Considering the reasons for death of bear individuals in Barová Cave, they were probably quite natural in the most cases, i.e. inadequate nutrition, injury, illness or higher age. Due to the notable share of bears from the cave bear group dead at the age of only 2–7 years (47.5% of individuals, see above), inadequate nourishment during the summer months can be considered a frequent cause of their death. The cave itself could occasionally become a natural trap, for example, during changing weather conditions (rapid floods, freezing, stone falls and slides). The number of the bears in the cave directly killed by the cave lions or cave hyenas was probably low, judging by the not-too-frequent traces of feeding activities on the bones.

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